

# Site fidelity, residence time and movements of red snapper *Lutjanus campechanus* estimated with long-term acoustic monitoring

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**ABSTRACT:** Residence time, site fidelity and movements for red snapper *Lutjanus campechanus* (Lutjanidae) were estimated from long-term telemetry monitoring (December 2005 to June 2010) at 6 sites (1 natural and 5 artificial reefs) in the northeastern Gulf of Mexico. Each site consisted of an array of 5 receivers, with 1 at the center reef site and 4 receivers placed 1100 m north, south, east and west of center (2 km radius detection area). Throughout the study, a stationary control transmitter was located 400 m south of the center receiver at each site to estimate changes in detection rates from environmental factors. These receiver arrays enabled fishery independent estimations 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 542 d, ranging from 1 to 1099 d, with 72% of fish staying at least 1 yr at the site. Some fish (n = 12) showed seasonal and directed movements to other sites (up to 8 km away) and returned to original sites up to 7 mo later. 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 in any previous study and show the importance of artificial reefs for this species.

**KEY WORDS:** Site fidelity · Acoustic telemetry · Seasonal movements · Red snapper · Artificial reefs

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## 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 & Shipp 1994, Szedlmayer 1997, Watterson et al. 1998, Peabody 2004, Szedlmayer & Schroepfer 2005). Although approximately 10 000 to 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 & Heath 1998, Schirripa & Legault 1999, SEDAR 2005, Shipp & 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 GOM oil rigs (Gitschlag et al. 2003, Lingo & Szedlmayer 2006, Wells & 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 & 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,

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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. Early studies examined the distribution of red snapper catches relative to habitat type, depth and season (Camber 1955, Moseley 1966, Bradley & Bryan 1975), and more recent studies have used mark-recapture (Beaumariage 1969, Fable 1980, Szedlmayer & Shipp 1994, Watterson et al. 1998, Patterson et al. 2001, Patterson & Cowan 2003, Diamond et al. 2007, Strelcheck et al. 2007) and ultrasonic telemetry (Szedlmayer 1997, Peabody 2004, Szedlmayer & Schroepfer 2005, Schroepfer & Szedlmayer 2006) to estimate site fidelity and movements. 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 (e.g. small artificial reefs, oil-gas platforms and natural reefs), hurricanes, transmitter detection range, fish size and 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 & Cowan 2003, Strelcheck et al. 2007). Patterson & Cowan (2003) estimated site fidelity at approximately 25% yr<sup>-1</sup> from declines in captures at tagging sites (minus an assumed natural mortality rate of  $M = 0.1$  and no fishing mortality). Strelcheck et al. (2007) used the same method, tagged fish at similar habitats and obtained site-fidelity rates of around 50% yr<sup>-1</sup>. 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 it is difficult to detect 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 & 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 individ-

ual fish, with a median residence time of 373 d and site fidelity of 50% yr<sup>-1</sup> from event analysis (Szedlmayer 1997, Szedlmayer & Schroepfer 2005, Schroepfer & Szedlmayer 2006). Peabody (2004) also used ultrasonic telemetry to monitor the residency and movements of small red snapper (<450 mm TL; n = 125) around oil-gas platforms 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 6 mo. After 70 d, however, there was only a 50% probability of detection of these fish at the release site, possibly due to 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 >50% yr<sup>-1</sup>. These previous tagging and telemetry studies have only addressed the movements and residency of smaller fish (<500 mm TL), with the exception those by Szedlmayer & Schroepfer (2005) and Schroepfer & Szedlmayer (2006). Red snapper can attain sizes up to 1 m or more, so questions still remain on the residency time of larger red snapper (Szedlmayer & Shipp 1994, Wilson & Nieland 2001). 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 & Schroepfer 2005, Topping 2009). 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 & Szedlmayer 2003, McCawley & 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 has been attributed to hurricanes (Watterson et al. 1998, Patterson et al. 2001) and cold fronts (Moe 1963, Moseley 1966, Bradley & 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 immi-

gration) at both artificial and natural habitats would help determine why these fish are associated with these structures.

In the present study, long-term (>3 yr) 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 yr) were used to assess these aspects of red snapper ecology. In addition, diel and seasonal movement patterns were examined along with the environmental factors that may have influenced these behaviors.

## MATERIALS AND 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 & Heath 1998). Red snapper were tagged on 1 natural and 5 artificial habitats. Artificial habitats included a pipeline covered with a concrete mat (Site A1 in Fig. 1), a 15 m sunken barge (A2), a  $4.4 \times 1.3 \times 1.2$  m steel metal cage (A3), an M-60 army tank (A4)

and a steel-frame pyramid (A5). The natural habitat (N1) was composed of a 20 m long drowned river bed (~1 m relief), with undercut banks lined with tree stumps (Fig. 1). The depths of the sites ranged from 20 to 30 m.

### Fish tagging

Large red snapper (>500 mm TL) were captured at the selected habitats via hook and line. Fish were brought on board the research vessel, placed in a 70 l container of seawater containing MS-222 ( $150 \text{ mg l}^{-1}$ ) and quickly anesthetized to Level 4 (Summerfelt & Smith 1990). Once sedated, the fish were temporarily removed from the anesthetic and an ultrasonic transmitter was implanted within the peritoneal cavity through a small (18 mm) vertical incision made with a No. 11 scalpel slightly above the ventral midline, and sutured with plain gut (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 a weighted line with an inverted

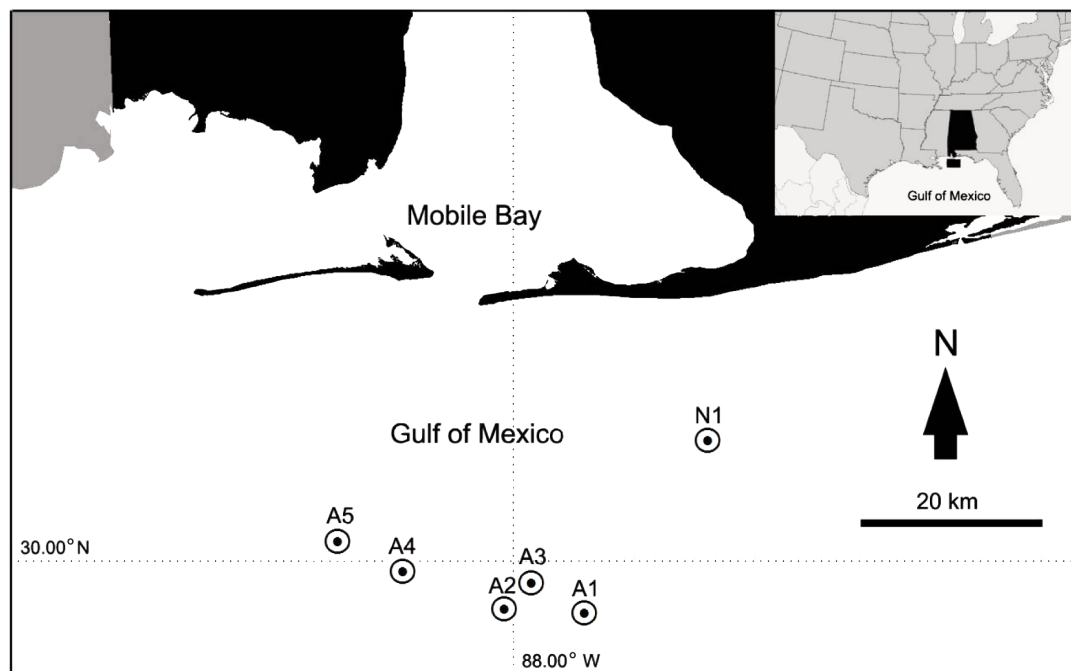


Fig. 1. Location of study sites in the northeast Gulf of Mexico. Inset in upper right shows Gulf of Mexico and study area (black box) offshore Alabama (black state), USA

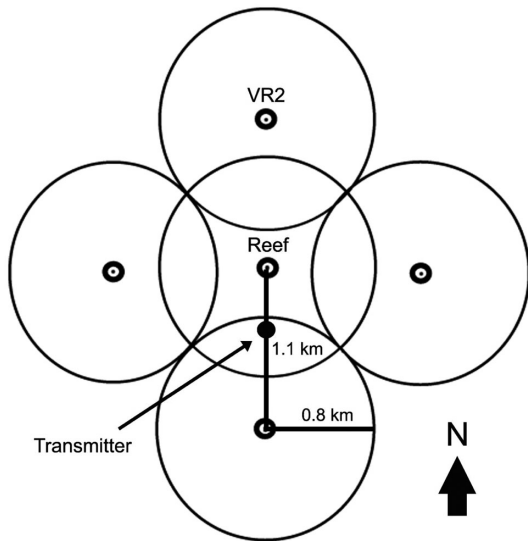


Fig. 2. Design of receiver array (Vemco VR2) for each site, with 1 receiver at the reef and 4 others surrounding the reef, 1.1 km (0.42 km for Sites A4 and A5) away to the north, south, east and west. Circles represent detection range of 0.8 km (0.3 km for Sites A4 and A5). A stationary control transmitter was placed 400 m south of the reef (150 m for Sites A4 and A5). Sites A4 and A5 used Sonotronics SUR-1 receivers

barbless hook that was attached to the fish’s lower jaw. Upon retrieval of the weighted line the fish were released at depth near the reef site.

Two types of transmitters were used in the present study; individually coded Vemco transmitters (V16-6L-R64K; code intervals: 20 to 69 s, 16 × 94 mm; battery life: 6 yr) were used at sites with Vemco VR2 receivers (A1, A2, A3, N1), and coded Sonotronics transmitters (CT-05-48, 16 × 79 mm; battery life: 4 yr) were used at sites where Sonotronics SUR-1 receivers were deployed (A4, A5).

### Continuous remote monitoring

An underwater acoustic receiver array was deployed at each site that included 5 separate omnidirectional receivers (Vemco VR2 or Sonotronics SUR) moored near the bottom (~5 m). For each array, 1 receiver was located at the release site (center, C) and the other 4 were placed at 1100 m (VR2) or 420 m (SUR) to the north (N), south (S), east (E), or west (W) of the center (Fig. 2). Receivers placed at 1100 m (or 420 m) 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 & 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 (Fig. 3). Fishing mortality was estimated from both the tag returns by fishers and from the 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 (last detected by center receiver). 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 a decrease in detection range from a transmitter that was lying on the bottom. The estimates of natural and fishing mortality were necessary to accurately assess

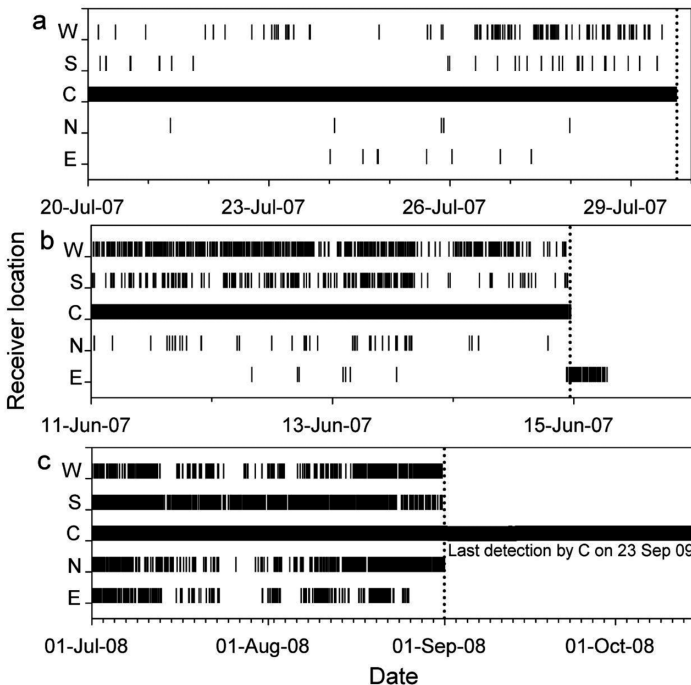


Fig. 3. *Lutjanus campechanus*. Detection plots showing examples of the detection patterns from fish experiencing (a) fishing mortality, (b) emigration, or (c) natural mortality events. Each plot shows a portion of the overall detections of a single fish by the center (C), north (N), south (S), east (E) and west (W) receivers at the release site. Vertical dotted lines: an event (mortality or emigration)

site fidelity and residence time with event analysis (Schroepfer & Szedlmayer 2006). Each site was periodically surveyed for tagged fish, using SCUBA aided by an underwater hand-held receiver (Sonotronics) to locate swimming fish with transmitters and dead fish (i.e. tags laying on the bottom). To increase the probability of tag returns by fishers, a tag return reward of USD 50 to 150 was advertised via internet fishing forums, posters distributed at local tackle stores and marinas, and newspaper coverage of the project.

### Detection rate and range validation

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 throughout the study period, and enabled contrasts between movements and mortality (Figs. 2 & 3; Topping 2009). This design also helped 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 (C = 400 m, S = 700 m, E = 1170 m, W = 1170 m, N = 1500 m). 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). A Vemco VR60 receiver with an omnidirectional hydrophone was also placed next to the transmitters to audibly verify the number of clear signal transmissions and collisions to ensure that the VR2 was recording properly. 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) at each site and converted to a percent of expected detections. Continuous water temperatures (1 h resolution) were recorded throughout the study by waterproof temperature loggers (Onset HOBO U22 Water Temp Pro v2) moored at each site near the bottom (~20 to 33 m) and midwater (~15 m). 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 proportion ( $S$ ) of fish residing at the site over time ( $t$ ). Emigration (event) times were analyzed by the product limit method of Kaplan & 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 (i.e. fishing and natural mortalities). The lifetest procedure in the statistical analysis system (SAS) program was used to estimate the Kaplan-Meier (K-M) survival function (Chambers & Leggett 1989, Allison 1995, Ohta & Kakuma 2004, Schroepfer & 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 defined as the proportion of fish remaining at the sites on Day 365. The K-M survival (residence) function  $S(t)$  is defined as the proportion of individuals residing, to  $t$ :

$$\hat{S}(t) = \prod_{t_j \leq t} (1 - d_j/r_j) \quad (1)$$

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

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

$$[\hat{S}(t)] \pm 1.96[\text{var}\hat{S}(t)]^{1/2} \quad (3)$$

### Data analysis

Residency and site fidelity were estimated based on an event analysis method. The effect of fish size (TL) on residence time was tested with a log-rank test of association within the SAS lifetest procedure (Kalbfleisch & Prentice 1980). A log-rank test for homogeneity (lifetest procedure) was used to compare between various residence curves (Klein & Moeschberger 1997). The number of fish emigrating in each season was compared to the null hypothesis of equal proportions of fish emigrating in each season (summer, beginning on 21 June; fall, 23 September;

winter, 21 December; spring, 21 March) with a likelihood ratio chi-squared test to examine seasonal emigration. A likelihood ratio chi-squared test was also used to test whether equal proportions of fish emigrated from the release site in N, S, E and W directions (Cody & Smith 2006). 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.

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 & Devlin 1988, Cohen 1999) of detection rates at 1 h intervals was also used to examine diel periodicity of movements. 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 on N, S, E and W receivers) by using a local regression to estimate regression surfaces fitted to data points (total detections per hour) within a chosen neighborhood (smoothing factor) of each value of

the independent variable (Cleveland 1979, Cleveland & 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 Akaike information criterion ( $AIC_{C1}$ ) statistic (Cohen 1999). The same time series used for the FFT analysis was analyzed with LOESS. Total detections per hour on the center receiver and the combined total detections per hour on outside receivers (N, S, E, W) for fish at a site were obtained each hour over 24 h diel cycles (00:00 to 23:00 h), with each day of the time series yielding 1 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 rate and range validation

Mean detections per transmitter per hour significantly decreased as the number of transmitters present next to a VR2 receiver was increased and was described by a negative logarithmic relation ( $r^2 = 0.99$ ,  $p < 0.0001$ ; Fig. 4). Detections per transmitter per hour decreased from 92 for 1 transmitter present to 15 detections per transmitter per hour when 15 transmitters were present. Total detections per hour increased to a maximum of 280 when 9 transmitters were present, but total detections decreased when  $>10$  transmitters were present due to excessive signal collisions ( $r^2 = 0.95$ ; Fig. 4). Based on these results, the maximum number of transmitters at each reef site (at any time) was 10 (fish + control).

The relation between number of fish (transmitters) present and detection rate was used to estimate the maximum detections of the control transmitter expected at each site for each day. A fish was considered present at a particular site only after it was detected a minimum of 5 times at that site on a particular day. The percentage of maximum expected detection rate was estimated from June 2006 to August 2008 over the distances these controls were placed

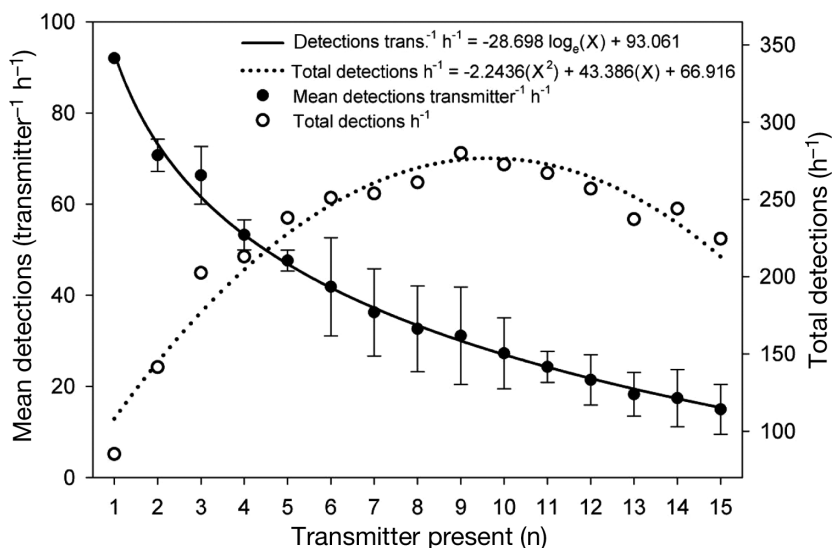


Fig. 4. Comparison of mean detections per transmitter per hour ( $\pm$ SD) to number of transmitters present showed a logarithmic negative relation (solid line;  $R^2 = 0.99$ ). Comparison of total detections per hour to transmitter number showed a quadratic relation (dotted line;  $R^2 = 0.95$ )

away from the C, S, E, W and N VR2s. There were seasonal periods when control transmitter detection rates were reduced below expected rates due to changing environmental conditions that reduced detection ranges (Fig. 5). A logistic relation was predicted from mean percent of maximum expected detections of the control transmitter to receiver distance (Fig. 6;  $r^2 = 0.98$ ,  $p = 0.03$ ). Mean percent of expected detections at 400 m was reasonably high (mean  $\pm$  SD:  $79 \pm 14\%$ ; Fig. 6), followed by 65% at 700 m. Detections of the control transmitter were about 25% lower at the N1 site at 400 m than at all other sites, which may be due to shallower 20 m (N1) versus 30 m depths (A1, A2, A3).

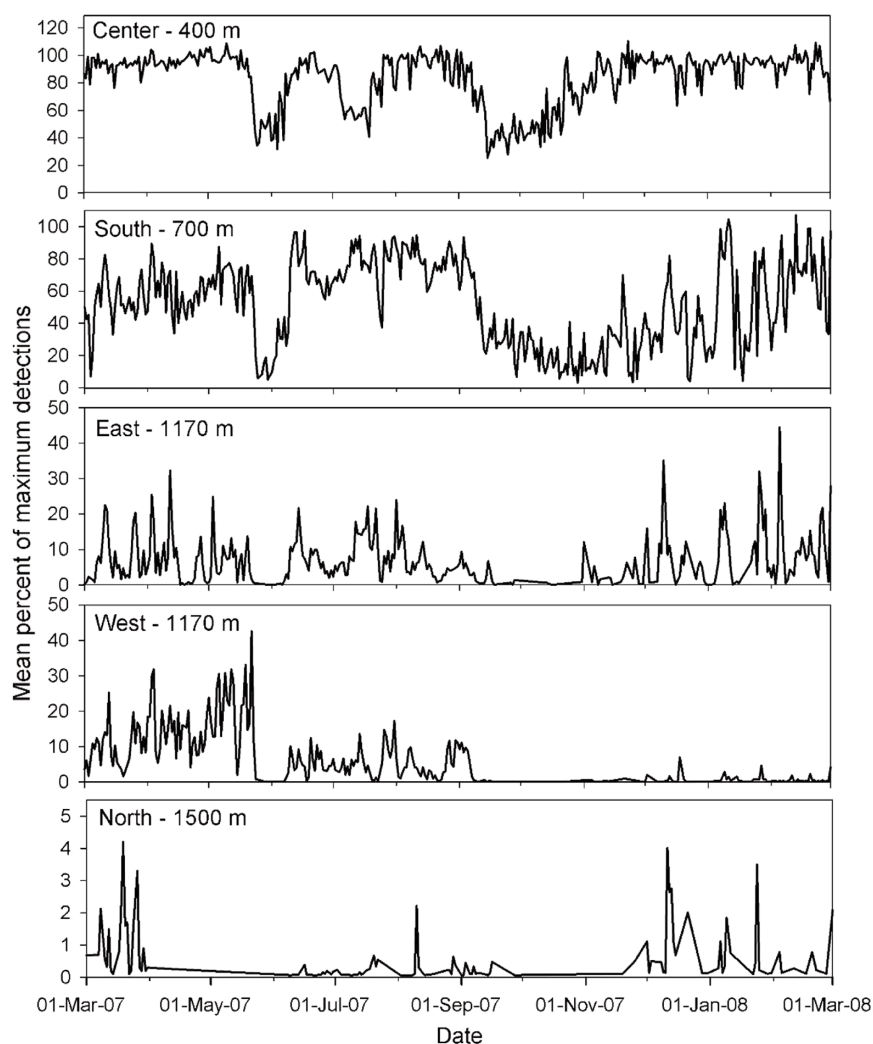


Fig. 5. Mean control transmitter detections at each distance (mean detections of Sites A1, A2 and A3 for center, south, east, west and north VR2s on each date) shown as the mean percent of the maximum expected detections. Expected detections were calculated from the relation of detections per transmitter per hour (see Fig. 4) to number of transmitters (fish) present at a given location. Note: different y-axis scales

### Residence time and site fidelity

Red snapper *Lutjanus campechanus* ( $n = 102$ ) were monitored at 6 different sites (A1 to A5, N1; Fig. 1) for up to 1275 d (December 2005 to June 2010). Red snapper size range was 501 to 860 mm TL (mean  $\pm$  SD =  $639 \pm 81$  mm; Table 1). Fish remained present at the sites until the end of the study, emigrated, died, or were removed by fishers, as determined by detections from the 5 receivers at each site and by fisher returns (Fig. 7). Individual fish were detected at sites from 1 to 1099 d (Table S1 in the supplement at [www.int-res.com/articles/suppl/m437p183.pdf](http://www.int-res.com/articles/suppl/m437p183.pdf)). 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 (maximum = 1099 d). 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. One day after release at Site A3, this fish was detected at 3 separate sites (A2 to A1 to A2), with an overall movement of 20 km in a 24 h period, then remained resident to A2 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 by the end of the study (10 June 2010). The fates of 6 fish were unknown, because their last detections occurred during periods when an outside receiver was not recording or removed during a hurricane. These fish were assumed to have emigrated based on 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 appropriate 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

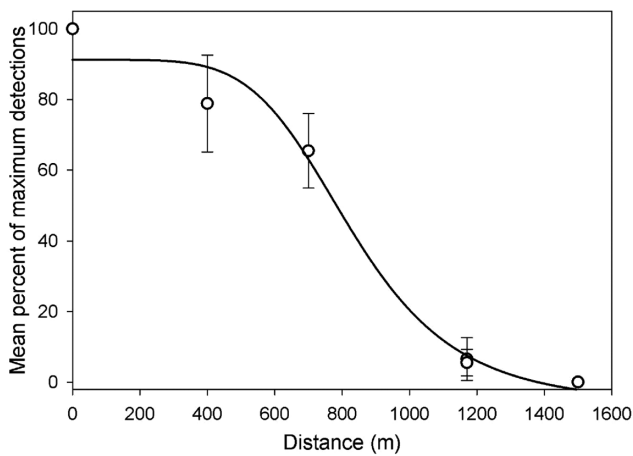


Fig. 6. Logistic relation of the mean percent of maximum expected detections of the control transmitter to VR2 distance ( $\pm$ SD;  $R^2 = 0.98$ ). Sites (A1, A2, A3 and N1) were averaged from June 2006 to August 2008

tagging. Red snapper ( $n = 85$  fish) median residence time (when 50% of fish still present) was 542 d (406 to 661 d, 95% confidence limits [CL]). The annual site-fidelity estimate was 72%  $\text{yr}^{-1}$  (Fig. 8). 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 ( $n = 102$  fish), median residence time was reduced to 411 d (375 to 571 d, 95% CL); however, a log-rank test of homogeneity did not detect a significant difference between these 2 K-M residence (survival) plots ( $p = 0.08$ ; Fig. 8). The K-M plot derived from all 102 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 61%  $\text{yr}^{-1}$  (Fig. 8).

### Storm effects on movement patterns

Some fish ( $n = 19$ ) 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 2 storms, wave heights in the study area were as high as 11 m and wind gusts were as high as  $100 \text{ km h}^{-1}$  (NOAA Buoy Station 42040, 102 km south of Mobile Bay), which reduced detection range and made it difficult to determine the fate of these fish. At least 1 fish died during these storms based on detections before and after storms (e.g. Fig. 3c). Before these storms 26 fish were present and immediately after the storms 18 fish remained.

One fish (No. 87) at Site N1 that was lost after these hurricanes, returned 2 mo later (24 October 2008) from the east, remained 1 mo, and then this fish and 3 others (Fish 74, 82, 86) emigrated to the east at the end of November 2008. Also, Fish 89 (A4) and Fish 94 (A5) emigrated in early December 2008 from deeper sites (25 m). These emigrations in November and December 2008 were during, or right after, several cold fronts passed over the area; however, 5 of these 6 fish returned to their respective sites as water temperatures increased ( $> 20^\circ\text{C}$ ) during several weeks in May and June 2009 (Fig. 9). Around the same time the following year, Fish 89 and 94 emigrated again, with Fish 94 returning again in May 2010. Fish 22 also showed movements associated with cold fronts and hurricanes. These movements were to another site  $\sim 2$  km E-SE of Site A1 (located during a 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 2 yr. Another large (810 mm TL) red snapper (Fish 70) released at Site A3 on 29 November 2007

Table 1. *Lutjanus campechanus*. Summary of dates each study site was active (receivers deployed; start date, end date, time) and final status of fish released at each site (present, emigrated, caught, dead, unknown). Min.: minimum number of days a fish was present at the site; max.: maximum number of days a fish was present at the site after release; mean TL: mean ( $\pm$ SD) total length of fish released at that site

Site	Start date	End date	Time (d)	Re-leased	Pres-ent	Emi-grated	Caught	Dead	Un-known	Min. (d)	Max. (d)	Mean TL (mm)
A1	13 Dec 2005	10 Jun 2009	1275	26	1	8	14	3	0	1	1099	658 $\pm$ 84
A2	27 Jul 2006	23 Sep 2009	1154	19	4	7	4	3	1	1	856	689 $\pm$ 75
A3	9 Aug 2006	23 Sep 2009	1141	25	3	12	2	4	4	1	895	634 $\pm$ 78
A4	29 Aug 2007	13 Apr 2010	958	13	2	5	5	1	0	168	958	632 $\pm$ 63
A5	21 Oct 2008	8 Jun 2010	595	7	1	3	3	0	0	34	595	627 $\pm$ 41
N1	11 Dec 2007	29 Oct 2009	688	12	2	7	0	1	2	3	687	545 $\pm$ 35
All	13 Dec 2005	8 Jun 2010	1638	102	13	42	28	12	7	1	1099	639 $\pm$ 81



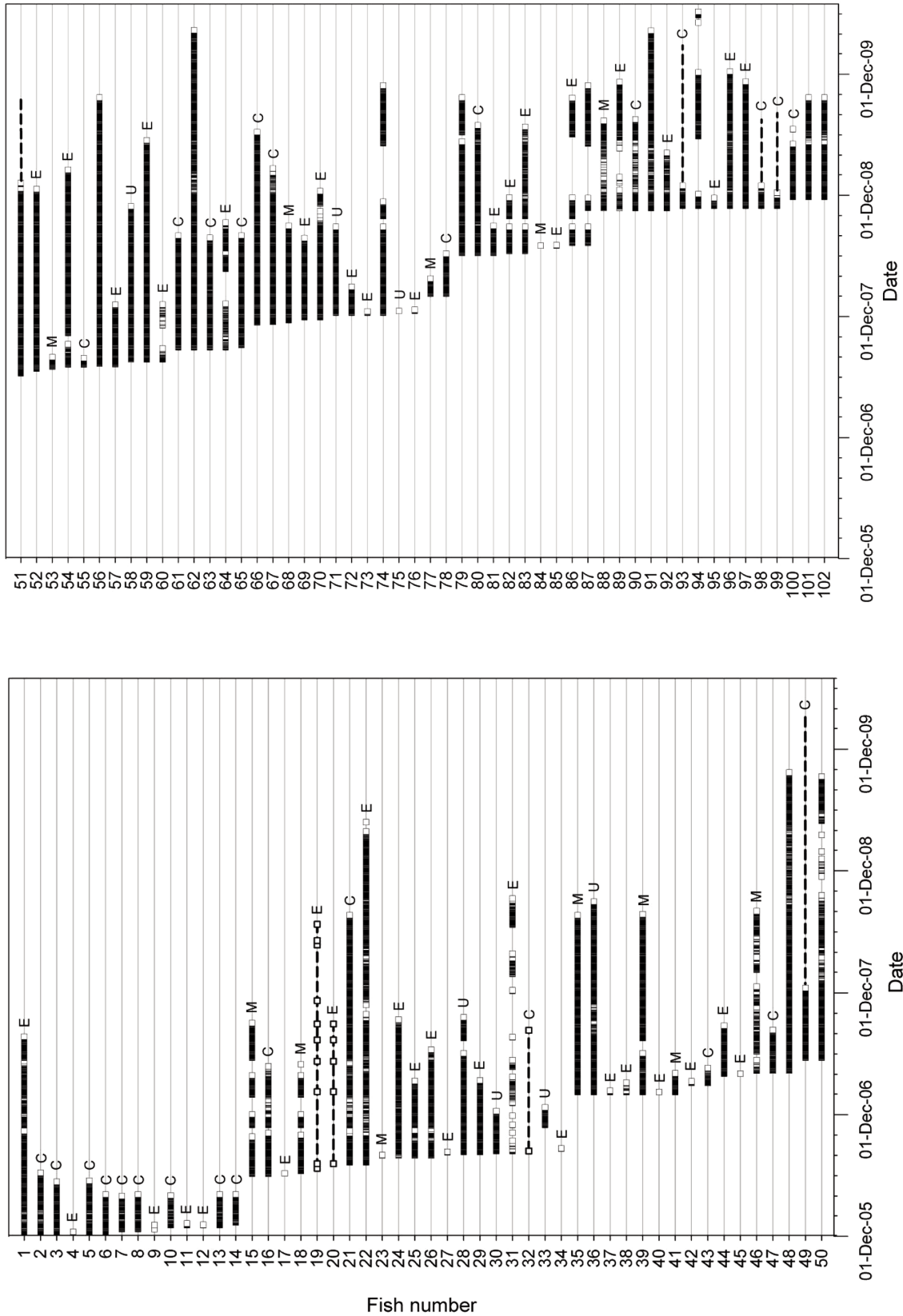


Fig. 7. *Lutjanus campechanus*. Daily presence of red snapper (n = 102) released at all sites. Open squares: dates fish were present (i.e. detected at least 5 times by any receiver); horizontal dashed lines: dates fish were occasionally relocated until the last known date present; letters: events (C: caught; M: natural mortality; E: emigration; U: unknown); fish without letters were still present at the end of the study

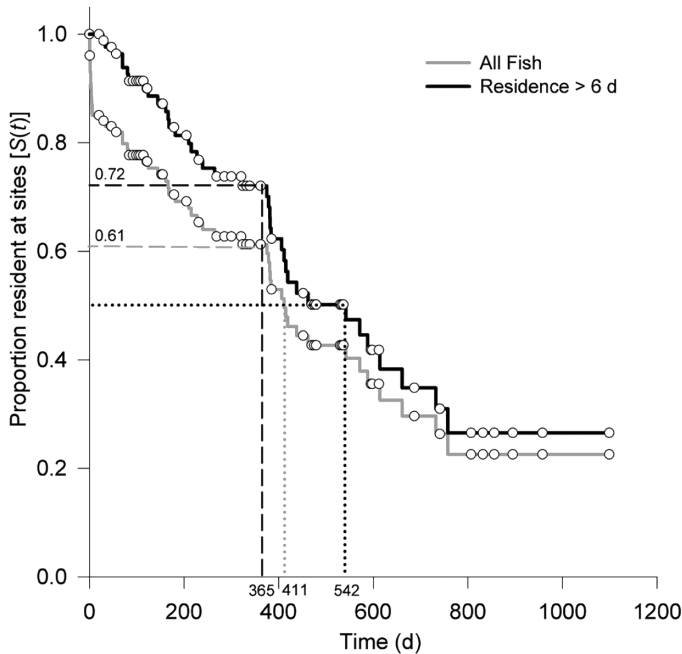


Fig. 8. *Lutjanus campechanus*. Kaplan-Meier survival (i.e. residence time) curves showing the proportion of red snapper remaining at study sites over time (d). Black line: fish remaining present longer than the 6 d post-release period (n = 85); gray line: all fish released (n = 102); dotted lines: median residence times (50% remaining); dashed lines: 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

moved to Site A1 (~6 km apart) on 2 separate occasions, staying at the alternate site for up to 21 d before returning to the release site. These directed movements all occurred as strong cold 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 these sites (15 to 350 d). Twelve fish moved to other locations, but returned to their release sites after long-term absences up to 7 mo, with some fish staying for the remainder of the study or again emigrating from the site.

The number of fish (n = 38) emigrating from the 12 km<sup>2</sup> 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 (37%), winter (26%), fall (29%) and spring (8%; likelihood-ratio:  $\chi^2 = 8.20$ , p = 0.04). There were also significant differences in the direction that fish emigrated from the release site, with 51% moving to the east, 26% to the south, 11% to the north and 11% to the west (likelihood-ratio:  $\chi^2 = 13.95$ , p = 0.003).

**Diel movement patterns**

Diel patterns of detections indicated that red snapper would move away from the reef sites at night. A time series of total detections per hour 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<sup>-1</sup> that indicated a daily sinusoidal cycle (Fig. 10a). These data were also analyzed with the LOESS procedure (local regression),

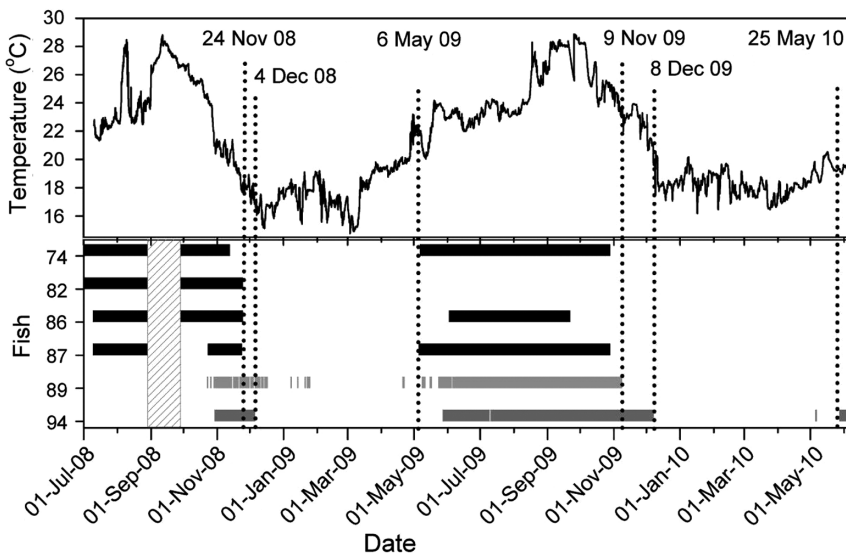


Fig. 9. *Lutjanus campechanus*. Daily detections of Fish 74, 82, 86 and 87 (Site N1, black), Fish 89 (A4, gray) and Fish 94 (A5, dark gray) at release sites represented by vertical dashes (bottom panel). Vertical dotted lines: cold fronts and storms when fish emigrated as water temperature decreased (top panel) and immigrated back to site as water temperature increased; hatched box: when receivers were removed due to hurricanes Gustav and Ike. Receivers were removed from Site N1 in October 2009, Site A4 in April 2010 and Site A5 in June 2010

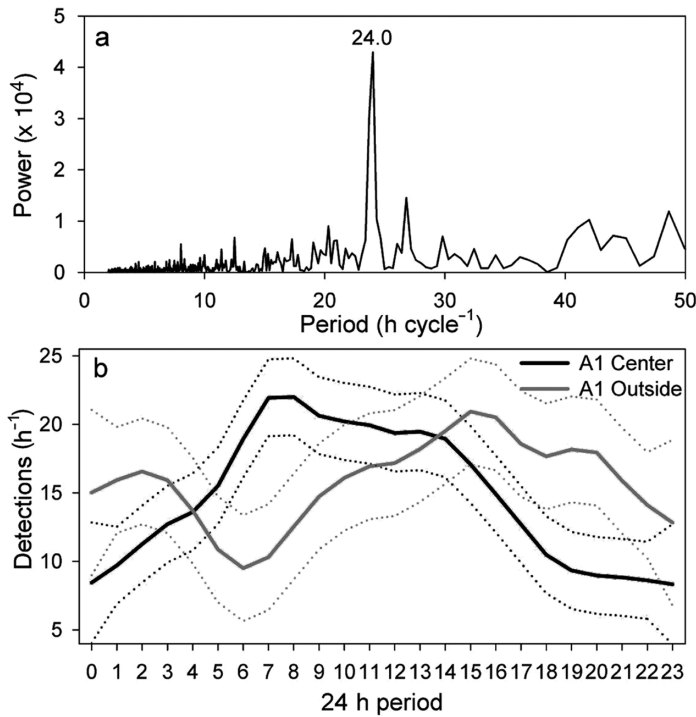


Fig. 10. *Lutjanus campechanus*. Time series of continuous receiver coverage ( $n = 78$  d) for red snapper ( $n = 10$ ) at Site A1 from 12 January to 31 March 2006 analyzed by (a) spectral analysis (periodogram) of total detections per hour of these fish by the center receiver and (b) local regressions (LOESS) of detections per hour by the center (black line) and outside (gray line) receivers. The periodogram shows a strong peak at a period of 24 h indicating a diel cycle in detection frequencies. The LOESS showed high detections when fish were close to the reef, and lower detections when fish were further from the reef. Dotted lines: 95% confidence limits

day, with a maximum at 15:00 h and remaining relatively high throughout the night (Fig. 10b). Based on detection range data (Fig. 6; detections decreased with increase in transmitter distance), fish showing these patterns (69%) 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. Fig. 10b).

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 21 moved toward the west, ~1 km away from the structure, during both night and day (Fig. 11). These movements from 1 to 17 July 2008 were significantly correlated with tidal stage. Although tidal effects were correlated with diel effects ( $r = 0.41$ ,  $p < 0.0001$ ), the influence of both tide and diel periods on detections per hour of Fish 21 by the west receiver were detected with a stepwise regression. Over this 18 d period, detections on 12 d were significantly affected by diel period ( $r^2$  range: 0.09 to 0.65,  $p < 0.02$ ) and detections on 7 d were significantly affected by tidal cycles ( $r^2$  range: 0.19 to 0.72,  $p < 0.006$ ). All  $r$ -values (correlation coefficients) were negative, indicating Fish 21 tended to move toward the west during low tides and at lower light levels (e.g. Fig. 11).

with an estimate of total detections per hour from each 1 h period of each day ( $n = 78$  d). Detections at the center receiver (near the structure) were greater during daylight hours (07:00 to 15:00 h), with a peak in detections at 07:00 h (around sunrise for this time of year). Pooled detections at the outside receivers (1.1 km away) were lowest at sunrise (07:00 h) and tended to increase throughout the

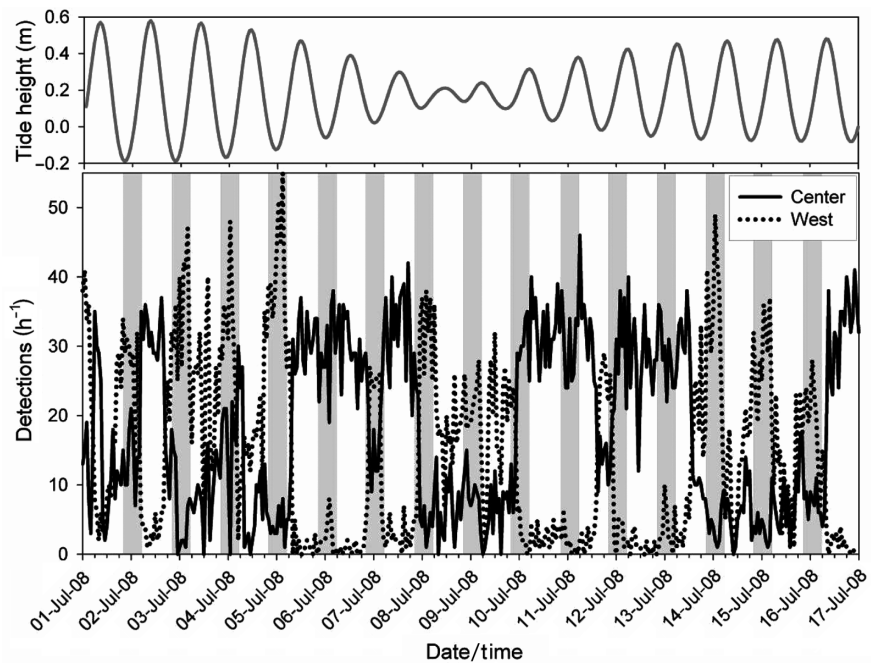


Fig. 11. *Lutjanus campechanus*. Total detections each hour of Fish 21 by the center (solid black line) and the west (dotted black line) receivers at Site A1 from 1 to 17 July 2008. Shaded bars show nighttime periods. Tidal cycle (solid gray line) is plotted in upper panel

## DISCUSSION

The residence, site fidelity and movement patterns of red snapper *Lutjanus campechanus* around various structured habitats off Alabama were successfully estimated with long-term telemetry, and the design of the receiver arrays enabled fishery-independent estimations of emigration, fishing and natural mortalities in an open water system. To date, this was the longest telemetry study for red snapper (twice as long), which contributed to the highest residence time and site-fidelity estimates obtained for this species for any habitat, with many fish resident for over a year ( $n = 37$ ) and some for as long as 2 yr ( $n = 9$ ). The high estimates of median residence time (542 d) and site fidelity (72%) were also due to being able to account for natural mortality, fishing mortality and post-release behaviors. Large red snapper (>500 mm TL) permitted the use of long-life transmitters (4 to 6 yr) that had detection ranges of 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, weaker signal strength transmitters (Peabody 2004, McDonough 2009). Also, unique to this study was the use of stationary control transmitters that allowed control of changing transmitter detection rates due to changing environmental parameters and more accurate estimation of mortality, movement patterns and residence.

### Detection rate and range validation

Residence studies typically release multiple fish at one location, but few account for changes in detection rate related to different numbers of ultrasonically tagged fish present (Simpfendorfer et al. 2008). Multiple Vemco Rcode transmitters within the detection range of a receiver significantly affected detection rate of individual transmitters due to signal collisions of transmitters with the same frequency (69 kHz). Significant changes in detections of the stationary control transmitter occurred as fish emigrated or were added to a site. If ignored, these detection changes of remaining fish would be interpreted as seasonal movement patterns.

Telemetry studies should consider detection range changes when determining seasonal movements from detection rate (e.g. Arendt et al. 2001, Starr et al. 2002, Szedlmayer & Schroepfer 2005, Topping et al. 2006, Meyer et al. 2007). A number of studies have

tested the detection range of the transmitters used in fish, but these tests are typically short term, used only to determine telemetry array set-ups (e.g. Arendt et al. 2001, Simpfendorfer et al. 2002, Finstad et al. 2005, Giacalone et al. 2005, Szedlmayer & Schroepfer 2005, Heupel et al. 2006, Hedger et al. 2008). If detection range is not measured throughout the study, there can be unknown gaps in detection within the array that allow fish to pass through undetected, and a reduced detection range (loss of detection) could be interpreted as fish leaving the study. The mean detection rate (mean proportion of expected detections), determined as distances increased from the control transmitter in the present study, was similar to detection range estimates from Szedlmayer & Schroepfer (2005). Both the present study and that of Szedlmayer & 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. 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. The mean detection range significantly varied over the study, and being able to account for this variability allowed for better interpretation of fish detection data.

### Residence time and site fidelity

Telemetry studies of red snapper and other species have detected an initial post-release emigration behavior that is likely related to the capture and handling stress associated with tagging procedures (Gurshin & Szedlmayer 2004, Peabody 2004, Schroepfer & Szedlmayer 2006, Lowe et al. 2009, McDonough 2009). Initial high declines (emigration plus mortality in the present 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 & Gavrilova 1991). In the present study, 17 of the 102 (17%) released fish emigrated or died within the first 6 d. These fish were never detected again and were not reported as captured by fishers. Schroepfer & Szedlmayer (2006) 'lost' 12 of 77 (16%) red snapper within 3 d, and they considered this initial loss of fish a tagging artifact. Peabody (2004) released 125 red snapper, but 28 (22%) of these fish were never detected or reported caught by fishers. McDonough (2009) released fish ( $n = 36$ ) at the same oil platforms ('the Circle') and at least 53% left the site (or were

not detected) over the 14 d study. Similar 'loss' patterns (30% loss in the first 6 d) were shown by various ultrasonically tagged fish species on oil platforms off California (Lowe et al. 2009). These early emigrations were most likely due to capture and tagging stress, and, after some initial recovery period, the remaining fish showed a significantly lower emigration rate.

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 previous studies showed the same initial post-release behavior (and mortality). If all tagging methods cause this behavior in red snapper, then previous estimates of site fidelity and residence time based on mark-recapture may be underestimated because conventional tagging cannot account for this effect (Szedlmayer & Shipp 1994, Patterson et al. 2001, Patterson & Cowan 2003, Diamond et al. 2007, Strelcheck et al. 2007). Patterson & Cowan (2003) calculated red snapper site fidelity ( $SF = e^{-Q}$ ;  $Q$  = instantaneous emigration rate) of approximately 25%  $yr^{-1}$ , with an instantaneous rate of decline of recaptures of  $D = 1.47 yr^{-1}$  for fish at their site, assuming no fishing mortality ( $F$ ), where  $Q = D - \text{instantaneous total mortality}$  ( $Z = 0.09$ ). Strelcheck et al. (2007) estimated an overall SF of 51.5%  $yr^{-1}$  from a  $D$  of 0.72  $yr^{-1}$ , assuming a  $Z$  or  $M$  of 0.10 (natural mortality, i.e. no fishing). Substantial differences among the present study and these 2 previous studies were the abilities of the present study to account for fishing mortality, natural mortality, emigration and the initial stress response. In addition, these previous studies assumed no tag shedding and that all recaptured tagged fish were correctly recognized. Accounting for these factors could easily be responsible for the higher site fidelity (72%  $yr^{-1}$ ) observed in the present study.

Another factor that may have attributed to differences in site-fidelity estimates between the present and previous studies was differences in tagged fish size. Since red snapper maturity (100%, 440 mm FL [forklength]; 50%, 275 mm FL) occurs at sizes smaller than those used in the present study (>500 mm TL), differences between these studies may be due to an ontogenetic change in movement patterns (Render 1995, Jackson et al. 2007). Three main hypotheses of size effects on movements have been suggested: (1) larger fish may move more since their size may make them less susceptible to predation, (2) smaller fish may move more or show less fidelity due to competitive exclusion from preferred habitat by larger conspecifics, and (3) larger fish may need to move over a

larger area to acquire the prey required to meet their energetic needs (Wakeman et al. 1979, Szedlmayer & Schroepfer 2005, Strelcheck et al. 2007, Gallaway et al. 2009, Topping 2009, Mudrak & Szedlmayer in press). The present 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 & Schroepfer (2005) were unable to correlate residence time to fish size, but did find that larger red snapper spent less time within receiver range. This movement pattern was also evident in a study that manually tracked large red snapper (>500 mm TL) at Sites A4 and A5 over 24 h periods, and found larger fish moved a greater mean distance from the reef than smaller fish (Topping 2009). In contrast, Peabody (2004) used telemetry methods for smaller red snapper on oil rigs, and estimated shorter residence times than those 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 a distinct thermocline, rather than fish size. Patterson et al. (2001) found that red snapper movements away from tagging sites increased with fish size, and Diamond et al. (2007) also showed a fish size effect whereby larger red snapper had a greater probability of movement. However, in general, Patterson et al. (2001) and Diamond et al. (2007) tagged much smaller fish on average (Patterson et al. 2001, 335 mm TL; Diamond et al. 2007, 363 mm TL) than those tagged in the present study.

The spatial scales on which site fidelity has been estimated were inconsistent among past studies and may affect what constitutes the high site fidelity of red snapper (Schroepfer & Szedlmayer 2006, Strelcheck et al. 2007). McDonough (2009) suggested that a better approach for estimating site fidelity would be in the context of a fish's home range (rather than the detection range of the transmitters used). However, definitions of home range can also 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, 2006). Strelcheck et al. (2007) suggested that since red snapper can live up to 50 yr (Wilson & Nieland 2001), they show relatively low site fidelity to small artificial reefs (0.1% of fish remaining after 10 yr). As shown in the present study, red snapper will stay at an 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 is considered it might be concluded that red snapper

showed low site fidelity to artificial reefs, but high habitat fidelity is apparent when accounting for quick movements followed by long-term 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 in 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 (>1000) of artificial structures in this area with a range of fishing mortalities (Topping 2009), and many of these structures were privately deployed with unpublished locations or have been relocated to unknown locations by hurricanes (Minton & Heath 1998, Turpin & 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 & Bortone 2002, Larsen 2005).

### Long-term movement patterns

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 7 mo. The directed movements (e.g. 8 km in 1.6 h) of some red snapper in the present study to other structured habitats indicate possible previous knowledge of these alternate sites. For example, Fish 70 emigrated from its original site (A3) to another site (A1) and then returned to A3. Also, over 2 consecutive years, Fish 22 would also move to another structure ~2 km to the east in spring and return to the release site in fall. 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 of other fish species to and from particular habitats appears important, as indicated from homing studies, and movement is probably due to prey availability, shelter and spawning opportunities, with different artificial reefs providing differing levels of these resources (Matthews 1990, Mitamura et al. 2005, Lowe et al. 2009). Homing of red snapper has not been verified in other tagging studies that have translocated this species to other habitats, but these fish did tend to leave the release site at a higher

rate than non-translocated fish (Patterson et al. 2001, Watterson et al. 1998, Peabody 2004).

Storms (e.g. cold fronts and hurricanes) appeared to initiate movement of red snapper in the present study. For example, the shallowest sites (N1, A4, A5) might be more affected by cold fronts compared to deeper sites. In November and December 2008, 6 fish emigrated from these sites towards the east right before or after several cold fronts, and when water temperatures warmed up in May and June 2009, 5 of these fish returned from an unknown location (>2 km away). Sites A4 and A5 are slightly deeper (25 m) than Site N1 (20 m), and the emigration of fish at the deeper sites was delayed ~10 d (water temperature cooled earlier at N1). It is possible that these fish were avoiding wave action and cold water masses by moving to deeper sites as suggested by Moseley (1966). Overall, 19 fish had movements that appeared related to storms, with some fish leaving the study site just prior (hours to 1 d) to the storm passing over the site. Heupel et al. (2003) found that blacktip sharks *Carcharhinus limbatus* may sense barometric pressure changes, as the sharks would leave the shallow bay to deeper water just prior to the arrival of a tropical storm. The present study also indicates that some fish may detect the pressure changes (decrease) associated with storm fronts and hurricanes.

Overall, 7 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<sup>-1</sup>. 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 (Peabody 2004, Szedlmayer & Schroepfer 2005). 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, Peabody 2004, Szedlmayer & Schroepfer 2005). The present study did find 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, Patterson 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 in various

directions from the study site (Patterson et al. 2001). The eastern emigration pattern of some fish in the present study provides evidence that higher fishing pressure to the east is not the only factor contributing to the apparent eastward redistribution of red snapper.

### Diel movements

Diel movement patterns were detected for red snapper in the present 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 & Schroepfer 2005, Meyer et al. 2007, McDonough 2009, Topping 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; Fig. 11) and patterns were not always consistent each day. When patterns were detected, most fish (69%) moved away from the structure late in the day or at sunset and returned sometime before sunrise. Both Peabody (2004) and Szedlmayer & 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, which supports the results of Peabody (2004) and Szedlmayer & Schroepfer (2005). Szedlmayer & Schroepfer (2005) used transmitters comparable to those in our study, and found some fish ( $n = 4$ ) showed diel patterns, with varied results between day and night detections. The diel movements for large red snapper in the present 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 (Ouzts

& Szedlmayer 2003, McCawley & Cowan 2007). Variability in the presence of reef and sand organisms during both day and night, and over seasons, may result in differences in diel movements that simply reflect food availability near the structure over diel and seasonal cycles (Ouzts & Szedlmayer 2003, McCawley & Cowan 2007). Intra-specific variability in movement patterns of fishes appears prevalent, and it will be necessary to continue to determine the causal factors (e.g. habitat, food availability, season, etc.) associated with this variability to better manage this species and others (Tolimieri et al. 2009).

In summary, this 4.5 yr study showed long-term residence of red snapper at both artificial and natural habitats in the northern GOM. 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 ( $12 \text{ km}^2$  at each site). The addition of a control transmitter to the design of this telemetry array allowed for the estimation of changes in detection range throughout the study. 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 our study have contributed to high site-fidelity rates ( $72\% \text{ yr}^{-1}$ ) and longer residence times (median: 542 d, range: 20 to 1099 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 may occur for various reasons; seasons, cold fronts and hurricanes appeared to affect the timing of red snapper emigration (and immigration) in the present study. Diel movements are probably related to foraging behavior as indicated by some diel diet shifts shown in previous studies (Ouzts & 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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