Fine-scale Movements and Home Ranges of Red Snapper *Lutjanus campechanus* Around Artificial Reefs in the Northern Gulf of Mexico

by

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A thesis submitted to the Graduate Faculty of
Auburn University
in partial fulfillment of the
requirements for the Degree of
Master of Science

Auburn, Alabama
December 12, 2011

Keywords: red snapper, *Lutjanus campechanus,* fine-scale movement,
home range, artificial reef, Gulf of Mexico

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Abstract

Few studies have examined fine-scale movement patterns of continental shelf marine fishes. For example, little is known about an important marine species, red snapper *Lutjanus campechanus*, and its fine-scale movement patterns around artificial reefs. Such information could provide insight on habitat use and help answer persistent questions concerning the ecological function of these structures for red snapper. Thus, the present study examined fine-scale movements (~1 m accuracy) of red snapper ($N = 5$) around artificial reefs in the northern Gulf of Mexico with the VR2W Positioning System (VPS, Vemco Ltd, Nova Scotia). This system enabled the continuous monitoring of tagged fish over extended durations (44–326 d) on various temporal scales (hourly, daily, and monthly). Red snapper showed a consistent close association with artificial reefs (mean ± SD distance = 19.3 ± 21.6 m). Home ranges (95% kernel density estimates, KDE) were significantly larger during daytime than nighttime periods. Monthly home ranges and core areas (50% KDE) were significantly larger in summer than in winter and positively correlated with changes in water temperature, suggesting colder temperatures reduced red snapper movement. Red snapper showed a high degree of site fidelity to the studied artificial reefs on multiple temporal scales, and these habitats provided a "home base" from which fish expanded area use to the immediately surrounding unstructured habitat.

Acknowledgements

This project was funded by Marine Resources Division, Alabama Department of Conservation and Natural resources, and is a contribution of the Alabama Agricultural Experiment Station and the Department of Fisheries and Allied Aquacultures, Auburn University. I thank my advisor, Dr. Stephen T. Szedlmayer, for his guidance and support throughout my time at Auburn. I also thank my committee members, Dr. Stephen A. Bullard and Dr. David L. Swann for their critical review of my thesis. A big thank you goes to Jenny Herbig, Danielle Horn, Pete Mudrak, Tara Syc, Claire Roberts, and Nick Wilson for their invaluable assistance in the field. I also thank Zy Biesinger for his help with data analysis. Finally, I am forever grateful for the endless love, support, and encouragement from my parents, sisters, and Joey Szczebak.

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INTRODUCTION

Red snapper *Lutjanus campechanus*, a commercially and recreationally valuable species in the Gulf of Mexico, is closely associated with natural and artificial reefs (Szedlmayer 1997; Szedlmayer and Schroepfer 2005; Schroepfer and Szedlmayer 2006; Topping and Szedlmayer 2011a), and is often the most abundant species present on those structures (Lingo and Szedlmayer 2006; Gallaway et al. 2009; Dance et al. 2011). However, the ecological function of artificial reefs for red snapper remains uncertain. Specifically, it is unclear if artificial reefs attract red snapper from surrounding areas and increase fishing mortality and stock depletion (Grossman et al. 1997; Cowan et al. 2011) or if they improve red snapper production and enhance fishery resources (Szedlmayer 2007; Gallaway et al. 2009; Shipp and Bortone 2009). Artificial reefs may increase fish biomass production by increasing food availability, feeding efficiency, and shelter from predation or fishes may be attracted to artificial reefs due to behavioral preferences (Bohnsack 1989). A better understanding of habitat use is required to clarify the role of artificial reefs for red snapper.

Diet analyses have differed in the identification of red snapper foraging habitats. Ouzts and Szedlmayer (2003) reported diets with reef- and sand-associated prey, while other studies observed red snapper diets dominated by pelagic and sand-associated prey (McCawley et al. 2006; Wells et al. 2008). Also, diel shifts in foraging habitats were observed, wherein red snapper fed opportunistically on reef or pelagic organisms throughout the day before moving off reefs at night to exploit nocturnal benthic organisms (Ouzts and Szedlmayer 2003; McCawley et al. 2006). Seasonal diet shifts have also been reported, but identification of foraging habitats based on prey items was inconsistent between studies (Bradley and Bryan 1974; McCawley et al. 2003). Thus, these diet studies do not offer a clear understanding of the value of artificial reefs or surrounding open habitat for red snapper diets. Analysis of red snapper fine-scale movement patterns would provide indirect evidence of foraging habitats as diel and seasonal movement patterns may be closely associated with foraging activity (Snedden et al. 1999; Haertel and Eckmann 2002; Bellquist et al. 2008; Andrews et al. 2009).

In addition to improving understanding of the value of artificial reefs, analyses of fine-scale movements may also provide insight into the use of open habitats surrounding the reefs. For example, predation by red snapper and other reef fishes can alter the distribution and abundance of open habitat prey (Kurz 1995; Bortone et al. 1998). Also, as the distance between artificial reefs decreases, foraging areas of nearby reefs overlap, access to prey is reduced, and reef fish biomass may decline (Lindberg et al. 1990; Jordan et al. 2005; Strelcheck et al. 2005). An evaluation of fine-scale movements will contribute to defining the size of open habitat forage areas, and direct the placement of future artificial reefs as to optimize their use and increase reef fish biomass (Bortone et al. 1998; Strelcheck et al. 2005).

Fine-scale movement patterns of red snapper have been investigated in the northern Gulf of Mexico (Topping and Szedlmayer 2011; McDonough 2009; Szedlmayer and Schroepfer 2005); however, those studies are limited to short temporal scales (hours-weeks). Szedlmayer and Schroepfer (2005) manually tracked red snapper (*N* = 4) overnight (9 or 16 hr periods) using surface-operated detection equipment. All fish remained near the reef throughout the tracking period and were closer to the reef at dusk than during the night and dawn. Topping and Szedlmayer (2011) manually tracked red snapper (*N* = 12) from the surface for longer tracking periods (24 hr) and showed that red snapper stayed near the reef and were generally closer to the reef during the day than at night. McDonough (2009) monitored fine-scale movement patterns of red snapper around oil platforms for two 2-week periods with a real-time radio-linked acoustic positioning system (VRAP, Vemco Ltd, Nova Scotia). Fish showed diel periodicity related to distance from the platforms, but patterns were variable throughout the study. Many questions remain regarding diel movement patterns and habitat use of red snapper due to low sample sizes of tracked fish and short tracking durations. No previous studies have monitored seasonal patterns of fine-scale movements by red snapper.

Recent advances in acoustic telemetry technology have greatly enhanced fine-scale tracking capabilities. The Vemco VR2W Positioning System (VPS) allows fine-scale (m), continuous, long-term, simultaneous tracking of multiple fish with greater accuracy than active manual tracking (Espinoza et al. 2011a). In the present study, the VPS was evaluated for use in the Gulf of Mexico, and was used to define red snapper home ranges, potential foraging distances, and diel and seasonal variations in movement patterns around artificial reefs. In turn, these data were used to help clarify the ecological function and importance of artificial reefs for red snapper.

METHODS

Study site.—Red snapper were tagged and tracked in the Hugh Swingle General Permit Area, 30 km south of Dauphin Island, Alabama, USA (Figure 1). Study sites (N = 2) were centered on steel cage artificial reefs (4.4 x 1.3 x 1.2 m) located 1.4 km apart at depths of 30 m. The reefs were deployed in February 2006 at unpublished locations and thus fishing mortality was limited.

Fish Tagging.—Adult red snapper (> 400 mm total length) were captured by hook and line, weighed, measured, and anesthetized onboard the research vessel in a 70 L container of seawater and MS-222 (150 mg tricaine methanesulfonate/L seawater for 2.5 min). Fish tagging and release procedures followed Topping and Szedlmayer (2011a). A uniquely coded acoustic transmitter (Vemco V16-6x-R64k; 69 kHz; transmission delay: 20–69 sec) was implanted within the peritoneal cavity through a vertical incision (20 mm) above the ventral midline, and the incision was closed with absorbable, sterile, surgical sutures (Ethicon 2-0 plain gut). For visual identification, all tagged fish were marked with individually numbered internal anchor tags (Floy®). After surgery, fish were held at the surface or in a 185 L container of seawater for recovery prior to release. When fin and gill movements resumed, an inverted barbless hook was inserted through the lower jaw, and fish were returned to the reef on a weighted line and released at the bottom.

Fine-scale tracking.—Fine-scale movements of tagged red snapper were monitored from July 2010 to August 2011 using the Vemco VR2W Positioning System (VPS). Each study site included an array of omni-directional acoustic receivers ($N = 5$; Vemco VR2W) moored ~4.5 m above the seafloor on lines anchored to the bottom. Receiver positions were chosen to maximize detection ranges and assure continuous, simultaneous detection of each tagged fish by at least three receivers. Preliminary detection range tests of receivers showed 100% detection of transmitters at 400 m. Thus, a receiver was positioned adjacent to the artificial reef (20 m north) at each site, and four additional receivers were placed 300 m north, south, east, and west of center to maximize overlap of detection ranges (Figure 2). At each site, temperature loggers ($N = 2$; Onset HOBO® U22 Water Temp Pro v2) were attached to the mooring line of the center receiver at the seafloor and near the receiver to monitor water temperature (1 hr intervals).

Synchronization transmitters (sync tags; Vemco V16-6x; 69 kHz; transmission delay: 540–720 sec) were attached to the mooring lines 1 m above all receivers to synchronize the receiver clocks. Time synchronization was critical for accurate positioning with the VPS as transmitter positions were calculated by triangulating the differences in arrival times of transmission detections at three or more receivers (Espinoza et al. 2011a). A stationary control transmitter was moored within each receiver array and its position was recorded using the depth finder and GPS onboard the research vessel. The accuracy of the VPS was evaluated by comparing VPS-calculated positions with known transmitter positions. Detection data was downloaded from the receivers periodically (1–2 months), post-processed using Vemco VPS Software (Vemco Ltd, Nova Scotia), and reported as fish positions over time.

Data Analysis.—Area use was calculated in R using two-dimensional kernel density estimation (Venables and Ripley 2002). Kernel density estimates (KDE) describe a probabilistic area within which an animal may be located (Worton 1989; Seaman and Powell 1996). Red snapper home ranges were defined by 95% KDE (< 5% excursions) and core area use was defined by 50% KDE. The effect of month on area use (i.e., 95% and 50% KDE) was tested using a one-way mixed model repeated measure analysis of variance (rmANOVA) with fish as a random factor and month as a repeated measure. Also, the effects of diel period (day and night), and hour (1 hr periods over 24 hr cycles) on area use were analyzed using two-way mixed model rmANOVA with fish as a random factor and month as a repeated measure. When significant differences were detected Tukey-Kramer multiple comparison tests were used to show specific differences in area use over time. The effect of water temperature on area use was analyzed using a linear regression model and the relation between diel periods and water temperature was compared with a two-way mixed model rmANOVA with fish as a random factor and month as a repeated measure. The effect of fish length on monthly area use was tested with rmANOVA. Distances between the artificial reef and red snapper positions (latitude, longitude) were calculated with the haversine formula (Sinnott 1984):

$$a = \sin^2(\Delta \mathrm{latitude}/2) + \cos(\mathrm{latitude}_1) \bullet \cos(\mathrm{latatitude}_2) \bullet \sin^2(\Delta \mathrm{longitude}/2)$$

$$c = 2\mathrm{arctan2}(\sqrt{a}, \sqrt{(1-a)})$$

$$d = Rc,$$

where R is the earth's radius (mean radius = 6,371 km). The haversine formula was also used to calculate distances between the known and VPS-calculated positions of the stationary transmitters.

RESULTS

VPS Accuracy

The accuracy of VPS-calculated positions was examined with stationary control transmitters. At site R1, the control transmitter was moored on its own line within the receiver array and the know position was based on the location of the float at the top of the mooring line. At site R2, the control transmitter was moored on a floated line tied to artificial reef and the known position was based on the location of the reef. The mean ± SD distance between the known position and VPS-calculated positions of control transmitters at site R1 (N = 42,652) was 0.98 ± 0.66 m, and at site R2 (N = 50,176) was 3.3 ± 0.55 m. The larger error observed at site R2 may be due to the known transmitter position because it was based on the location of a larger object than at site R1.

Tagging Efforts and Outcome

Adult red snapper (N = 33) were tagged with acoustic transmitters and released on steel-cage artificial reefs (N = 2) in the northern Gulf of Mexico. All red snapper were grouped into three categories based on the status of the tagged fish after 2 d at liberty: tracked, lost, or stationary (Table 1). Tracked fish (N = 5) were monitored with the VPS for 42–326 d between July 2010 and August 2011. Lost fish (N = 15) left the receiver array, and most (N = 13) were not detected again after this initial loss. However, two of the lost fish were detected intermittently ~80 m south of the receiver array. Fish status (i.e., active or stationary) and movements of these two fish could not be analyzed due to low accuracy of VPS-calculated positions outside the receiver array. Stationary transmitters (N = 13) were defined as red snapper mortalities and showed zero movement immediately after the fish's release (N = 9) or within 90 min (N = 3) or 2 d (N = 1) of release. Divers recovered stationary transmitters (N = 9) from the seafloor using VPS-calculated positions (latitude, longitude), while the others (N = 4) could not be recovered due to low visibility conditions, or inability of divers to locate transmitters within the reef structure.

Fine-scale Movements

KDE were used to describe red snapper space use relative to artificial reefs, rather than distances, because KDE are robust to autocorrelation and are not sensitive to outlying positions (Worton 1989; Seaman and Powell 1996). Core areas were significantly larger in June and July 2011 than December 2010 – April 2011 ($P < 0.05$; Figure 3). Similarly, home ranges were larger May–July 2011 than in January and February 2011 and were also larger in March 2011 than May 2011 and larger in April 2011 than June 2011 ($P < 0.05$; Figure 3). No significant differences in monthly area use were detected during months when only one fish was tracked (i.e., July–October 2010, August 2011; $P > 0.05$). Area use was significantly positively correlated with water temperature (home range: $P < 0.001$, $r^2 = 0.63$; core area $P < 0.001$, $r^2 = 0.63$; Figure 3).

Diel and hourly differences in red snapper area use were analyzed with the effect of month removed. Home ranges were significantly larger during the day than the night ($P < 0.01$; Figure 4). Also, there was an increasing trend in hourly home range size throughout the day, with a peak from 1700 to 1800 hours, followed by a decline into the night periods. The smallest hourly home ranges were observed between 0400 and 0500 hours and between 2100 and 2200 hours (Figure 5).   No significant differences in core area size were detected between day and night periods (P = 0.47) or across hourly periods (P = 0.27).   Water temperatures were not significantly different between day and night periods (P = 0.99). Fish size (570–719 mm total length) was not significantly correlated with home range (P = 0.20) or core area (P = 0.17).

DISCUSSION

VPS Accuracy

VPS estimates of control transmitter positions showed up to sub-meter accuracy. This high degree of accuracy was further verified by our ability to recover non-moving transmitters (N = 9) on the seafloor from apparent red snapper mortalities by diving on VPS-calculated positions. The accuracy of the VPS was first validated in a southern California estuary (< 4 m depth), where the mean ± SD distance between known positions and VPS estimates of stationary transmitters was 2.13 ± 1.31 m (Espinoza et al. 2011a). The VPS was then applied to gray smooth-hound sharks *Mustelus californicus* (N = 22; 5–145 d) in the estuary and successfully identified fine-scale patterns in habitat use, including diel movement patterns (Espinoza et al. 2011). The present study showed the VPS is also highly applicable for monitoring fine-scale movements of fishes in open waters in the Gulf of Mexico, and the frequency and accuracy of red snapper positions achieved with the VPS exceeded that of manual tracking (Topping and Szedlmayer 2011).

Residence and Site Fidelity

Past studies of red snapper movement patterns, site fidelity, and residence around artificial reefs in the Gulf of Mexico reported varying results. Several mark-recapture studies suggested red snapper showed little site fidelity to artificial reefs (Watterson et al.

1998; Patterson et al. 2001; Patterson and Cowan 2003) and moved extensively (mean distance 29.6 m; Patterson et al. 2001). Strelcheck et al. (2007) used similar methods, but observed higher site fidelity than other mark-recapture studies. Ultrasonic telemetry studies of red snapper around the same oil-gas platforms off Louisiana concluded red snapper had high short-term site fidelity and low long-term site fidelity (Peabody 2004), or low short-term site fidelity (McDonough 2009). In contrast, high site fidelity and long-term residence was reported in ultrasonic telemetry studies of red snapper around smaller artificial reefs, with median residence times of 373 d and 542 d (Szedlmayer and Schroepfer 2005; Schroepfer and Szedlmayer 2006; Topping and Szedlmayer 2011a). The present study supports the contention of high site fidelity and close association of red snapper with artificial reefs, based on new methods of fine-scale tracking with the VPS. Red snapper showed high site fidelity and long-term residency on artificial reefs, after excluding early (2 d) emigrations and mortalities that were likely a tagging artifact. After 2 d (recovery period) most tagged fish (80%) were present up to the last day of tracking, while one fish had emigrated from the receiver array after 68 d of continuous residency.

Seasonal Movements

This study was the first to continuously monitor fine-scale movement patterns of red snapper for extended durations (42–326 d). Red snapper remained relatively close to artificial reefs throughout the study (mean ± SD distance = 19.3 ± 21.6 m), but showed seasonal changes in habitat use. During spring and summer months, home ranges (95% KDE) were ~5-fold larger and core areas (50% KDE) were ~15-fold larger than during fall and winter months. These seasonal movement patterns were correlated with water temperature, suggesting colder temperatures may have reduced movements of this subtropical species. Seasonal changes in movement and home range size have not been reported previously for red snapper, as long-term telemetry studies with this species were not capable of detecting such fine-scale changes in proximity to a reef (Szedlmayer 1997; Szedlmayer and Schroepfer 2005; Topping and Szedlmayer 2011a). Patterns of smaller area use during colder months may reflect changes in red snapper metabolism as metabolic rate is positively related to temperature (Gillooley et al. 2001), and food intake decreases at lower water temperatures (Hidalgo et al. 1987).

Seasonal changes in area use may also result from seasonal prey availability. Red snapper stomach contents contained the greatest variety of prey during summer, and the least during winter (Bradley and Bryan 1975). Consistent with this pattern, species diversity on artificial reefs in the northern Gulf of Mexico was highest during the summer, and was affected by fluctuations in the epifaunal community and forage base (Dance et al. 2011). Additional studies of seasonal diets are needed to clarify red snapper foraging behavior during months of reduced movement.

Diel and Hourly Movements

In the present study, red snapper home ranges were significantly larger during the day than the night, while previous manual tracking indicated larger area use patterns at night compared to day periods (Szedlmayer and Schroepfer 2005; Topping and Szedlmayer 2011). For example, present home ranges were smallest from 2100 to 2200 hours and from 0400 to 0500 hours. During similar time periods (2100–0200 hours) Topping and Szedlmayer (2011) reported maximum distances from the reef and larger home ranges and core areas during the night than the day. Similarly, Szedlmayer and Schroepfer (2005) observed the largest area used between 1800 and 2100 hours, and reported red snapper farther from the reef during night than the morning. Though all studies had low sample sizes of tracked fish, the present study examined fine-scale movement patterns over much longer time periods, with greater accuracy (~1 m) and frequency of locations than these previous studies. Even so, differences in study design may have resulted in differing movement patterns among these studies. For example, compared to the present study, previous manual tracking of red snapper was over larger reefs (army tank and concrete pyramid), at shallower depths (~ 20 m), and only during summer periods (Szedlmayer and Schroepfer 2005; Topping and Szedlmayer 2011). Further, research vessel noise and movement during previous manual tracking may have altered fish behavior, as red snapper were often attracted to the research vessel during sampling over artificial reefs (author, unpublished).

The diel changes in home range observed in this study may reflect changes in foraging habitats as diel movement patterns of predatory fishes are often closely related to foraging activity (Snedden et al. 1999; Haertel and Eckmann 2002; Bellquist et al. 2008, Andrews et al. 2009). Studies of red snapper feeding periodicity suggested red snapper fed opportunistically on pelagic and reef-associated organisms during the day, and moved over open sand at night to consume nocturnal benthic organisms (Ouzts and Szedlmayer 2003; McCawley et al. 2006). These foraging behaviors were the opposite of habitat use patterns observed in this study, where home range expanded during the day to include larger areas of open habitat. Diel movement patterns of marine fishes are also commonly associated with shifts between foraging and refuge habitats (Emery 1978). The smaller nocturnal home ranges observed in this study suggest artificial reefs may be used for refuge under low light conditions.

Mortality

A large number (39.4%) of transmitters showed no movement within 2 d of releasing tagged red snapper onto artificial reefs. The short time period between fish tagging and no movement suggests tag loss was unlikely, and stationary transmitters were the result of fish mortality. While the cause of high early mortality is difficult to identify, tag and release procedures were probably not the immediate cause, because tagging methods were the same as applied to previous work with very low initial release mortality (e.g., only 2.2% of tagged fish died within 6 d of release, Topping and Szedlmayer 2011a). Abiotic factors may have contributed to the higher rates of mortality in the present study as tagging sites were located in deeper water with sharp thermoclines that were not apparent in previous studies. Depth of capture and exposure to thermoclines are known to affect red snapper by increasing the frequency of barotraumas and inhibiting reflex responses, burst swimming speeds and predator avoidance (Campbell et al 2009). Also, recovery time of captured red snapper was directly related to depth and temperature differentials between surface and bottom waters (Campbell et al 2009). The inhibitory effects of depth and thermoclines, coupled with the effects of anesthesia used during surgery, may have increased early mortality rates of tagged fish.

In combination with abiotic factors, predation may have contributed to high rates of early mortality. Sharks (spinner shark *Carcharhinus brevipinna*, Atlantic sharpnose shark *Rhizoprionodon terraenovae*, and other unidentified species) and bottlenose dolphins *Tursiops truncatus* were observed while fishing and diving at the study sites during tagging and tracking periods. Also, red snapper were captured by spinner sharks and bottlenose dolphins during sampling trips at nearby sites. Beginning immediately after release, one tagged fish showed large, erratic movements throughout the receiver array for 2 d before the transmitter became stationary. These movement patterns were inconsistent with those of other red snapper, indicating the transmitter may have been swallowed by a predator and excreted after 2 d.

Emigration

Initial rates of emigration observed in this study (45.5% within 2 d) were higher than previously reported by other red snapper telemetry studies (16% within 3 d, Szedlmayer and Schroepfer 2005; 17% within 6 d, Topping and Szedlmayer 2011a). Early emigrations in these previous studies reportedly occurred during an initial recovery period and were attributed to abnormal behavior caused by tagging stress (Szedlmayer and Schroepfer 2005; Topping and Szedlmayer 2011a). While a portion of early emigrations in the current study may be due to tagging stress, exceptionally high early emigration rates suggest additional factors contributed to the observed behavior. For example, McDonough (2009) reported 30% of tagged red snapper left the receiver array, or were not detected, within 2 d of tagging, and suggested predation by a migratory predator may have contributed to the initial loss of tagged fish. Transmitters from lost fish in this study may have been consumed by predators that subsequently moved out of the receiver array. Also, strong thermoclines may have increased fish stress during the tag and release procedure, and altered red snapper behavior to increase emigration.

Seasonal and directed movements among artificial reefs have been reported previously, where red snapper moved to different structures for extended periods and returned to the original release site (Topping and Szedlmayer 2011a). Also, Szedlmayer (1997) relocated the majority of red snapper that emigrated from the release site at other artificial reefs 88–760 m away. These observations suggest red snapper lost from the receiver arrays in this study may have moved to nearby artificial reefs outside the receiver detection ranges. Future work is needed to improve understanding of movement patterns and habitat use of tagged red snapper after emigrating from a release site.

Conclusions

Overall, this study showed red snapper were closely associated with specific artificial reefs and relatively small surrounding areas on multiple temporal scales, and these structures were an important habitat for this species. This study was the first to report seasonal changes in fine-scale proximity to artificial reefs, where red snapper used smaller areas in colder months than warmer months, suggesting movements were affected by water temperature. Diel patterns in habitat use were the opposite of previous studies with smaller home ranges observed during the night than the day in the present study. The immediately surrounding open habitat around reefs was also used regularly, and may be an important forage area for red snapper. If forage areas from nearby reefs overlap, reef fish abundance, richness, and biomass, may be inhibited by a decline in open habitat prey availability (Lindberg et al. 1990; Bortone et al. 1998; Jordan et al. 2005). Therefore, fine-scale area use estimates from this study may be used in defining the size of potential forage areas, and in providing management efforts with information that could optimize artificial reef placement.

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TABLE 1. Summary of the tagging effort and outcome of red snapper *Lutjanus campechanus* tagged with ultrasonic transmitters and released on two artificial reefs (R1 and R2) in the northern Gulf of Mexico. Tagged fish were tracked with the VPS, lost (left the receiver array within two days of release), or transmitters became stationary (fish mortality) with two days of release.

Reef	Tagged	Outcome		
		Tracked	Lost	Stationary
R1	23	4	10	9
R2	10	1	5	4
Total	33	5	15	13

TABLE 2. Summary of acoustic telemetry data for red snapper *Lutjanus campechanus* tracked in the vicinity of artificial reefs in the northern Gulf of Mexico. P: fish was present at the tagging site on the last day of tracking; E: fish emigrated from the receiver array prior to the last day of tracking.

Tag ID	Site	TL (mm)	Wt (kg)	Tracking period	No. days tracked	Status
3	R1	539	2	Jul 2010 - Jul 2011	326	P
14	R1	578	2.8	Nov 2010 - Jul 2011	240	P
16	R1	719	5.9	Dec 2010 - Jul 2011	223	P
19	R1	689	4.8	Apr 2011 - Jun 2011	68	E
25	R2	570	2.6	Jun 2011 - Aug 2011	42	P

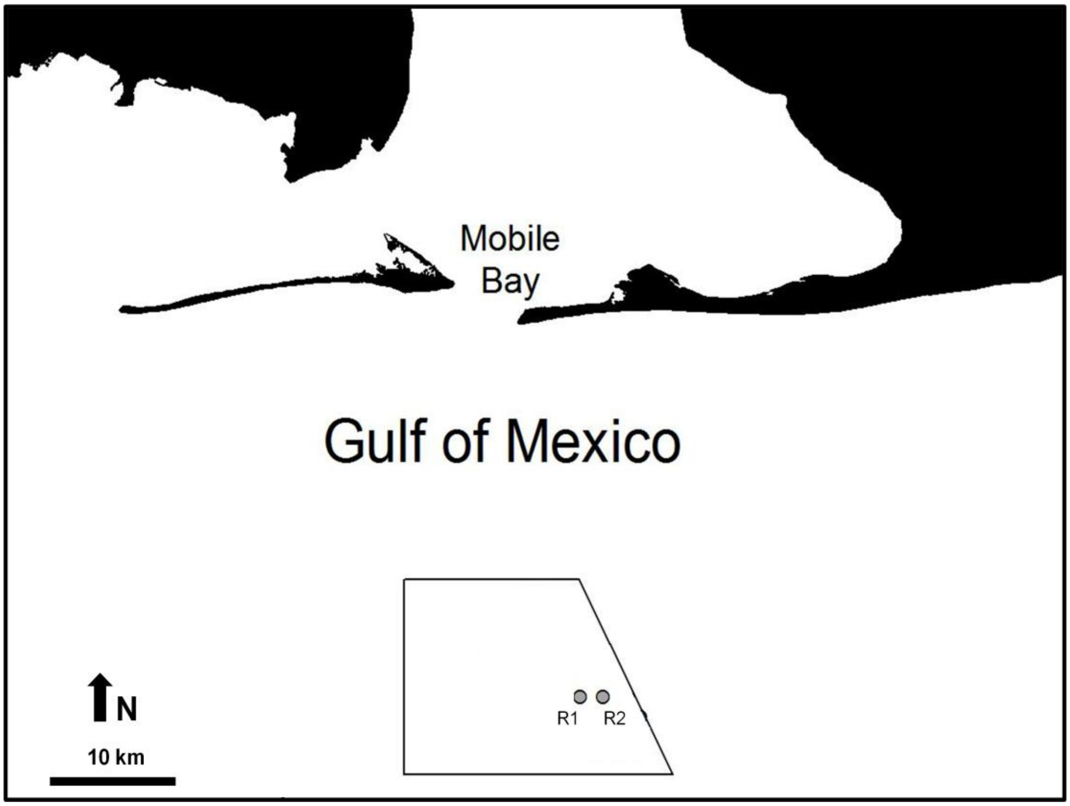

FIGURE 1. Northern Gulf of Mexico and the Hugh Swingle General Permit Area; circles indicate study sites at artificial reefs R1 and R2.

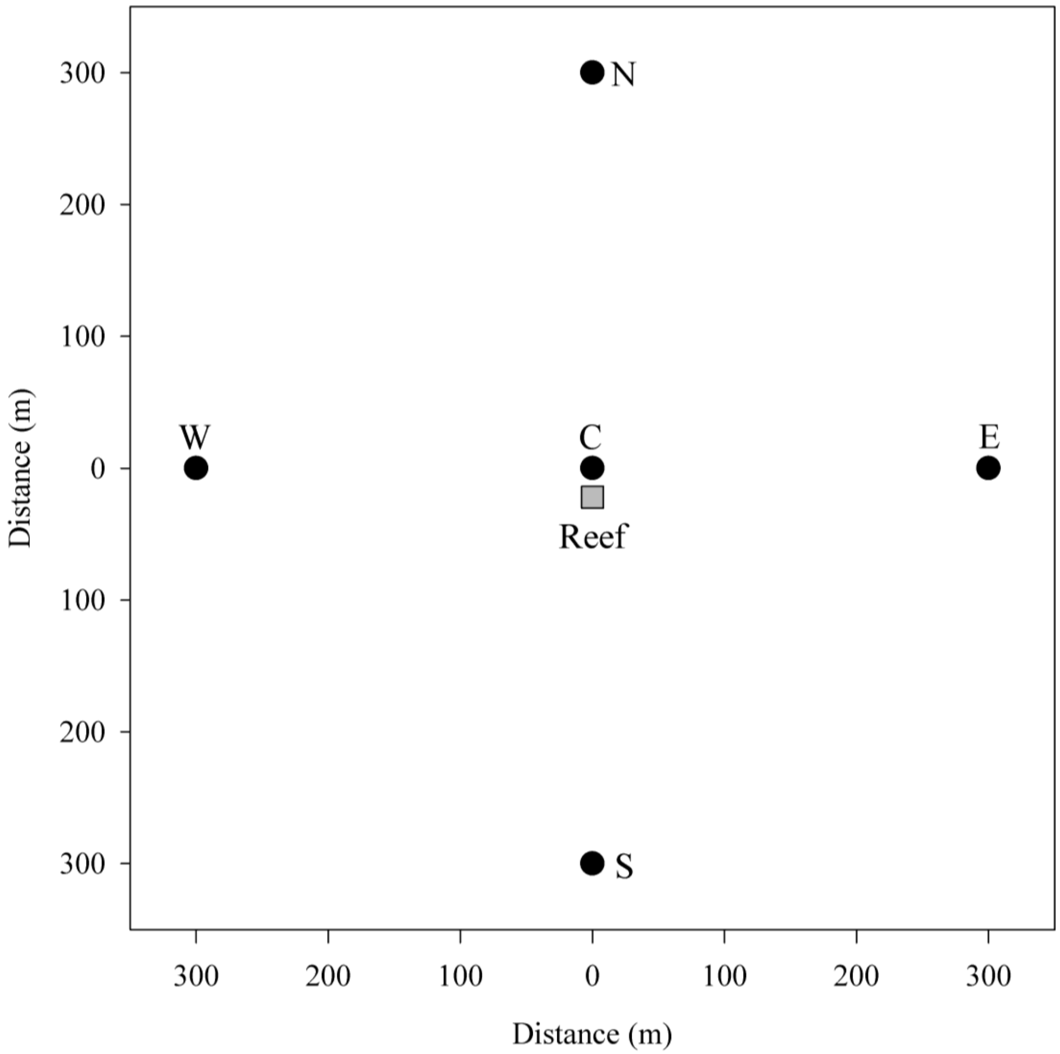

FIGURE 2. Receiver array used to examine fine-scale movements of red snapper *Lutjanus campechanus* around artificial reefs in the northern Gulf of Mexico. The same receiver array design was used at sites R1 and R2. Circles: receivers and co-located synchronization transmitters; square: artificial reef.

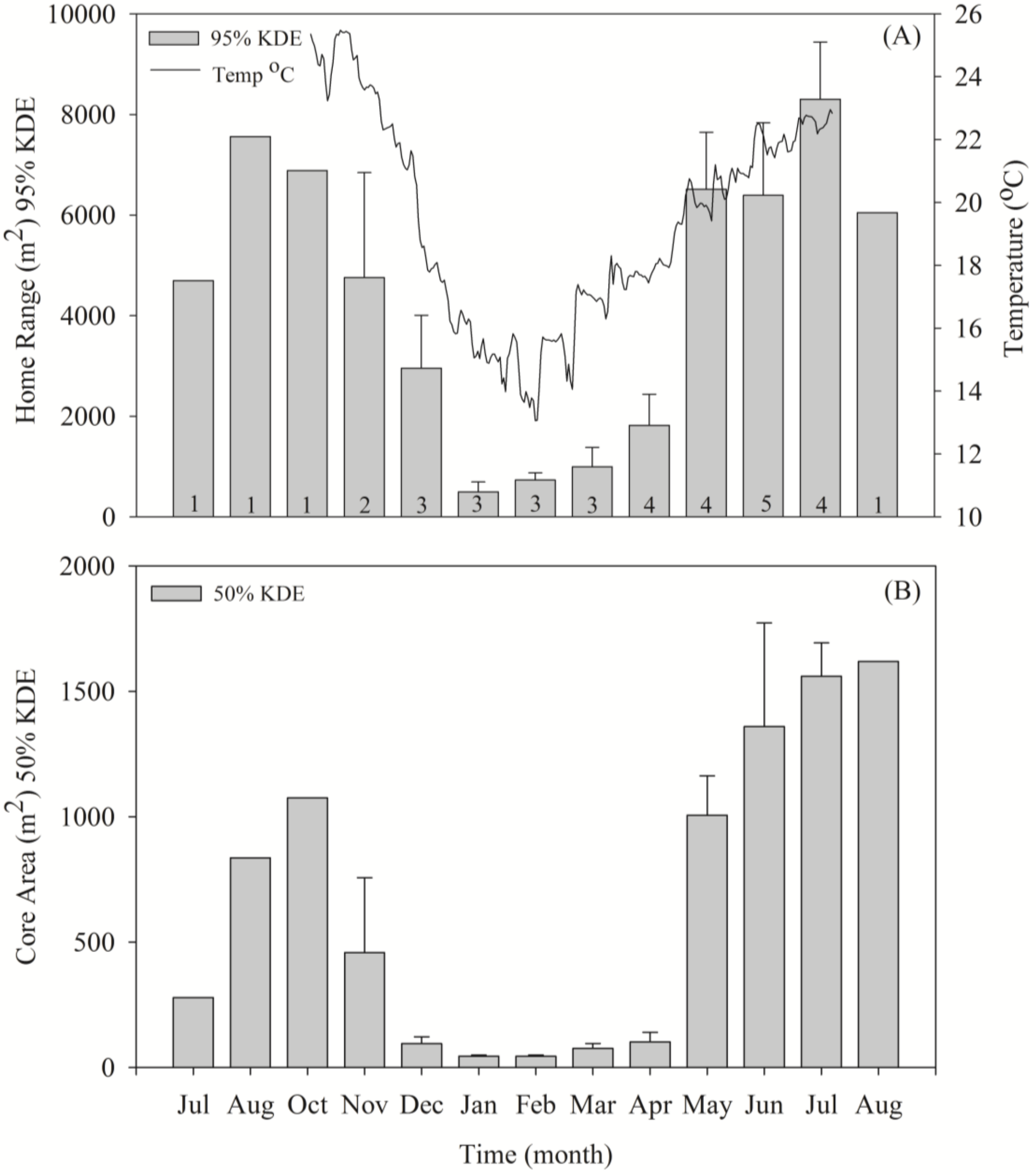

FIGURE 3. Mean monthly **(A)** home ranges (95% KDE + SE) and **(B)** core areas (50% KDE + SE) of red snapper *Lutjanus campechanus* around artificial reefs in the northern Gulf of Mexico. Numbers within bars indicate monthly sample sizes of tracked fish, and the black line indicates mean daily water temperatures at a depth of 26 m.

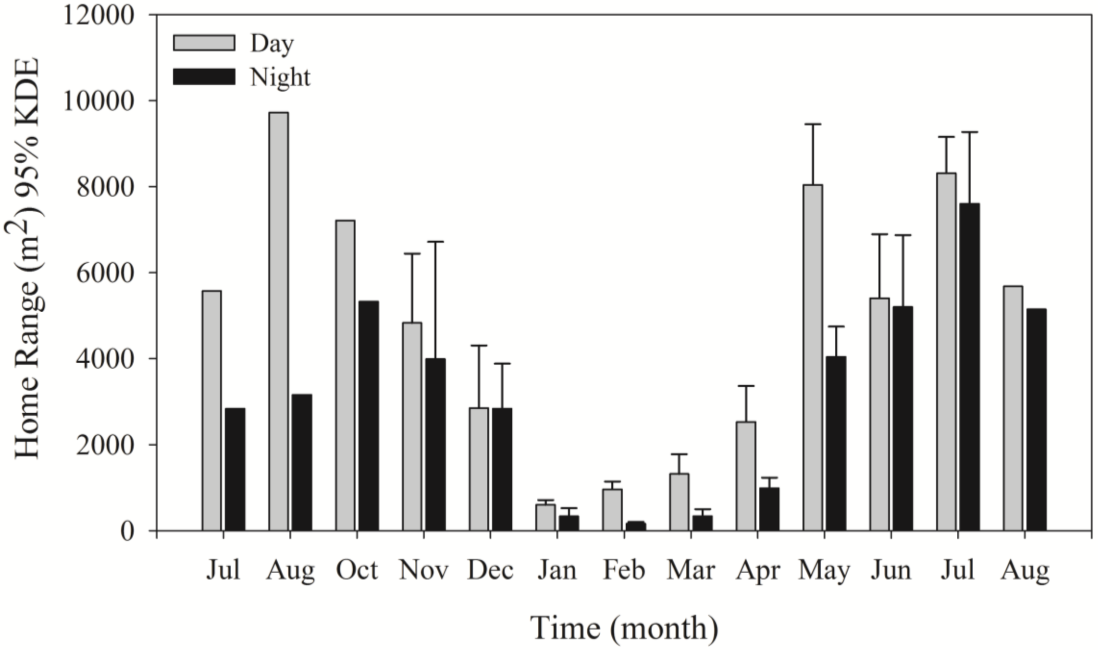

FIGURE 4. Comparison of mean monthly diurnal (gray bars) and nocturnal (black bars) home range estimates (95% KDE + SE) for red snapper *Lutjanus campechanus* around artificial reefs in the northern Gulf of Mexico. Overall, home ranges were significantly larger during the day than at night ($P < 0.001$). Day and night core area sizes (50% KDE, not shown) were not significantly different ($P = 0.47$).

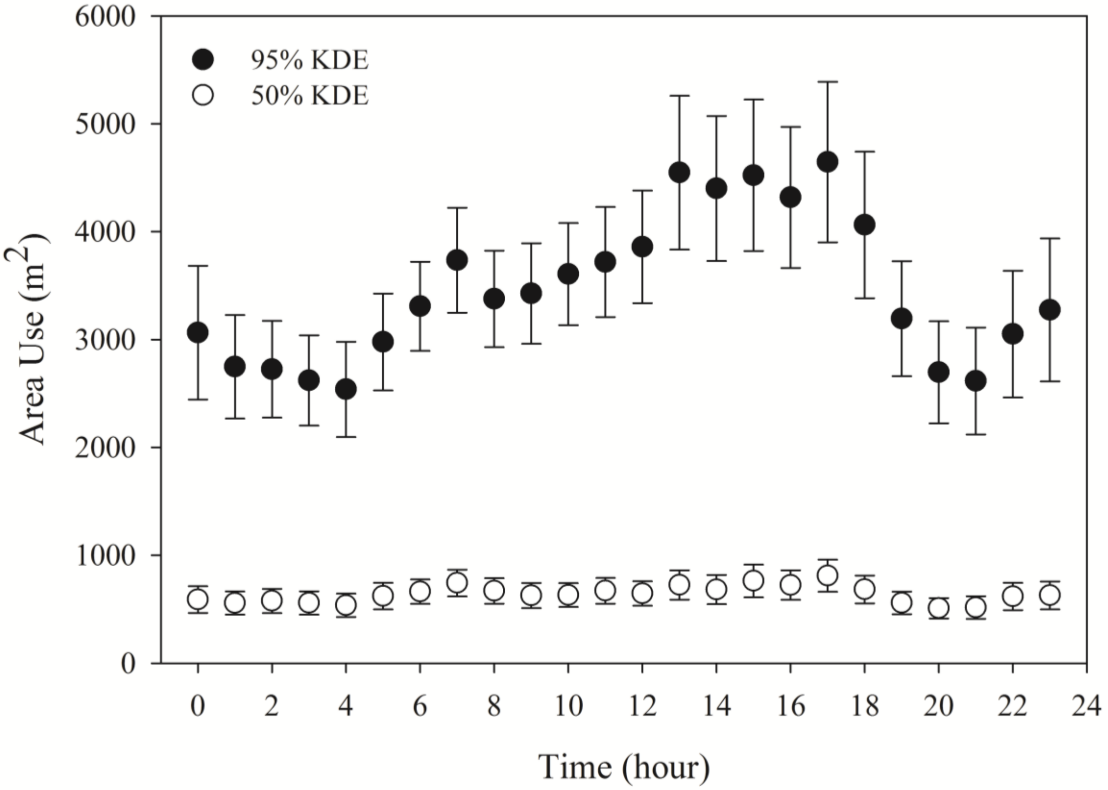

FIGURE 5. Mean hourly estimates of home range (black circles; 95% KDE ± SE) and core area (white circles; 50% KDE ± SE) of red snapper *Lutjanus campechanus* around artificial reefs in the northern Gulf of Mexico throughout the complete tracking duration.