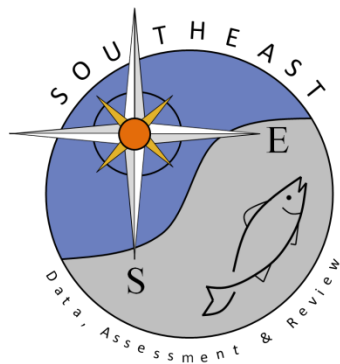


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Maria N. Piraino & Stephen T. Szedlmayer

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ARTICLE

Fine-Scale Movements and Home Ranges of Red Snapper around Artificial Reefs in the Northern Gulf of Mexico

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Abstract

Red Snapper *Lutjanus campechanus* are generally associated with artificial reef habitats in the northern Gulf of Mexico, but whether this association results in fish production is still controversial. Information on fine-scale habitat use patterns would be helpful in evaluating this. Little is known about the fine-scale movement patterns of Red Snapper around artificial reefs. The present study examined fine-scale (~1-m accuracy) movements of Red Snapper with the Vemco VR2W Positioning System. This system enabled continuous monitoring of tagged fish from 100 to 694 d. Locations of individual fish were recorded approximately every 10 min and totaled over 1.9 million accurate locations of Red Snapper from August 2010 through May 2012. Red Snapper showed close association with the reef structure (mean \pm SD distance = 26.3 ± 35.4 m) but differential habitat use in relation to both diel and seasonal periods. Home range areas (95% kernel density estimates [KDE]) were significantly larger during day than night periods and showed the lowest area use at dawn and dusk. Monthly home ranges (95% KDE) and core areas (50% KDE) were significantly larger in spring, summer, and fall than in winter and were significantly correlated with water temperature, suggesting colder winter temperatures reduced Red Snapper movement. Home range area was significantly correlated with fish size (407–590 mm standard length), and the fish in this study showed the highest site fidelity (88% still present after >10 months) of any Red Snapper in other previous studies. Red Snapper also showed use of multiple reefs within the monitoring area, as home ranges (95% KDE) showed a second peak around other artificial reefs. The high site fidelity, long-term use, and concentrated use of multiple artificial reefs confirm the importance of structured habitat for Red Snapper.

The Red Snapper *Lutjanus campechanus* 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 in the northern Gulf of Mexico (Lingo and Szedlmayer 2006; Gallaway et al. 2009; Dance et al. 2011). However, it is still unclear whether artificial reefs attract Red Snapper from surrounding areas and increase fishing mortality and stock depletion (Grossman et al. 1997; Cowan et al. 2011) or whether 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 (Redman and Szedlmayer 2009; Mudrak and Szedlmayer 2012), 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 ecological function of artificial reefs for Red Snapper.

Questions concerning on-reef versus off-reef foraging behaviors are important when examining Red Snapper habitat use patterns around artificial reefs. Past studies have differed in habitat use patterns based on prey consumption and do not offer a clear understanding of the value of artificial reefs or surrounding open habitat for Red Snapper (Bradley and Bryan 1975; McCawley et al. 2003; Ouzts and Szedlmayer 2003; McCawley et al. 2006; Wells et al. 2008). Analysis of Red Snapper fine-scale movement patterns would provide indirect

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evidence of foraging habitats, as 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 the 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 would contribute to defining the size of open-habitat forage areas and direct the placement of future artificial reefs 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 (Szedlmayer and Schroepfer 2005; McDonough 2009; Topping and Szedlmayer 2011b). However, these studies were limited to short temporal scales (hours to weeks). Szedlmayer and Schroepfer (2005) manually tracked Red Snapper ($n = 4$) overnight (9- or 16-h 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 at dawn. Topping and Szedlmayer (2011b) manually tracked Red Snapper ($n = 12$) from the surface for longer tracking periods (24 h) 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, 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 examined 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; Vemco, Nova Scotia) allows fine-scale (m), continuous, long-term tracking of multiple fish with far 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. These data were then used to help clarify the ecological function and importance of artificial reefs for Red Snapper.

METHODS

Study area.—Red Snapper were tagged and tracked in the Hugh Swingle General Permit Area in the northern Gulf of Mexico. Study sites were centered on steel-cage artificial reefs (2.5 m × 1.3 m × 2.4 m; $n = 3$) labeled R1, R2, and R3. Reefs R1 and R2 were located 30 km south of Dauphin Island, Alabama, at depths of 30 m, and R3 was 25 km south of Dauphin Island at a depth of 20 m (Figure 1). The reefs were deployed at unpublished locations and thus fishing mortality was limited.

Fish tagging.—From July 2010 to September 2011, adult Red Snapper (>400 mm total length; $n = 46$) were captured by hook and line, weighed, measured, and anesthetized (level 4; Summerfelt and Smith 1990) on the research vessel in a 70-L container of seawater and tricaine methanesulfonate (150 mg tricaine methanesulfonate/L seawater for 2.5 min). Fish-tagging procedures followed Topping and Szedlmayer (2011a). A uniquely coded acoustic transmitter (Vemco V16-6x-R64k; 69 kHz; transmission delay: 20–69 s) was implanted within the peritoneal cavity through a vertical incision (20 mm) above the ventral midline, and the incision was closed with interrupted stitches using absorbable, sterile, plain gut surgical sutures (Ethicon, number 2, 3.5 metric). For visual

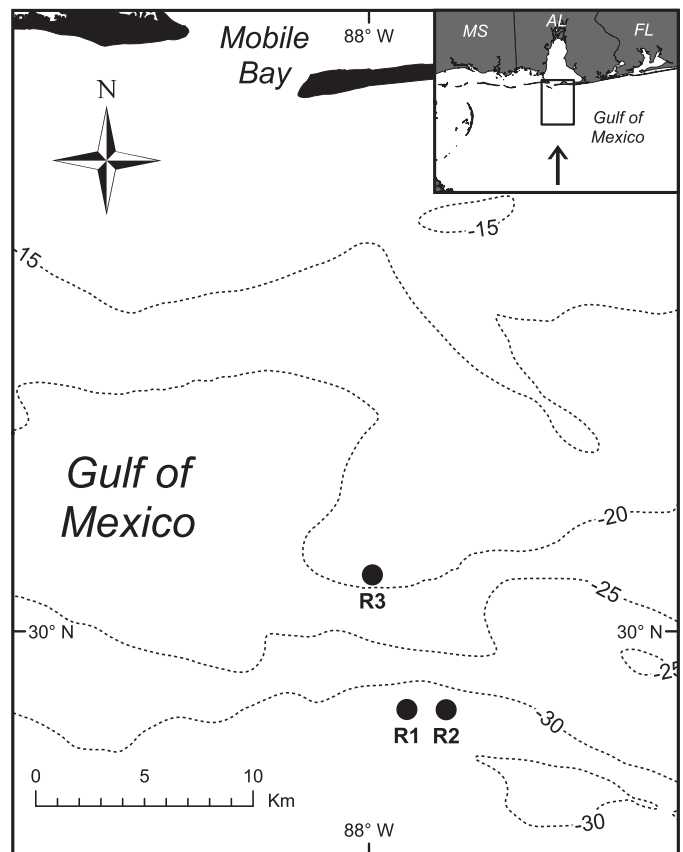


Figure 1. Study site locations in the northern Gulf of Mexico. Circles show VPS study reef locations for R1, R2, and R3.

identification, all fish were also marked with individually numbered internal anchor tags (Floy). Fish tagged between July 2010 and July 2011 were held at the surface or in a 185-L container of seawater after surgery 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. Fish tagged in August 2011 were returned to depth in cylindrical cages (plastic-coated wire; one fish per cage; 40.6 cm high, 61 cm in diameter). After ~2 h, scuba divers opened the cage doors on the bottom and released the fish close (2–3 m) to the reef.

Fine-scale tracking.—Fine-scale movements of tagged Red Snapper were monitored from July 2010 to May 2012 using the VPS. Each study site included an array of omnidirectional 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 the overlap of detection ranges (Figure 2). At each site,

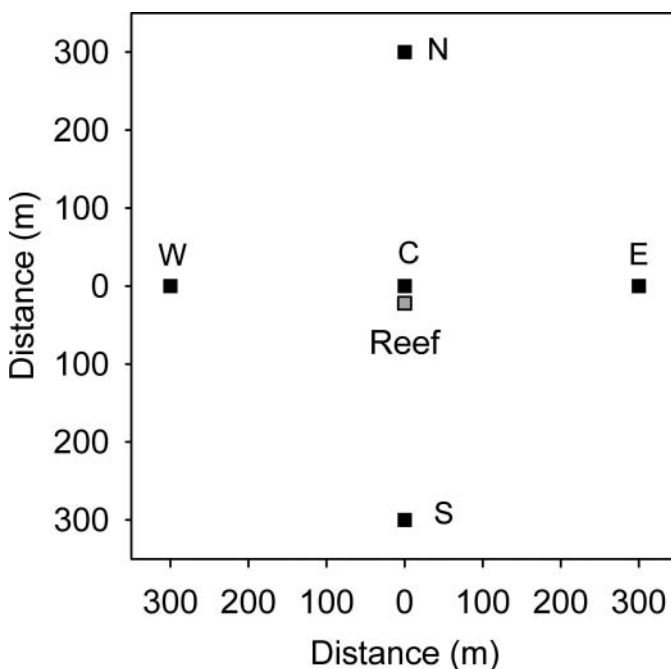


Figure 2. Receiver array used to examine fine-scale movements of Red Snapper around artificial reefs in the northern Gulf of Mexico. Receivers were placed 300 m north, south, east, and west of the artificial reef and center (C) receiver. The same receiver array design was used at all the sites. The black squares are the receivers and synchronization transmitters and the gray square is the artificial reef.

temperature loggers ($n = 2$; Onset HOBO U22 Water Temp Pro v2) were attached to the center mooring line near the receiver and at the seafloor to monitor water temperature at 1-h intervals.

Synchronization transmitters (sync tags; Vemco V16-6x; 69 kHz; transmission delay: 540–720 s) 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 with a three-receiver time-difference-of-arrival positioning algorithm (Espinoza et al. 2011a). Stationary control transmitters were moored within the receiver arrays and their positions were recorded using sonar and a Global Positioning System (GPS; latitude and longitude) onboard the research vessel. Also, to validate the accuracy of VPS-calculated positions, a control transmitter was suspended from the research vessel and was allowed to drift over the VPS array. Latitude, longitude, and time were recorded as the vessel moved over the array. The accuracy of the VPS was evaluated by comparing VPS-calculated positions with the stationary and drifting control transmitter positions recorded with the GPS. Transmitter detection data were downloaded from the receivers periodically (1–2 months), postprocessed by Vemco, and reported as fish positions over time.

Data analyses.—Distances between the artificial reef and Red Snapper positions (latitude, longitude) were calculated with the haversine formula (Sinnott 1984):

$$a = \sin^2(\Delta\text{latitude}/2) + \cos(\text{latitude}_1) \cdot \cos(\text{latitude}_2) \cdot \sin^2(\Delta\text{longitude}/2)$$

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

$$d = Rc,$$

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 control transmitter. Fish distance from the reef was compared with area use by linear regression.

Area use was calculated in R statistical software using two-dimensional kernel density estimation (Venables and Ripley 2002). Kernel density estimates (KDEs) 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 areas were defined by 50% KDE. The effect of season on area use was tested with one-way, mixed-model repeated-measures analysis of variance (rmANOVA) with fish as a random factor and season as a repeated measure. The effect of diel period (1-h intervals over 24 h) on area use was tested with rmANOVA with fish as a random factor and 1-h intervals 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. Linear regression was used to test

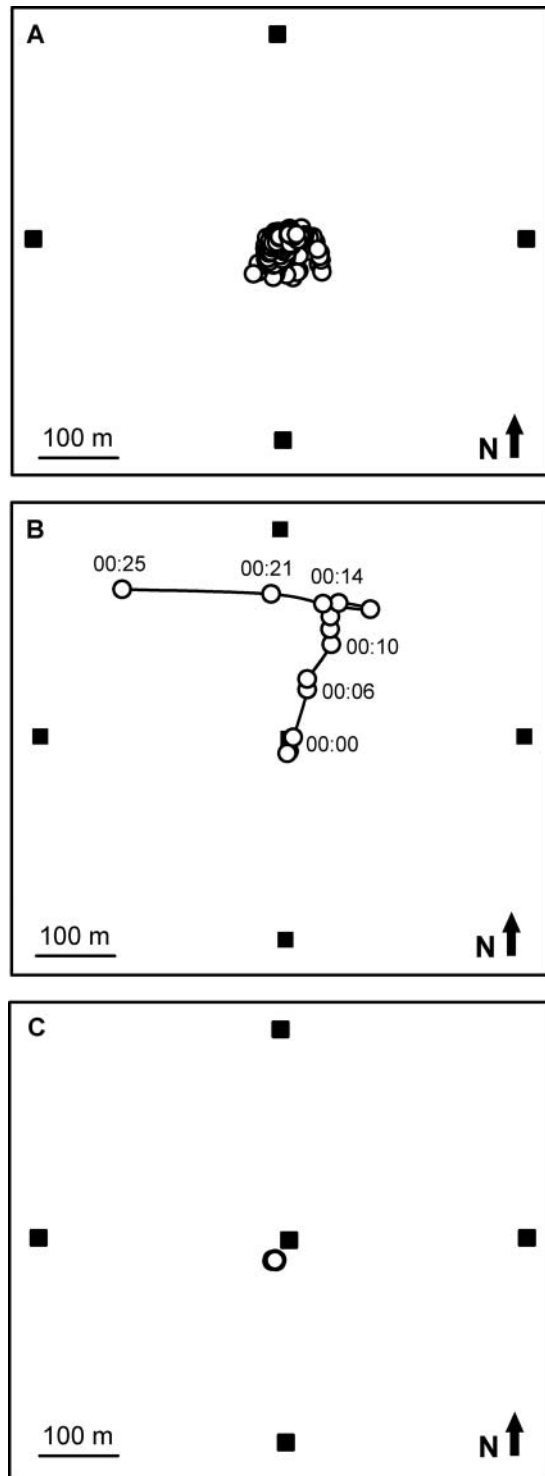


Figure 3. Examples of different tracking patterns observed for Red Snapper at artificial reefs in the northern Gulf of Mexico: (A) tracked, (B) lost (emigration), and (C) stationary (mortality). Patterns for tracked and stationary fish are shown over a 24-h period. The emigration example occurred over a 25-min time period. The black squares are receivers and synchronization transmitters and the white circles are fish positions identified with the VPS.

TABLE 1. Status of Red Snapper tagged with ultrasonic transmitters and released on three artificial reefs in the northern Gulf of Mexico.

Reef and total	Number tagged	Status		
		Tracked	Lost (emigration)	Stationary (mortality)
R1	25	6	10	9
R2	14	4	6	4
R3	7	7	0	0
Total	46	17	16	13

the effect of water temperature on Red Snapper KDE area use and to compare fish length and area use from July 2010 through May 2012.

RESULTS

Fish Tagging

All tagged Red Snapper were grouped into three categories 4 d after release: tracked, lost (emigration), or stationary (mortality) (Table 1; Figure 3). The VPS receiver arrays enabled the continuous monitoring of tracked fish ($n = 17$) over extended durations (100–694 d; Table 2). Individual tracked-fish locations were recorded approximately every 10 min and totaled over 1.9 million accurate locations of Red Snapper from August 2010 through May 2012 (Figure 4). The stationary control transmitter used to examine the accuracy of VPS-calculated positions showed a mean \pm SD distance of 0.98 ± 0.66 m between the known position and VPS-calculated positions ($n = 42,652$). Lost fish ($n = 16$) left the receiver array within 4 d of release, and most ($n = 14$) were not detected again after this initial loss (Table 1). However, two of the lost fish were detected intermittently ~ 80 m south of the R1 receiver array. Fish status (i.e., active or stationary) could not be determined outside the receiver array due to reduced accuracy of VPS-calculated positions and failure to detect fish on at least three receivers. Stationary transmitters were defined as Red Snapper mortalities and showed zero movement immediately after the fish's release ($n = 9$), within 90 min of release ($n = 3$), or 2 d ($n = 1$) after release. Divers recovered most stationary transmitters ($n = 10$) from the seafloor using VPS-calculated positions (latitude, longitude), but three transmitters were not recovered due to poor visibility or loss within the reef structure.

Only a few (15%) of the tagged and released fish were successfully tracked 4 d after release when fish were released by drop weight prior to August 2011. After this, in August 2011 we changed our procedure to releasing the fish from cages. Fish were held in cages on the seafloor for ~ 2 h prior to release in an effort to reduce emigration and mortality rates of tagged fish. This new release method increased survival and

TABLE 2. Red Snapper tracked around three artificial reefs (R1, R2, and R3) in the northern Gulf of Mexico. Abbreviations are as follows: Cage = predator exclusion cage used during release, P = fish was present at the tagging site on the last day of tracking, and E = fish emigrated from the receiver array prior to the last day of tracking.

Fish tag ID	Site	SL (mm)	TL (mm)	Weight (kg)	Tag date	Number of days tracked	Cage	Status
3	R1	423	539	2.0	Jul 9, 2010	694	No	P
14	R1	462	578	2.8	Nov 23, 2010	557	No	P
16	R1	590	719	5.9	Dec 10, 2010	540	No	P
19	R1	561	689	4.8	Apr 14, 2011	100	No	E
25	R2	455	570	2.6	Jun 24, 2011	170	No	P
34	R3	407	508	2.0	Aug 16, 2011	291	Yes	P
35	R3	493	622	3.5	Aug 16, 2011	291	Yes	P
36	R3	432	544	2.2	Aug 16, 2011	291	Yes	P
37	R3	462	571	2.6	Aug 16, 2011	291	Yes	P
38	R1	422	524	2.2	Aug 18, 2011	289	Yes	P
39	R1	447	565	2.5	Aug 18, 2011	289	Yes	P
40	R3	460	572	3.0	Aug 18, 2011	289	Yes	P
41	R3	424	524	2.4	Aug 18, 2011	289	Yes	P
42	R3	524	662	4.4	Aug 18, 2011	289	Yes	P
43	R2	421	532	2.4	Aug 23, 2011	284	Yes	P
44	R2	429	598	3.0	Aug 23, 2011	284	Yes	P
46	R2	414	515	3.0	Aug 23, 2011	284	Yes	P

the ability to track fish to 92%, and from August 2011 to May 2012 these cage-released fish were actively tracked at their release sites. Only one fish was lost out of 13 released from cages, and this fish was lost on the day it was released and not observed again.

Red Snapper showed high site fidelity and long-term residency on these artificial reefs. After excluding losses due to

early emigrations and mortalities within 4 d of tagging (defined here as a tagging effect), the next emigration did not occur until 100 d after tagging (Fish 19). Most (15 out of 17, or 88%) tracked fish were present for a minimum of 10 months, but some fish were present up to 23 months after tagging and until the last day of tracking (May 31, 2012; Figure 4).

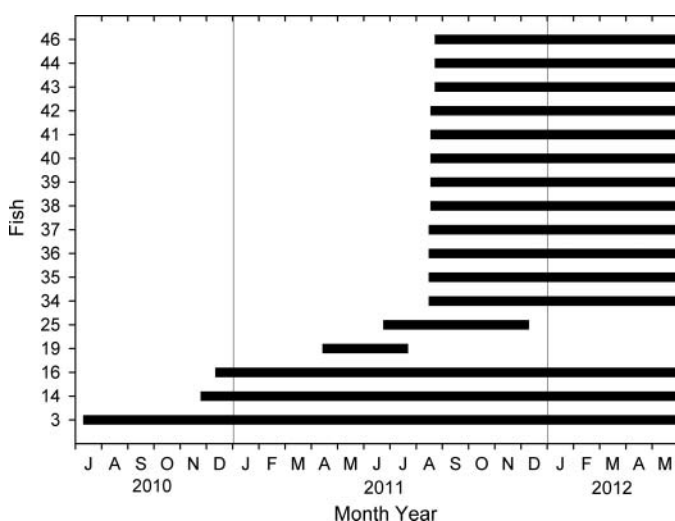


Figure 4. Continuous tracking durations for each transmitter-tagged Red Snapper ($n = 17$) released on three artificial reefs in the northern Gulf of Mexico. Fish still present after the last day of tracking ($n = 15$; May 30, 2012) were all active. Letters along the x-axis represent the sequential months of the year, beginning with July, August, September, etc.

Fine-Scale Movements

Red Snapper showed close association with the reef structure (mean \pm SD distance = 26.3 ± 35.4 m) but differential habitat use patterns in relation to both diel and seasonal periods. Fish mean distance from the reef was positively correlated with area use (KDE home range: $F_{1,15} = 5.1$, $P = 0.04$, $r^2 = 0.25$; KDE core area: $F_{1,15} = 8.3$, $P = 0.01$, $r^2 = 0.35$). The KDEs were used to describe Red Snapper habitat use patterns relative to artificial reef positions, rather than mean distance, because KDEs are robust to autocorrelation and are not sensitive to outlying positions (Worton 1989; Seaman and Powell 1996).

Some Red Snapper (53%) showed homing behavior. At all three VPS sites a second reef was located within the detection range of the receivers. These second reef sites were repeatedly visited by different tagged Red Snapper released on the center reef. Fish closely tied to the center reef at the site of release quickly moved to the other reef site, stayed there for short periods, and returned to the original center reef site (Figure 5).

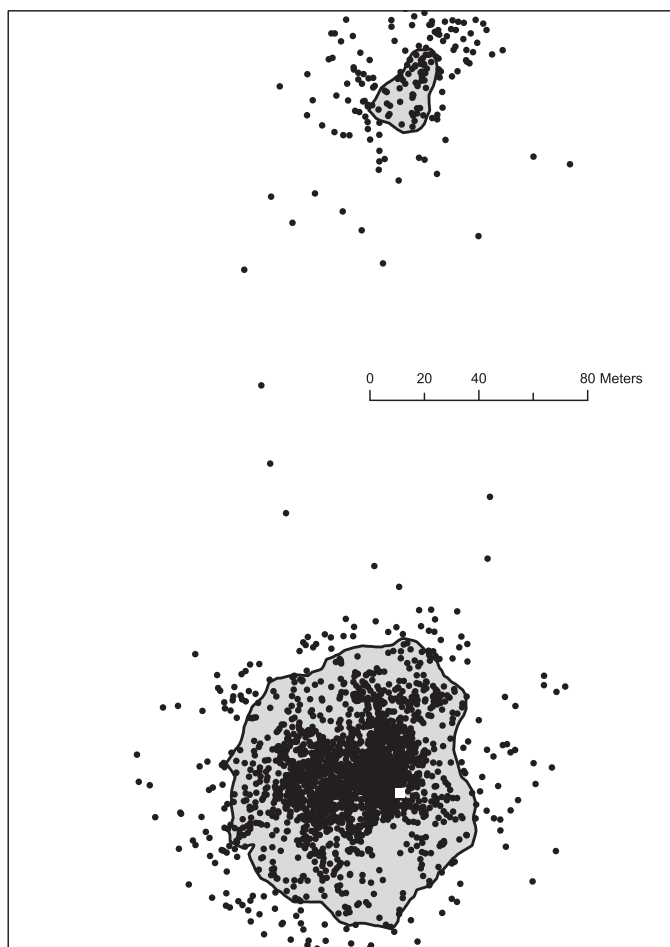


Figure 5. Example of home range (95% KDE; shaded polygon at the bottom of the figure) and individual fish locations (black dots; $n = 15,323$) for one Red Snapper (Fish 3) at site R1 over 1 month (August 2010). This is an example of homing behavior for Fish 3, who would regularly visit another artificial reef (steel cage) site near the north receiver but still within the array (shown by the shaded polygon at the top of the figure), then return to the original release site. The white square is the artificial reef release site.

Seasonal patterns of area use were observed such that home ranges and core areas were significantly smaller in winter (January–March) than in summer (July–September), fall (October–December), or spring (April–June) (rmANOVA, home range: $F_{3, 44} = 15.3, P < 0.001$; core area: $F_{3, 44} = 18.9, P < 0.001$; Figure 6). Red Snapper area use was significantly affected by temperature (home range: $F_{1, 18} = 16.7, P < 0.001, r^2 = 0.48$; core area: $F_{1, 18} = 16.2, P < 0.001, r^2 = 0.47$; Figure 7). Thus, diel patterns in Red Snapper area use were analyzed with the effect of month removed. Home ranges and core areas were significantly larger during the day than during the night and minimum at dawn and dusk (rmANOVA, home range: $F_{23, 368} = 12.5, P < 0.001$; core area: $F_{23, 368} = 6.4, P < 0.001$; Figure 8). Fish size (407–590 mm standard length) was positively correlated with home range

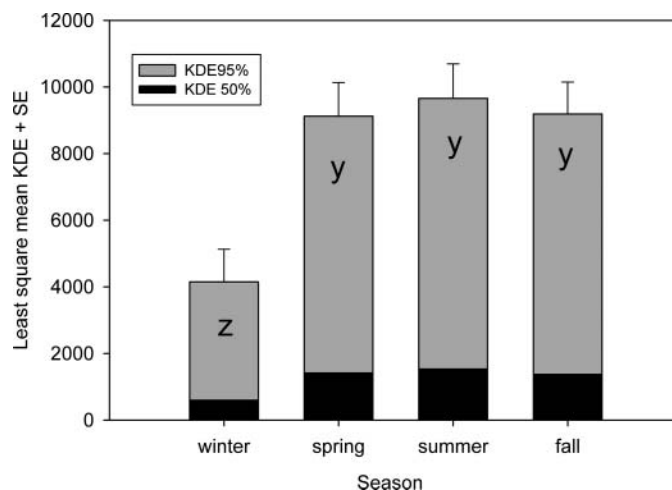


Figure 6. Seasonal patterns in home range (95% KDE) and core area (50% KDE) for Red Snapper around artificial reefs in the northern Gulf of Mexico. Different letters show significant differences for both home range and core area.

($F_{1, 15} = 6.1, P = 0.02, r^2 = 0.31$), but no relationship was detected with core area ($F_{1, 15} = 1.01, P = 0.31, r^2 = 0.06$; Figure 9).

DISCUSSION

Accuracy of the VPS

The VPS estimates of the stationary control transmitter position showed 1-m accuracy. This high degree of accuracy

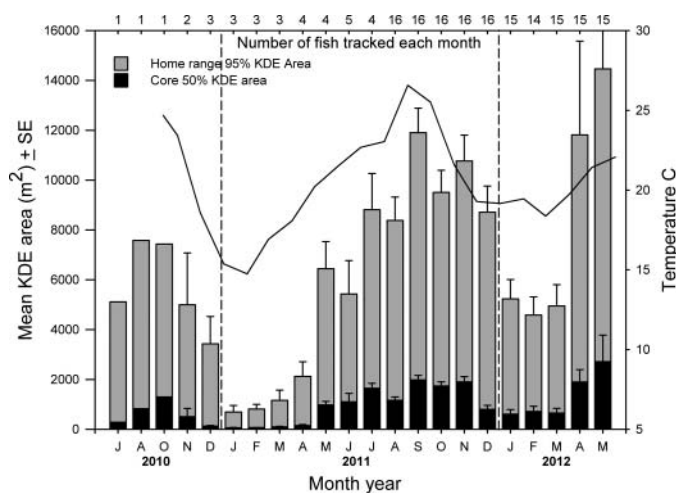


Figure 7. Comparison of water temperature and mean monthly home ranges (95% KDE) and core areas (50% KDE) of Red Snapper around artificial reefs in the northern Gulf of Mexico. Numbers at the top indicate the number of tracked fish for a particular month and the black line indicates mean daily water temperature at a depth of 26 m. Letters along the x-axis represent the months of the year, beginning with July, August, skipping September 2010 because receivers were not deployed, and continuing sequentially with October, November, etc.

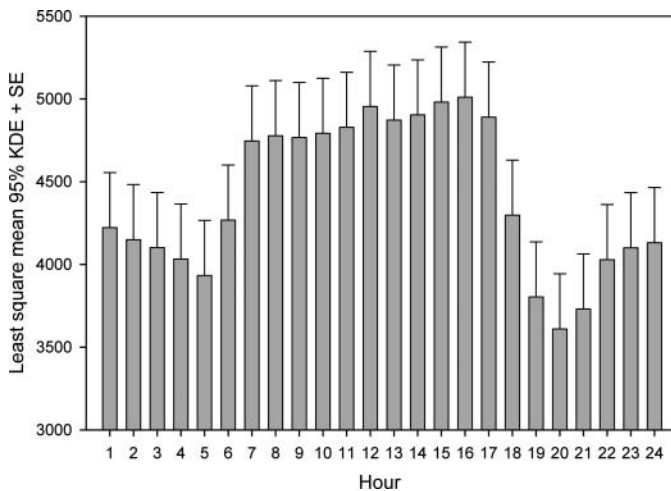


Figure 8. Mean area use by hour over a 24-h period (starting at midnight, with each h representing the time of day) for Red Snapper in the northern Gulf of Mexico. Home ranges were significantly larger during the day than at night and reached minimum values at dawn and dusk ($P < 0.01$). Day and night core area sizes (50% KDE; not shown) were not significantly different ($P = 0.42$).

was further verified by our ability to recover stationary transmitters ($n = 10$) 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 deep), where the mean \pm SD distance between known positions and VPS estimates of stationary transmitters was 2.1 ± 1.3 m (Espinoza et al. 2011b). The VPS was then applied to Gray Smoothhound *Mustelus californicus* ($n = 22$; 5–145 d) in the estuary, and it successfully identified fine-scale patterns in habitat use, including diel movement patterns (Espinoza et al. 2011a). The present study showed that the VPS is also highly applicable for monitoring fine-scale movements of fish in open waters in the Gulf of Mexico, and the frequency and accuracy of Red Snapper positions achieved with the VPS far exceeded that of manual tracking (Topping and Szedlmayer 2011b).

Residence and Site Fidelity

Past studies of Red Snapper movement patterns, site fidelity, and residence around artificial reefs in the Gulf of Mexico have reported different results. Results ranged from low site fidelity and a mean annual movement of 29.6 km (Watterson et al. 1998; Patterson et al. 2001; Patterson and Cowan 2003; Peabody 2004; McDonough 2009) to high sight fidelity (median residency up to 542 d) and a mean annual movement near 2 km (Szedlmayer and Shipp 1994; Szedlmayer and Schroepfer 2005; Schroepfer and Szedlmayer 2006; Strelcheck et al. 2007; Topping and Szedlmayer 2011a). The present study supports the higher site fidelity (88% still present after 10 months) and close association of Red Snapper with artificial reefs. Further, the present study was based on a new and

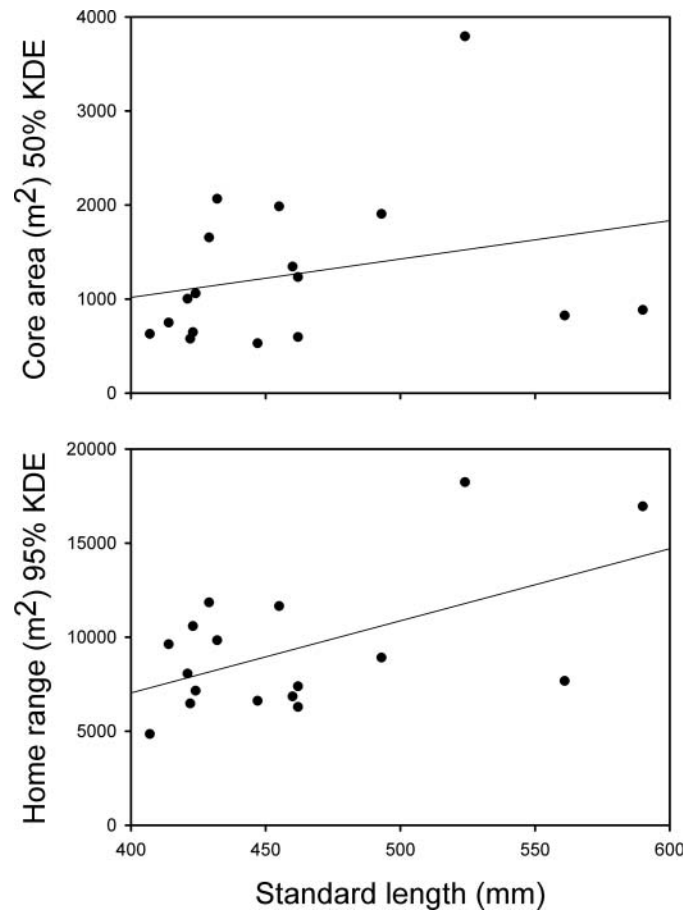


Figure 9. Red Snapper standard length in relationship to core area (top panel) and home range (bottom panel). The black dots are measurements of individual fish. Fish size was positively correlated with home range, but no significant relation was detected with core area.

far more accurate method of fine-scale tracking using the VPS, including unprecedented short time intervals between fish positions and much longer tracking periods than any previous study (up to 23 months).

Emigration and Mortality

The initial rates of emigration (32.6% within 4 d) observed in this study 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). We suspect that predation events may have contributed to increased early emigrations in the present study when tagged Red Snapper were consumed by predators and the ingested transmitters were carried away. Increased predation as a result of tagging was also directly identified when

transmitters showed no movement within 4 d of release. The short time between fish tagging and no movement suggests that tag loss from active fish was unlikely and that stationary transmitters were fish mortalities. The idea of predation mortality occurring immediately after the fish were released is supported by frequent observations of sharks (Spinner Shark *Carcharhinus brevipinna*, Atlantic Sharpnose Shark *Rhizoprionodon terraenovae*, and Sandbar Shark *Carcharhinus plumbeus*) and bottlenose dolphins *Tursiops truncatus* at the study sites during tagging and tracking periods. Further, 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. Regardless of if the fish suffered predation or emigrated, these events within the first 4 d were considered tagging artifacts and were not used in the present Red Snapper KDE estimates.

Most (92%) of the fish tagged in August 2011 ($n = 12$) and released in cages were still present at the end of the study in May 2012. One fish was lost within 4 d, and another fish emigrated from the reef immediately after release from the cage but returned to the same reef after 12 d and remained there until the end of the study. The lack of emigration and mortality observed for fish released in cages supports the conclusion that earlier initial high losses were a tagging artifact and did not reflect natural Red Snapper behavior. This substantial increase in survival and residency with cage release methods brings into question any tagging study of Red Snapper that does not somehow protect newly released fish. We especially discourage the mark and release of Red Snapper at the surface and contend that such methods will produce erroneous emigration and mortality rates. For example, if as many as 85% are lost due to tagging artifacts when fish were released at the bottom without protection, we expect that surface releases would only increase this problem.

To date the present study provides the best evidence of homing behavior in Red Snapper. Red Snapper showed use of other reefs within the VPS arrays. They spent relatively little time over open water and most of their time in close association with the original release site; occasional movements to other sites within the receiver arrays were followed by quick returns to the original release site. Previous studies found little evidence to suggest homing behavior in Red Snapper. Workman et al. (2002) found limited evidence of homing behavior in juvenile Red Snapper with only 4 out of 45 tagged fish returning after a 0.4 km displacement, while Patterson et al. (2001) found only 1 out of 111 Red Snapper at its original release site after being displaced 4 km. That marine fish show homing behavior is not surprising considering the extreme examples shown for Pacific salmon *Oncorhynchus* spp. (Dittman and Quinn 1996). The patterns shown by Red Snapper in the present study clearly show that Red Snapper “know” their

habitat and take advantage of nearby structured habitats (at least up to 300 m away) over a long-term basis (years). How far this use of “other” reefs extends cannot be estimated in the present study, but in a previous study Topping and Szedlmayer (2011a) showed back-and-forth movements from one reef release site to another over a distance of 8 km. The implications of such homing behavior is that the foraging base of a single artificial reef would most likely not limit Red Snapper but rather that a host of potential surrounding reefs with their associated epifaunal communities and surrounding prey communities are supporting particular groups of Red Snapper.

Seasonal Movements

This study was the first to continuously monitor fine-scale movement patterns of Red Snapper for extended durations (100–694 d). Red Snapper remained relatively close to the artificial reefs throughout the study (mean \pm SD distance = 24.5 ± 28.5 m) and showed seasonal changes in habitat use. Movement patterns were significantly correlated with water temperature such that home ranges and core areas were larger during spring, summer, and fall than in winter months. 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 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).

Diel Movements

In the present study, Red Snapper home ranges were significantly larger during the day than during the night and minimum at dawn and dusk, while previous manual tracking indicated patterns of larger area use at night compared with day periods (Szedlmayer and Schroepfer 2005; Topping and Szedlmayer 2011b). The advantage of the present study was its examination of fine-scale movement patterns over much longer time periods (100–694 d compared with 9–24 h) and with far greater accuracy (~ 1 m) and frequency of fish locations (about every 10 min). Even so, differences in study design may have resulted in the different movement patterns found in past studies and the present study. For example, previous manual tracking of Red Snapper was over larger reefs (army tank and concrete pyramid) and only during summer periods (Szedlmayer and Schroepfer 2005; Topping and Szedlmayer 2011b). Further, research vessel noise and movement may have altered fish behavior during manual tracking (Slabbekoorn et al. 2010).

Typically Red Snapper were considered an apex predator on reef structure in the northern Gulf of Mexico, and their diel

movement patterns were usually viewed as related to their predatory foraging behavior. Previous studies of Red Snapper feeding periodicity suggested that they 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; Topping and Szedlmayer 2011b). However, such apex predator foraging behaviors were the opposite of the habitat use patterns observed in the present study in which movements of Red Snapper were more similar to reef fish prey species.

For example, it is well established that predator fishes become more active at twilight periods (dawn and dusk) than at other times over a 24-h period, especially in structured reef systems (Hobson 1972; Helfman 1986; Danilowicz and Sale 1999; Holbrook and Schmitt 2002). Prey species, on the other hand, become cryptic or hide within reef structure, especially at dawn and dusk (Hobson 1972; McFarland et al. 1979; Helfman 1986). These crepuscular periods (dawn and dusk) are often called a “quiet” period when few fish are evident above the reef, indicating that predation intensifies during these periods (Collette and Talbot 1972; Hobson 1972; Helfman 1986; Hixon 1991). Typical of a prey fish, Red Snapper in the present study were more closely tied to the reef structure at dawn and dusk and showed greater area use in daylight than during other time periods. Such patterns are first revealed in the present study due to the advancement of tracking that far exceeded previous tracking studies. Lastly, the drastic increase in survival after the application of cage release methods indicated that predation pressure on Red Snapper was an important aspect of the ecology of this species on these reef structures.

Conclusions

This study showed that Red Snapper were closely associated with specific artificial reefs and relatively small surrounding areas on multiple temporal scales and that these structures were an important habitat for this species. At the same time, Red Snapper showed homing behavior with short-term use of nearby reefs followed by quick returns to their release sites, indicating that individual reef structures are most likely not the sole source of prey but rather that several reefs may provide the forage base for particular groups of Red Snapper. This study was the first to report seasonal changes in fine-scale proximity to artificial reefs; Red Snapper used smaller areas in colder months than in warmer months, suggesting movements were affected by water temperature. Diel patterns in habitat use were the opposite of those found in previous studies; smaller home ranges were observed during the night than during the day and were the smallest at dawn and dusk. Such diel patterns, along with the large change in survival after using cage release methods, indicate that Red Snapper are subject to substantial predation pressure, and their movement patterns suggest that they are a prey species rather than apex predators.

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