

**Red Snapper, *Lutjanus campechanus*, Mortality, Movements,
and Habitat Use Based on Advanced Telemetry Methods**

by

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Abstract

Ultrasonic telemetry was used to estimate the success of a new release method, mortality, movements (m to km), and depth patterns for red snapper, *Lutjanus campechanus*, ($n = 86$) around artificial reefs in the northern Gulf of Mexico. Mortalities, fine-scale movements (~ 1 m accuracy) and emigrations were estimated over 3 years from > 5 million fish positions, based on a VEMCO Positioning System (VPS, Vemco Ltd, Nova Scotia) deployed at four different reef sites. In addition a surrounding array (64 m^2) of 22 receivers, located on other reef sites at 1.6 km distances was used to validate emigrations and larger movement patterns (km). A remotely opening cage was used to release transmitter tagged fish and successfully (100%) protected fish from predation following release. The VPS system validated the fate of 98% of the released fish around the artificial reefs (independent of fishery). A high fishing mortality and low natural mortality were observed during short federal recreational fishing seasons (42 to 9 days). For all years combined total instantaneous mortality (Z) was 0.45 (0.28 – 0.67). Red snapper movements showed high residency (34 months) and site fidelity ($85\% \text{ y}^{-1}$) to artificial reefs. Depth patterns, two-dimensional (2D) and three-dimensional (3D) home range (95% kernel density estimates; KDE) and core areas (50% KDE) significantly changed over seasonal, monthly, and diel time periods. In the winter months, deeper depths (mean \pm SD, $26 \text{ m} \pm 3 \text{ m}$) and fewer movements (area and volume) were observed, with fish mostly (99% of time) staying near their VPS site.

During fall and summer months, shallower depths ($18 \text{ m} \pm 5 \text{ m}$) and larger movements were observed with up to 31% of time spent on secondary sites within the VPS array. Over diel periods, most red snapper (3 out of 4 VPS sites) showed larger movements during the day, smaller areas during the night, and least movement during dusk and dawn. The surrounding receiver array showed that red snapper typically moved short distances ($\sim 1.5 \text{ km}$), remained on these secondary sites for prolonged periods (23 – 336 d), were then caught, emigrated out of the array, or returned to their release sites. The long-term use of the VPS reefs ($> 1,095 \text{ d}$) showed high residency, site fidelity and mortality for larger red snapper. Red snapper movement patterns were most likely related to foraging, spawning and predator evasion (*i.e.*, quick movements over open habitat, short emigration distances, paired emigrations, and reduced movements at dawn and dusk).

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CHAPTER 1:
A CAGE RELEASE METHOD TO IMPROVE FISH TAGGING STUDIES

Abstract

The return and survival of tagged fish to their depth of capture has proved difficult due to barotrauma and predation in previous telemetry studies. Tagging stress can slow and disorient the fish upon release, and reduce the ability to return to depth, relocate their home habitat site, and evade predators. To reduce these initial tag and release artifacts we designed and tested a remotely opening cage for use with reef fish in the northern Gulf of Mexico. Our objectives were to quickly return transmitter tagged fish to depth (20 – 30 m) in close proximity (< 10 m) to their capture site, and to increase survival by providing predator protection during an initial recovery period. This cage release method proved successful for both red snapper, *Lutjanus campechanus* (n = 62 out of 71, 87%) and all gray triggerfish, *Balistes capriscus* (n = 24) that were tagged and released on artificial reefs. All tagged fish were released from November 2012 to September 2014, no initial tag induced mortalities were observed, and after tagging, fish were successfully tracked for extended periods (for the entire 2 y study period).

Introduction

In both conventional and acoustic tagging studies, increased stress, emigration, and mortality of fish after tag and release has been reported for several different release methods (Szedlmayer 1997; Starr et al. 2000; Humston et al. 2005; Szedlmayer and Schroepfer 2005; McDonough and Cowan 2007; Westmeyer et al. 2007; Topping and Szedlmayer 2011b; 2013; Piraino and Szedlmayer 2014). Immediate and prolonged tagging mortality due to barotrauma and stress from the tagging procedure have been examined in multiple species (Parrish and Moffitt 1992; Davis 2002; McGovern et al. 2005; Jarvis and Lowe 2008; Diamond and Campbell 2009; Pribyl et al. 2009; Campbell et al. 2010; Sumpton et al. 2010; Hannah and Rankin 2011; Pribyl et al. 2011; Hannah et al. 2012). These studies showed increased stress due to the rapid change in pressure, substantial changes in water and air temperature, fish handling, and time spent on the surface (Parrish and Moffitt 1992; Davis 2002; Jarvis and Lowe 2008; Diamond and Campbell 2009; Campbell et al. 2010).

While the effects of barotrauma stress have been examined, the effects of different release methods on tagged fish were rarely reported. Methods of release include surface release (Fable 1980; Gitschlag and Renaud 1994; Szedlmayer and Shipp 1994; Patterson et al. 2001; McDonough and Cowan 2007; Hannah and Rankin 2011), drop weights (Szedlmayer and Schroepfer 2005; Topping and Szedlmayer 2011a; 2011b; Piraino and Szedlmayer 2014), underwater tagging and release by SCUBA divers (Tong 1978; Gitschlag 1986; Parrish and Moffitt 1992; Szedlmayer 1997; Starr et al. 2000; Sigurdsson et al. 2006), surface tagging and underwater release by divers (Szedlmayer

1997; Nemeth et al. 2007), and surface tagging, caging, and delayed release by divers (Piraino and Szedlmayer 2014).

In most cases, studies of release methods have not considered predator protection, but have focused on cost, time, training, and fish condition (*e.g.*, surface release, drop weights, underwater tagging). For example, the drop weight release method was quick, inexpensive, and returned fish to their depth of capture (Szedlmayer and Schroepfer 2005; Topping and Szedlmayer 2011a; 2011b; Piraino and Szedlmayer 2014). However, during descent tagged fish were not protected against predators. This protection may be extremely important following tagging, because even fish with little sign of barotrauma can still have loss of equilibrium and reduced mobility (Tytler and Blaxter 1977; Gitschlag and Renaud 1994; Cooke and Philipp 2004; Danylchuk et al. 2007; Jarvis and Lowe 2008; Campbell et al. 2010; Raby et al. 2013). The early escape of disoriented fish during decent at mid-depths can substantially increase emigration and predation. In an effort to reduce predation effects, cage release methods were tested for transmitter tagged red snapper, *Lutjanus campechanus* (Piraino and Szedlmayer 2014). The cages were lowered to bottom near the capture reef site, and after ~ 2 h, SCUBA divers opened the cage doors on the bottom and released the fish close (2 – 3 m) to the reef. This cage release method required more time and training, but successfully reduced tag induced emigrations and predation mortality of tagged red snapper from 85% to 8%.

A release method that provides protection from predators is especially important in regions with a high abundance of predators. In recent years shark abundances have apparently increased based on SCUBA diver encounters 20 to 50 km south of Dauphin Island, AL. For example in 2014, SCUBA diver fish surveys on artificial reefs had

frequent encounters (~ 45%) with large (> 2 m) carcharhinid sharks, while past diver surveys (> 1000) over 20 years prior to 2010 only had rare (< 10) shark encounters (unpublished data Szedlmayer, S.T). These larger sharks include many species that commonly occur in our study area (10 – 40 m), for example, blacktip shark, *Carcharhinus limbatus*, bull shark, *C. leucas*, sandbar shark, *C. plumbeus*, spinner shark, *C. brevipinna*, nurse shark, *Ginglymostoma cirratum*, scalloped hammerhead, *Sphyrna lewini*, and tiger shark, *Galeocerdo cuvier* (Drymon et al. 2010). Thus, in our study area with substantial shark populations, the use of SCUBA divers to release tagged fish from submerged cages became difficult due to safety considerations.

In the present study, we further examine cage release methods to reduce predation and tag induced early emigrations with an untested species, gray triggerfish, *Balistes capriscus*, as well as continue studies with red snapper. Importantly, we develop a remote release method that eliminates the use of SCUBA divers and the risk of shark encounters.

Methods

The cage and release method was tested from November 2012 to 2014 on transmitter tagged red snapper and gray triggerfish 20 – 50 km south of Dauphin Island, AL in the northern Gulf of Mexico. Tagging methods followed Topping and Szedlmayer (2011a; 2011b). Temperature and dissolved oxygen levels were measured at depth prior to tagging. If the dissolved oxygen values were lower than 2.5 mg/L fish were not

tagged. If surface temperatures were higher than temperatures at depth of capture we chilled both the anesthesia container and the recovery container with ice. Fish were captured by hook and line, weighed, measured, and anesthetized 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 were tagged internally with an acoustic transmitter and externally with an anchor tag. During the tagging procedure the swim bladder was punctured for easy insertion of the transmitter. After tagging, fish were held until they showed signs of recovery (active fin and gill movements) and then placed in the release cage. The tagging procedure was complete in < 10 min.

The release cage (84 x 62 x 62 cm) was constructed of vinyl coated wire mesh (16 gauge, 3.8 cm mesh), and fastened with stainless steel connectors (Figure 1-1). Four 0.25 kg lead weights were attached to the bottom corners of the cage and three weights to the cage door. A nylon rope (1.5 cm diameter) was attached to the inside of the door and passed through a stainless steel ring over the top of the cage, which allowed opening and closing of the cage door. This ring was attached to a 10 cm buoy to keep the rope suspended above the cage (Figure 1-1). Initial testing without fish was observed by SCUBA divers and confirmed that the cage descended to the seafloor and opened correctly.

Once a tagged fish recovered from anesthesia it was placed into the release cage and held at the surface (1 m depth), and observed for about 10 – 20 sec to confirm that the fish was upright and actively swimming. After confirming normal swimming behavior, the caged fish was lowered to the bottom (20 – 30 m). As the cage was lowered to the bottom the line was kept tight to keep the release door closed. Once the

cage reached the seafloor the line was released which allowed the cage door to open. The weights on the cage door passively caused the door to fall open. The cage door weights continued to keep the door open until retrieval and allowed the tagged fish to leave on its own initiative (Figure 1-2). Cages were retrieved after allowing at least 10 min for gray triggerfish and 15 min for red snapper to leave the cage. The cage was retrieved either by hand or by winch depending on the preference of the crew members. If a tagged fish remained in the cage after this release period it was not released and removed from the study. Video cameras (GoPro Inc., San Mateo, California, USA) were attached to a subset ($n = 6$) of the cage releases to visually assess fish releases.

All tagged fish were released on artificial reefs surrounded by an acoustic array (VEMCO, VR2W Positioning System, Vemco Ltd, Nova Scotia; Piraino and Szedlmayer 2014) and their fine-scale positions (~ 1 m accuracy) were monitored for extended time periods (up to 2 years). Survival was evaluated based on the fine-scale movements of tagged fish within the VPS array. If a tag showed movement within the array, it was assumed that the fish was alive. However, if a tag was stationary it was defined as a mortality. Emigrations were detected when a fish made progressive movements away from the center of the reef (Piraino and Szedlmayer 2014). Some emigrations were confirmed by detections on additional VR2W receivers on nearby reefs (~ 1 km). In addition, diver observations of active, normal, swimming behavior of tagged fish provided further survival validations in later months.

Results

We used this new cage release method with tagged red snapper and gray triggerfish on artificial reef habitats (22 to 35 m depths) in the northern Gulf of Mexico. Video recordings confirmed that the cage door successfully opened onto the seafloor for all the recorded releases (n = 6; Figure 1-2). Most tagged red snapper (n = 62 out of 71, 87%) and all tagged gray triggerfish (n = 24) left the cage of their own initiative. Based on video recordings red snapper and gray triggerfish left the cage within 1 to 14 min.

We identified mortality and emigration based on fine scale (1 m) fish position data within VPS arrays (Piraino and Szedlmayer 2014), and broader scale movements based on detections at single receivers 1 km from the release site. After fish left the cage, no mortalities were detected within the VPS arrays during an initial 4 d post release recovery period. At the single receivers, we detected three (27%) emigrations of tagged red snapper and one (33%) emigration of a tagged gray triggerfish, among fish that left their release site within the recovery period. These emigrating red snapper remained at their new reef sites for extended periods (> 30 d). After this initial 4 d recovery period most red snapper (82%) and gray triggerfish (83%) remained on the release site for extended periods. For example, one tagged red snapper remained at its release site for 559 d, and was subsequently caught and reported by a private fisher. After the initial 4 d recovery period, no natural mortalities were recorded for red snapper, while one mortality was detected in a gray triggerfish 8 d after release. Emigrations were detected 6 – 367 d after release for red snapper, and 21 – 563 d after release for gray triggerfish.

Discussion

The present cage release method provides several advantages (*e.g.*, less training and greater predator protection) over past release methods and has proved successful for both red snapper and gray triggerfish. Several telemetry studies have observed a substantial percentage of tagged fish emigrating shortly (< 8 d) after release presumably due to the tagging stress: *e.g.*, 15%, 8 out of 54 fish (Szedlmayer and Schroepfer 2005), 16%, 14 out of 87 (Topping and Szedlmayer 2013), and 35%, 7 out of 20 fish (McDonough and Cowan 2007). In the present study, red snapper emigrations (18% 11 out of 62) and gray triggerfish emigrations (17%, 4 out of 24) during the initial 4 d recovery period were similar to these previous studies.

We detected no mortalities in tagged fish immediately following release (≤ 4 d), but identified a single mortality in a gray triggerfish 8 d after release. This mortality occurred shortly after the post-release recovery period and may have still been related to tag and release effects. Topping and Szedlmayer (2013) reported a low mortality (2%, 2 out of 87 fish) for tagged red snapper within 6 d of release. In contrast Piraino and Szedlmayer (2014) reported a high release mortality (39%, 13 out of 33 fish) within 4 d of release.

The high mortality reported by Piraino and Szedlmayer (2014) was likely caused by shark predation. In the present study, SCUBA divers frequently encountered 1 to 3 large (> 2 m) sandbar and bull sharks on the same artificial reefs used by Piraino and Szedlmayer (2014) and diver release of tagged fish from cages was discontinued for safety considerations. We then developed the present cage release method and continued

tagging on the same sites that showed this high predation level and detected no predation and reduced emigration of transmitter tagged fish.

In the present study, red snapper had similar emigration rates compared to earlier telemetry studies in the Northern Gulf of Mexico when predation effects were less apparent (Szedlmayer and Schroepfer 2005; Topping and Szedlmayer 2013). Piraino and Szedlmayer (2014) lost 39% of their tagged fish to known predation using the drop weight release method. They also detected a high (45%) loss to emigration that may include additional predation. During the present study, the video recording showed the presence of predators *Carcharhinus* spp., and bottlenose dolphin, *Tursiops truncatus*, around the cages, confirming the continued predation risk. However, the present cage release method protected the tagged fish from predation based on the high survival (100%) observed.

A review of the camera videos showed that tagging recovery time varied from 1 to 14 min. The longest recovery time was for red snapper confirming that this post-release protection provided by the cage may be particularly important for this species. The cage provided protection for a minimum of 15 min and allowed red snapper to recover from tagging stress and exit on their own initiative. A recompression study on Pacific rockfish that used similar methods (hook and line and cage release) found that the degree of impairment due to barotrauma varied by species, increased with depth of capture (greatest > 40 m depth), and that observations of barotrauma made while the fish was on the surface poorly predicted the degree of behavioral impairment observed underwater (Hannah and Matteson 2007). Similarly, in the present study there were no

detectable differences in fish recovery behavior observed at the surface before lowering the cage among tagged fish that took 1 to 14 min to exit the cage.

In the future, cameras should be used to record all cage releases. The recordings in the present study were valuable in showing not only the threat of predation but also the importance of maintaining tension on the line while lowering the cage. In addition, it showed that the cage functioned correctly with the cage door opening after it reached the seafloor. The future use of camera recording would allow evaluations of all releases and potentially identify any difficulties.

In the present study, the cage was dropped close to the reef (< 10 m). The close proximity of the caged fish to the reef site likely allowed the fish to quickly swim from the cage to the reef to avoid predation. We suggest that the combination of the cage protection and longer-term predator protection of the reef site substantially contributed to the high survival of tagged fish in the present study.

The present cage release method was successfully used to release transmitter tagged fish on artificial reefs at depths up to 30 m in the northern Gulf of Mexico. In the northern Gulf of Mexico, there is little natural reef habitat (Parker et al. 1983; Dufrene 2005) and artificial habitats are typically surrounded by flat sand or mud bottom. Therefore, there were few obstructions around the reef that would prevent the cage door from opening. The success of the present cage release method on natural habitats may be reduced due to the increased complexity of the reef surface that may impede the cage door from opening. In addition, this method was used in relatively shallow waters (≤ 30 m), and it is unclear how the cage would function at deeper depths.

Conclusion

The cage release in the present study provides an effective method that improved the survival and residency estimates of reef-oriented fish. The cage was designed to release fish at depth, and increased predator protection for tagged fish immediate (~ 15 min) after release. We also suggest that release of fish within close (< 10 m) proximity of their capture site also provided longer-term predator protection. The advantages of the present cage release methods are: 1) it can be made with readily available and inexpensive material (wire mesh, rope, and floats), 2) it reduces effort by eliminating the need for SCUBA divers, and 3) it only releases fish in good condition as fish exited the cage on their own initiative. This method was successful for the release of transmitter tagged red snapper and gray triggerfish, but may also be successful with other species in the northern Gulf of Mexico.

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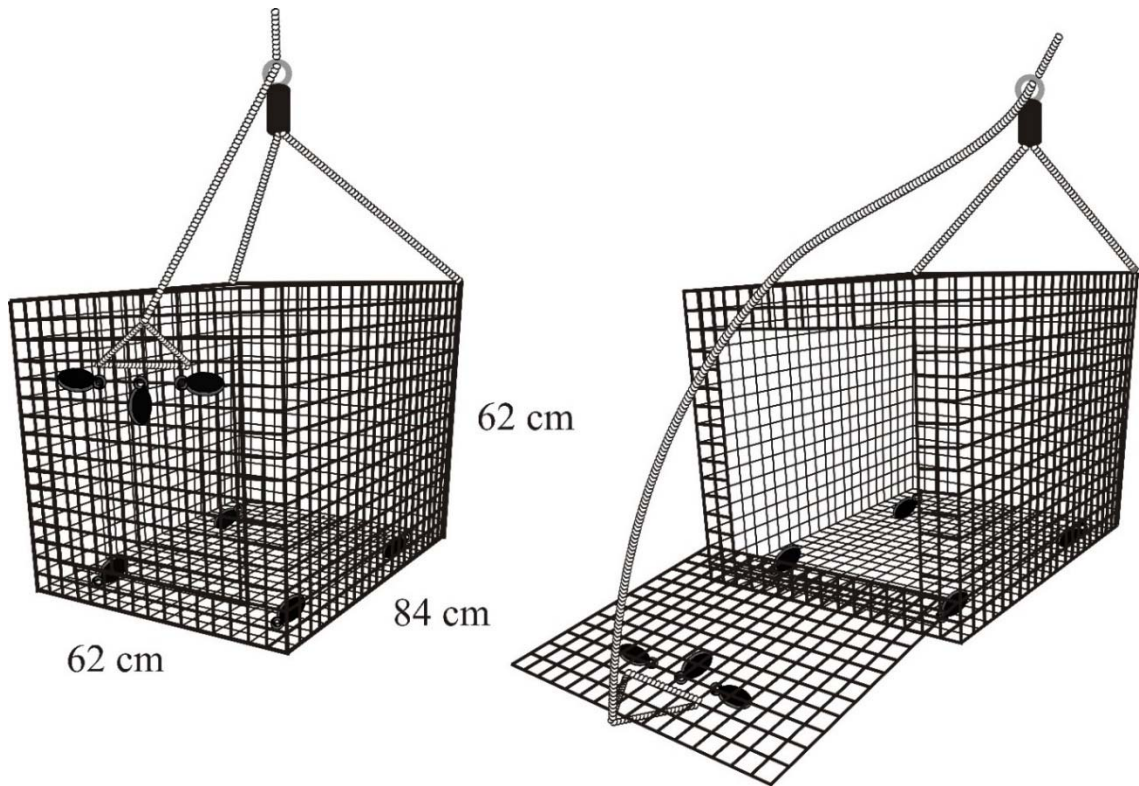


Figure 1-1: Vinyl coated wire mesh cage (16 gauge wire, 3.8 cm mesh size) with individual 0.25 kg weights fastened to the bottom of the cage and to the outside of the cage door. A nylon rope (1.5 cm diameter) is attached to the inside of the door and runs through a stainless steel ring over the top of the cage. This ring is attached to a small buoy (black; 10 cm) to keep the rope suspended above the cage.

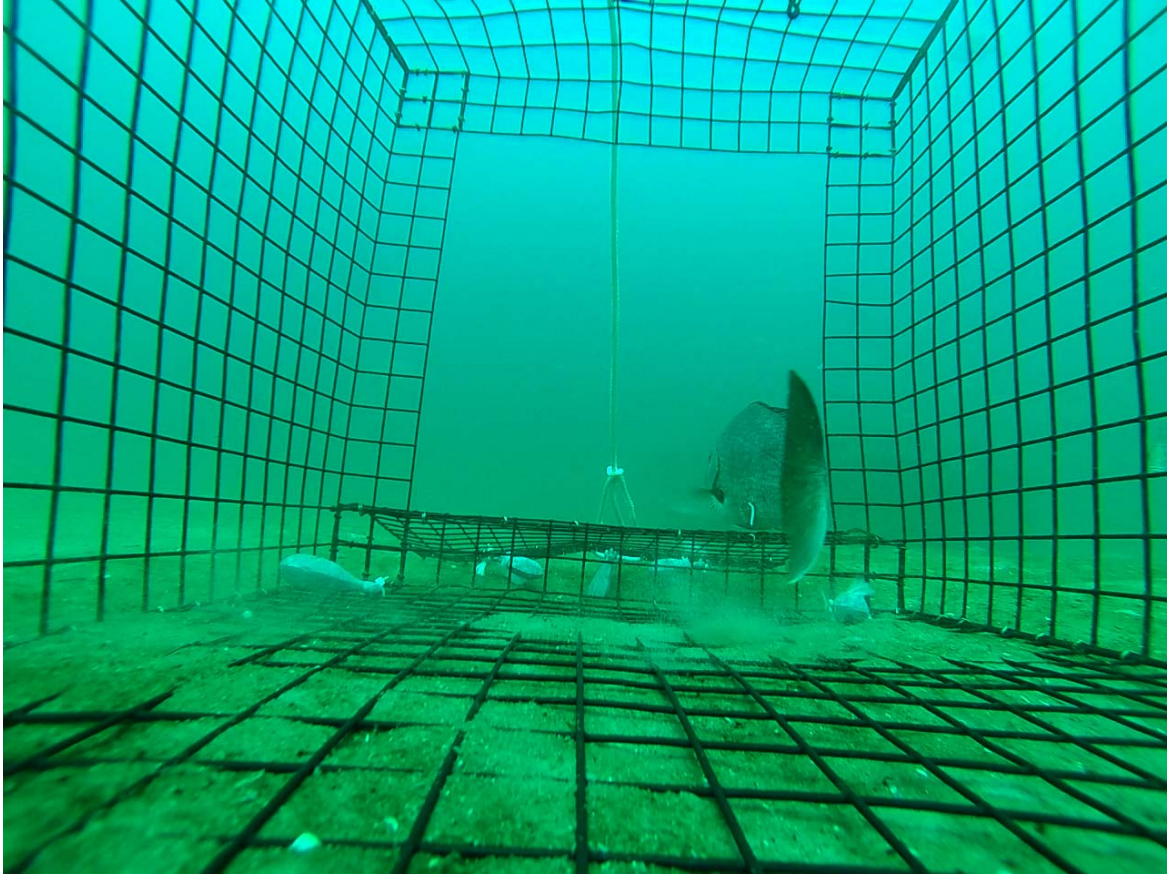


Figure 1-2: A transmitter red snapper, *Lutjanus campechanus*, exiting the cage. The camera was attached to the bottom of the cage and is facing towards the opened cage door.

CHAPTER 2:
MORTALITY ESTIMATES FOR RED SNAPPER, *LUTJANUS CAMPECHANUS*,
BASED ON ULTRASONIC TELEMETRY IN THE
NORTHERN GULF OF MEXICO

Abstract

We used the VEMCO Positioning System to estimate mortalities from the fine-scale movements (~1 m accuracy) of red snapper, *Lutjanus campechanus*, on artificial reef sites (n = 4) in the northern Gulf of Mexico from 2012, 2013, and 2014. Additional receivers (n = 22) on surrounding reef sites validated emigrations of tagged red snapper from the VPS-monitored sites. Telemetry tracking patterns identified fish status as active, emigrated, caught (*F*), or dead (*M*) at monthly intervals. We tagged and released 86 red snapper and after a 6-d tagging recovery period 61 fish were still present and were tracked for extended periods (17 to 1096 days). Among the tracked fish, 16 emigrated and 23 were caught by fishers on VPS-monitored reef sites. For all years combined, annual fishing mortality was $F = 0.41$ (0.25 – 0.62, 95% CL). In 2012, $F = 0.72$ (0.35 – 1.31) and was higher than other years, but the number of fish available for recapture at the start of the sport fishing season was low (n = 15). In 2013, $F = 0.18$ (0.07 – 0.41; n = 31) and in 2014, $F = 0.34$ (0.17 – 0.64; n = 29). One natural mortality (*M*) was detected

in 2012, and $M = 0.12$ ($0.02 - 0.69$), subsequently no natural mortalities were detected in 2013 and 2014 ($M = 0$). Total instantaneous mortality (Z) for all years was $Z = 0.45$ ($0.28 - 0.67$). We attributed the low M to the high fishing mortality, but caution that sample sizes were small, typical of telemetry studies. The fates of 60 (98 %) transmitter-tagged red snapper were successfully identified based on the VPS technology. Increases in F from 0.18 (2013) to 0.34 (2014) occurred when the fishing season was decreased (42 to 9 days) and indicated that fishers increased effort during the shortened fishing seasons, and management goals of reduced catch may not have been achieved.

Introduction

Red snapper, *Lutjanus campechanus*, is one of the most important sport and commercial species in the northern Gulf of Mexico, and the stock is still considered overfished (SEDAR 2013; Cass-Calay et al. 2015). The Gulf of Mexico Fishery Management Council and NOAA Fisheries are responsible for managing and setting harvest limits (total allowable catch, TAC) to ensure sustainable fisheries. Critical to these management plans are accurate measures of mortality, and perhaps more important is the separation of total mortality (Z) into its component parts of fishing mortality (F) and natural mortality (M). Prior to telemetry based methods, partitioning total mortality into F and M required several assumptions, and previous M estimates were indirectly calculated. With the advent of telemetry based methods, direct empirically derived estimates became obtainable (Hightower et al. 2001; Topping and Szedlmayer 2013).

In most mark-recapture studies, F was based on the number of tagged fish that were caught and reported by fishers. However, there were usually difficulties with non-reporting and tag shedding. Fishing mortality was then subtracted from total mortality (*e.g.*, estimated from age frequency distributions) to estimate M . Estimates of red snapper M were also derived theoretically from a combination of life history characters and environmental measures, and varied from $M = 0.10$ to 0.36 (Topping and Szedlmayer 2013). Present management plans use $M = 0.10$ (SEDAR 2013).

New technology in telemetry systems allows for the direct estimate of M in both freshwater and marine fish species (Hightower et al. 2001; Heupel and Simpfendorfer 2002; Pollock et al. 2004; Starr et al. 2005; Melnychuk et al. 2007; Karam et al. 2008; Topping and Szedlmayer 2013). Topping and Szedlmayer (2013) used an array of overlapping receivers and tag detection frequencies to directly estimate F and M for red snapper. Especially important with new telemetry systems is the ability to directly estimate F independent of fisher returns, and M from stationary transmitters. Kaplan-Meier staggered entry methods (Kaplan and Meier 1958; Pollock et al. 1989) estimated mortalities, $M = 0.11$ (range = $0.06 - 0.20$) and $F = 0.27$ (range = $0.11 - 0.54$), and showed a decrease in F and increase in M that followed reductions in TAC (Topping and Szedlmayer 2013).

In the present study, we estimated natural, fishing, and total red snapper mortality independent of fishers using a new fish positioning system (VEMCO Positioning System [VPS], Vemco Ltd, Nova Scotia). The VPS technology offers major advantages over traditional overlapping receiver arrays where fish positions were typically plus or minus 100's of m, compared to this new VPS approach with fish position accuracy around ~ 1 m

(Piraino and Szedlmayer 2014). This new VPS technology also provides unprecedented frequencies of detections, about every 5 min, continuously for long periods (only limited by 6 to 10 year battery life of transmitters).

Methods

Study Sites

The study area was in the Hugh Swingle General Permit Area located approximately 20 – 50 km south of Dauphin Island, Alabama, USA, in the northeast Gulf of Mexico. The study sites (n = 26) consisted of steel-cage artificial reefs (2.5 x 1.3 x 2.4 m) deployed from 2006 to 2010 at unpublished locations (Figure 2-1). We selected unpublished or “private” reef locations to provide a more accurate estimate of mortality, because there are far more “private” reef sites (87.3%) compared to “public” reef sites (12.6%; S. T. Szedlmayer and P. A. Mudrak, unpublished). Distances between steel cages ranged from 1.4 – 1.6 km and water depth ranged from 20 to 35 m (Figure 2-1). Four VPS-monitored sites were among these reefs for estimating fine-scale movements, while 22 surrounding sites were for estimating larger-scale presence and absence data (Figure 2-1).

Fish Tagging and Release Procedures

Fish tagging procedures followed previous red snapper tagging methods described by Topping and Szedlmayer (2011a; 2011b; 2013) and Piraino and Szedlmayer (2014). All tagged red snapper in the present tagging study were susceptible to both commercial

and sport fisheries, because all released fish were greater than the 2012 – 2014 commercial (> 330 mm TL) and sport (> 406 mm TL) federal minimum size limits. Fish were caught by hook-and-line (8/0 circle hook baited with Gulf menhaden, *Brevoortia patronus*) and immediately anesthetized with MS-222 (150 mg tricaine methanesulfonate/L seawater for 2 – 3 min) in a 70 L seawater tank. Each fish was weighed (kg), measured (mm SL, FL, TL), and tagged internally with a unique acoustic transmitter (Vemco V16-6x-R64k, with transmission delays = 20 – 69 sec). The transmitter was surgically implanted into the peritoneal cavity through a small vertical incision (20 mm) above the ventral midline. The incision site was sealed with absorbable, sterile, plain gut surgical sutures (Ethicon 2-0, metric 3). Each fish was externally tagged for visual identification by SCUBA divers and fishers, with a unique anchor tag (Floy[®]). Tagged red snapper were observed in a 185 L seawater recovery tank on the research vessel until they showed active opercula pumping and fin movements (~ 2 min).

All red snapper were returned to depth in a predator protection cage within 10 m of the artificial reef site of capture. The specific type of release cage was different among study years. For the first release method, we used a closed circular cage (height = 40.6 cm, diameter = 60 cm) made of vinyl coated 12.5 gauge wire mesh (Piraino and Szedlmayer 2014). Transmitter-tagged fish were held in the cage at depth for a minimum of 1 hour, before SCUBA divers visually inspected fish condition. Only tagged fish in “acceptable” condition were released by manually opening a cage door. Tagged fish were considered acceptable for release if observed oriented in an upright position, swimming, and responding to diver presence (*e.g.*, swimming against the cage trying to

escape from divers), while fish were considered unacceptable for release if observed lying on their side and not responding to divers. This SCUBA diver release method was discontinued after divers had increasing encounters with larger (≥ 2 m) sandbar shark, *Carcharhinus plumbeus*, and bull shark, *Carcharhinus leucas*.

We modified our release method in November 2012, and red snapper were subsequently released through the use of a remotely opening rectangular cage (46 x 61 x 61cm) made with vinyl coated 16 gauge wire mesh (Williams et al. 2015). Tagged fish were placed into the cage at the surface and the door was closed. The cage remained closed during descent, but automatically opened when the cage reached the sea floor. The cage protected tagged fish from predators in the water column and at depth until fish exited the cage on their own initiative. The release cage was retrieved after a minimum of 15 minutes. If a tagged fish did not exit the cage and was brought back to the surface, it was considered in poor condition and not released.

Long-term Position Monitoring

We measured fine-scale movements of tagged red snapper from January 2012 to December 2014 using the VEMCO Positioning System (VPS). For each VPS-monitored site, five Vemco VR2W receivers were positioned as described by Piraino and Szedlmayer (2014): a central receiver was positioned 20 m north of the artificial reef and four additional receivers were placed 300 m to the north, south, east, and west of the central receiver (Figure 2-2). The receivers were attached to an anchor line ~ 4.5 m above the sea floor. A synchronization transmitter was attached 1-m above each receiver to calibrate receiver timing (sync tags; Vemco V16-6x; 69 kHz; transmission delay: 540

– 720 sec) and a float was attached 1-m above each sync tag. The arrangement of receivers at 300 m from the center reef site allowed for transmitter-tagged fish to be simultaneously detected by at least three receivers at all times within the VPS array, because the maximum distance from any receiver was 424 m (*i.e.*, transmitters signals were detected 100% of the time at 400 m; Piraino and Szedlmayer 2014). Highly accurate (~ 1 m) fish positions were calculated based on time differential of signal arrival at three or more receivers (Vemco data post-processing; Vemco Ltd., Nova Scotia). Stationary control transmitters with known locations were attached to anchors within the receiver arrays to determine the accuracy of Vemco VPS-calculated positions.

The status of a tagged fish was based on VPS positions and time intervals among positions. Each fish was either classified as “active” (detections show frequent movements around the reef) or having undergone an event. Events included “emigration” (sequential detections away from the reef), “fishing mortality” (abrupt disappearance of detections around the reef), and “natural mortality” (stationary detections or irregular large-scale movement patterns). We used surrounding site receivers (n = 22) for additional validation of emigrations detected by the VPS analysis. Fish that emigrated were frequently detected on nearby surrounding sites, while VPS identification of fishing mortality and natural mortality would lack detections on surrounding sites. Fishing mortalities were also confirmed by fisher returns. To increase the probability of fisher returns, a high reward (\$150 USD) was offered and posted at local marinas, marine supply, and bait shops, and an easily accessible website was created to reach larger audiences. It was assumed that fish within the VPS-monitored

arrays experienced similar fates (*i.e.*, mortality rates) to red snapper outside of the VPS arrays (Topping and Szedlmayer 2013).

Validating Detection Data

Telemetry receivers can generate false detections that are not valid transmitter-tagged fish (Pincock 2012). False detections can result from incomplete transmission due to interference (*i.e.*, noise) or collision of signals from two or more transmitters that simultaneously reach a receiver (Pincock 2012). False detections that produced unknown tags were removed from analysis. Transmitter detections of known tags were further screened before acceptance as a valid tagged fish presence. Transmitter detections were accepted as valid fish presence if there was at least one short interval between detections and more short intervals than long intervals. In the present study, the short interval time was set at 23 min (30 times the average transmitter delay: 20 – 69 sec, mean = 45 sec) and the long interval was set at 9 h (720 times the mean = 45 sec transmitter delay; Pincock 2012).

Estimates of Survival and Mortality

A known fate model was applied in the “MARK” program to estimate conditional survivals, total survivals, standard error (SE), and 95% confidence limits (CL; Topping and Szedlmayer 2013). Annual estimates were based on monthly time intervals (Jan to Dec) for each year (2012, 2013, and 2014). The “MARK” program calculated survival estimates based on the maximum likelihood binomial (MLE; Edwards 1992):

$$\mathcal{L}(\theta|n_i, y_i) = \prod_{i=1}^t S_i^{y_i} (1 - S_i)^{(n_i - y_i)}$$

This equation describes the survival model for the monthly time interval (θ), the number of individuals active during each interval (n_i), the number surviving each interval (y_i), and the MLE of survival during each interval (S_i). In this model, survival was estimated from conditional probabilities of surviving specified events (*i.e.*, emigration or mortality). For example, the probability of surviving a mortality event (i) was determined by calculating the number of individuals at risk of dying (n_i) and the number of individuals that survived (y_i) for that time interval (t). Fish that emigrated or suffered a mortality not under consideration were removed (*i.e.*, “right censored”). For example, when M was estimated all emigrations and F mortalities were removed.

Instantaneous annual (12 month) mortality rates were based on total survival after 36 months (study period) adjusted to 12 months, *i.e.*, annual $S = \text{total } S^{(12/36)}$ for each mortality type. For example, annual $F = -\log_e S^{(12/36)}$ from fishing mortality, annual $M = -\log_e S^{(12/36)}$ from natural mortality, and annual $Z = -\log_e S^{(12/36)}$ from all mortality (Starr et al. 2005). Confidence limits for instantaneous mortality rates were calculated from the 95% confidence limits estimated from the MLE of the survival functions at 1 year (12 months; Klein and Moeschberger 2003; Topping and Szedlmayer 2013). The reported sample sizes for the mortality estimates were the number of fish available for recapture on the opening day of the sport fishing season for each year.

Results

The fine-scale movements of red snapper were continuously recorded at four different VPS-monitored sites (Figure 2-1) for 36 months (January 2012 to December 2014). All transmitter-tagged red snapper were greater than the Gulf of Mexico federal recreational length minimum, 406 mm TL, with a mean size = 600 mm TL and a range of 454 to 877 mm TL. We tagged and released 86 red snapper, and after allowing for an initial 6-d tagging recovery period, 61 fish survived and were tracked for extended periods (17 to 1096 days) with most (98%) fish tracked for more than 30 days. Emigrations of fish from the VPS-monitored arrays within the first 6 d ($n = 25$) were considered tagging stress behaviors (Topping and Szedlmayer 2011b; 2013) and were removed from further analyses. For example, tagging stress was apparent in fish-92, which immediately left the tagging site (R1) on the same day that it was released, was present on a surrounding reef (S20) for six days and then returned on day seven. Beginning on day seven, this fish was tracked on the original release site for five months and included in analyses, then emigrated to a location outside the R1 receiver array (Figure 2-1).

Fish status was determined (active, emigrated, mortality) by the VPS technology for all fish ($n = 61$) that remained after the 6-d tag recovery period. At the end of this study, 22 fish were still being tracked (active) on the VPS-monitored reef sites (Figure 2-3). Emigrations ($n = 16$) from VPS-monitored sites occurred from 17 to 978 days after release and all occurred outside of the federal sport fishing season during the winter and spring months. Total fish susceptible to emigrations were similar among years ($n = 37$ in

2012 and 2014; $n = 34$ in 2013). Three fish emigrated in 2012, nine fish in 2013, and four fish in 2014. A few red snapper ($n = 4$) were residents at their VPS-monitored release sites for long periods (240 – 978 d) then emigrated and remained away for 90 – 344 d, then returned to their release site. These fish were classified as active when on their release site and as emigrations (right censored) when they were away from their release site.

Fishing mortality occurred in 23 transmitter-tagged red snapper. All F mortalities were identified by VPS position patterns, but many ($n = 15$) were also verified by fisher reported recaptures. Total survival from all fishing mortality over the 36 month study period was $S_F = 0.29$ (0.16 – 0.47, 95% CL). Adjusted to annual survival $S_F^{(12/36)} = 0.29^{(12/36)} = 0.66$, thus annual $F = \log_e 0.66 = 0.41$ (0.25 – 0.62; Table 2-1).

Fishing mortality rates varied across years on the VPS-monitored sites. In 2012, $S_F = 0.48$ (0.27 – 0.70) with $F = 0.72$ (0.35 – 1.31), and was higher than other years with 9 fisher mortalities among the 15 tagged red snapper available for recapture on opening day (1 June). Fishers reported five recaptures, while four additional recaptures were identified from the VPS analysis (56% fisher reporting rate). In 2013, 31 fish were available for recapture on opening day (1 June), and we observed a lower fishing mortality with $S_F = 0.84$ (0.67 – 0.93) and $F = 0.18$ (0.07 – 0.41; Table 2-1). Fishers reported three recaptures, while two additional recaptures were identified from the VPS analysis (60% fisher reporting rate). In 2014, a similar number of red snapper ($n = 29$) were available for recapture on opening day (1 June), and fishing mortality increased, with $S_F = 0.71$ (0.53 – 0.84) and $F = 0.34$ (0.17 – 0.64; Figure 2-4; Table 2-1). Fishers

reported seven recaptures, while two additional recaptures were identified from the VPS analysis (78% fisher reporting rate).

One natural mortality was observed in 2012, with $S_M = 0.89$ (0.50 – 0.98) and $M = 0.12$ (0.02 – 0.69). The VPS analysis showed that fish-46 disappeared close to the center of the tagging site (R3) on 20 July 2012. However, the transmitter was subsequently detected over 800 times on multiple VPS-monitored sites and surrounding reef sites (R1, R3, S12, & S13). Some of detections were validated after we applied the false detection screening criteria (at least one short interval of < 23 min between detections and greater short intervals than long 9-h intervals). This detection pattern was unique and did not match any other observed red snapper fine-scale or large-scale movement patterns (based on > 5 million fish positions) in the present study. The high number of erratic detections over wide areas were most likely caused by the movements of a larger predator that had preyed upon the tagged red snapper. However, the long duration of erratic detections (> 2 y) is difficult to explain, as a consumed transmitter within the gut cavity of a larger predator would likely be expelled after a short period. We can only speculate that the transmitter somehow became trapped within the predator, perhaps in the spiral valve of a shark predator. No other natural mortalities were observed in 2013 or 2014 ($M = 0$). For all years (2012 – 2014), $M = 0.04$ (0.01 – 0.23), $F = 0.41$ (0.25 – 0.62) and total Z ($F + M$) = 0.45 (0.28 – 0.67; Table 2-1).

The fate of one fish in this study was undetermined after extensive tracking (~ 1 year) and right censored from subsequent survival analyses. The fate of fish-41 was unknown because receivers were removed from VPS-monitored reef sites due to an

impending tropical storm. When the receivers were reinstalled after a 16 d absence (24 Aug to 10 Sep 2012) this fish was no longer present.

To test the effectiveness of the false detection screening, the criteria was first applied to all transmitter-tagged fish that showed a VPS-identified fishing mortality and transmitters were returned by fishers. The number of false detections from the 11 transmitters that were returned and turned off varied, ranging from 0 to 63 detections (Table 2-2). The highest number of false detections was from a fish caught during the 2014 fishing season. It was falsely identified 63 times in the 5 months after recapture. We applied the false detection screening criteria to the 11 returned transmitters for any detections after capture date, and all subsequent detections were identified as false detections. The false detection criteria was then applied to all post-capture detections of mortalities without returned transmitters (fisher reported but not returned and VPS identified mortalities) and all were identified as false detections (Table 2-2).

Discussion

The VPS telemetry arrays enabled continuous highly accurate (1 m accuracy; Piraino and Szedlmayer 2014) tracking of red snapper on artificial reef sites for 3 years. In the present study, we were able to estimate mortalities independent of fisher returns, because the fate of tagged red snapper was known within the VPS-monitored arrays (Hightower et al. 2001; Heupel and Simpfendorfer 2002; Bacheler et al. 2009; Topping and Szedlmayer 2013). The present annual estimate of $F = 0.41$ was higher than the

suggested maximum fishing mortality rate ($F_{\text{MAX}} = 0.094$) used in the 2013 stock assessment models (SEDAR 2013). In addition, the present study estimate of F was higher than a previous telemetry-derived estimate of $F = 0.27$ (Topping and Szedlmayer 2013), and the stock assessment estimate for hook-and-line in the eastern Gulf of $F = 0.15$ for 2007 – 2011 (SEDAR 2013). The present estimate of F does fall within the range of $F = 0.29 – 0.47$ from the 1999 stock assessment (Schirripa and Legault 1999).

Compared to previous studies, the higher F estimates from the present study occurred during the shortest federal sport fishing season to date. The sport fishing seasons decreased from 46 days in 2012, to 42 days in 2013, to 9 days in 2014 due to fishers exceeding catch quotas during previous years (NMFS 2014). In the present study, most fishing mortalities (96%) occurred during these shortened sport fishing seasons. In 2012, we observed the highest fishing mortality ($F = 0.72$), but there was little change in sport fishing season between 2012 (46 days) and 2013 (42 days). We suggest that 2013 and 2014 likely provided more accurate mortality estimates due to larger sample sizes. Topping and Szedlmayer (2013) reported that F rates decreased as sport season and bag limits decreased. For example, in 2006, $F = 0.62$ ($n = 26$) with a 194 day season and 4-fish bag limit; in 2007, $F = 0.22$ ($n = 51$) with a 194 d season and 2-fish bag limit; and in 2008, $F = 0.14$ ($n = 41$) with a 65 day season and 2-fish bag limit (Topping and Szedlmayer 2013). In the present study bag limits remained the same, surprisingly, F increased from 0.18 (2013) to 0.34 (2014), when the sport season was reduced by 78%. In addition, F estimates in the present study from 2013 and 2014 with shorter sport seasons (42 and 9 days), were similar or higher than previous F estimates in 2007 and 2008 with longer sport seasons (194 and 56 days, Topping and Szedlmayer 2013). In the

present study, the increase in F despite severe reductions in fishing seasons suggested that fishers concentrated their effort and total catch may not have been reduced. Thus, the present study supports stock assessments and management efforts that have reduced red snapper fishing seasons, even with the increase in TAC to 14.3 million pounds (SEDAR 2013; NMFS 2014; Southeast Fishery Bulletin 2015). However, F may vary by region and reef type (*i.e.*, artificial, natural, private, public) and this variation should be considered in future studies and management efforts.

In several previous studies, increased fishing mortality has been associated with fish species that congregate at “known” locations (*e.g.*, Gadidae, Salmonidae; Roughgarden and Smith 1996; Hutchings 2000; Worm et al. 2009). Similarly, the association of red snapper with known locations of artificial reefs may have contributed to increased fishing mortality. At the same time, long-term (> 1 y) telemetry studies in the study area have shown high site fidelity for red snapper (> 72% y^{-1} ; Szedlmayer 1997; Szedlmayer and Schroepfer 2005; Topping and Szedlmayer 2011a; 2011b; Piraino and Szedlmayer 2014). We suggest that such high site fidelity may have partially resulted from high fishing mortality ($F = 0.27$, Topping and Szedlmayer 2013; $F = 0.41$, in the present study). For example, as fish are removed by fishers competition is reduced and remaining fish are more likely to stay. Thus, the association of red snapper with artificial reefs may lead to a negative feedback system such that once a reef is located with abundant red snapper, fishers can continue harvest until most resident fish are captured.

In addition, fishing mortality most likely varies on reefs with unpublished (private) versus published (public) locations. Higher fishing pressure would typically be

expected on reef sites with publically known locations compared to reef sites with unpublished coordinates (Jaxion-Harm and Szedlmayer 2015). Jaxion-Harm and Szedlmayer (2015) measured red snapper density on smaller unpublished reef sites (*e.g.*, steel cages and pyramids) and published reef sites of all sizes (*e.g.*, pyramids, army tanks, barges) and showed that legal-sized red snapper were abundant on all reef types, but the greatest percentage of larger red snapper (> 650 mm TL) were observed on unpublished reef sites. In the present study, the selected unpublished reef sites likely reflect a reduced fishing effort compared to published reef sites simply because they are more difficult to locate, thus present estimates would likely be conservative and less than overall fishing mortality in the region.

One natural mortality was observed during this study in 2012 (with $M = 0.04$ for all years 2012 – 2014). Topping and Szedlmayer (2013) estimated $M = 0.11$ from 2006 to 2008, but varied by year: $M = 0$ (2006), $M = 0.19$ (2007), and $M = 0.21$ (2008). We suggest that the low M estimate in the present study was most likely related to combined effects of high fishing mortality and that we tagged relatively young fish (4 to 10 years) compared to the maximum life expectancy (> 40 years; Szedlmayer and Shipp 1994; Wilson and Nieland 2001). The long-term (3 y) estimate of $M = 0.04$ (0.00 – 0.99) in the present study supports the use of low $M = 0.1$ that has been applied in the most recent red snapper stock assessment (SEDAR 2013).

Estimated fisher recapture reporting rates have historically been indirectly calculated based on a combination of secretly planted tags, fisher or port surveys, catch information, or the use of multiple tags (Pollock et al. 2001; Pine et al. 2003). In multiple tag studies, high-reward tags were assumed to be 100% reported, and the relative

difference between the standard tag reporting and the high-reward reporting was considered the “actual” reporting rate (Pollock et al. 2001; Bacheler et al. 2009; Hightower and Pollock 2013). In the present study, the 65% reporting rate of high-reward tags indicates that assuming a 100% reporting rate for high reward tags may cause underestimates in F (Pollock et al. 2001; Pine et al. 2003). The fisher reporting rate in the present study (65%) falls within the upper range of fisher reporting rates that were directly estimated by previous telemetry studies (17%, Hightower et al. 2001; 89%, Topping and Szedlmayer 2013). A great advantage of telemetry studies is that they can provide fisher-independent F and M estimates, but fisher reported recaptures are still important in validating the telemetry-based estimates (Hightower and Pollock 2013; Topping and Szedlmayer 2013). In addition, fisher returns can provide a unique opportunity to understand fisher behavior (Pine et al. 2003) and generate species specific tag reporting rates. The 65% reporting rate in the present study was low compared to the 89% reporting rate from a previous study (Topping and Szedlmayer 2013), and may be attributed to many factors including tag shedding, unintentional non-compliance, or intentional non-reporting due to disagreement over present management restrictions.

Similar to Pincock (2012), there were false detections recorded on receivers that were removed from analyses based on a screening criteria developed in the present study. Pincock (2012) estimated that 10 to 15 transmitters with an average transmission delay of 60 seconds in a fixed area would generate a false detection every 5 to 7 hours. In the present VPS study, false detections on single receivers were not important, because in post-processing analyses we needed at least three simultaneous receiver detections to triangulate the position of a transmitter-tagged fish. However, false detections can be

problematic on single receivers outside the VPS-monitored array. Such false detections may interfere with the correct identification of mortality and emigration events. For example, a tagged fish that was identified as an F mortality from VPS analyses, but subsequently shows up on an outside receiver at a later date. Clearly, as we have accomplished in the present study, it is important to correctly identify these post-event false detections and remove them from analyses.

In the present study, we successfully used VPS telemetry to identify the fates of 98% of transmitter-tagged red snapper on four artificial reefs independent of fisher returns. The present estimate of low M can be attributed to the young ages of the fish tagged compared to their long life expectancy, and also the high fishing mortality rate as fishers have become extremely efficient at catching red snapper in our study area. Direct estimates of mortality showed that fishing mortality was high in all study years. Increases in F from 0.18 to 0.34 (2013 to 2014) when the sport fishing season was decreased from 42 to 9 days was unexpected, and indicated that fishers increased effort such that total catch may not have been reduced despite the shortened fishing seasons. The high site fidelity of red snapper with particular artificial reefs in known areas likely contributed to increased fishing mortality. Overall, the present telemetry based red snapper mortality estimates on artificial reefs in the northeast Gulf of Mexico support the present management restrictions of short fishing seasons; however, fisher success and effort likely varies by region and reef type and such aspects of fisher mortality need further examination.

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Table 2-1: Red snapper, *Lutjanus campechanus*, instantaneous annual mortality rates (Z = total mortality, F = fishing mortality, M = natural mortality) estimated from VPS telemetry by the known fate model in the “MARK” program. Mortality was estimated for each year (2012, 2013, and 2014), and for all years (3 years). Values in parentheses are 95% confidence limits. The numbers of fish (n) were the numbers of tagged fish available for recapture at the opening of the federal sport fishing season and days were the season durations for each year.

Year(s)	n	Z	F	M	Days
2012	15	0.84 (0.42–0.47)	0.72 (0.35–1.31)	0.12 (0.02–0.69)	46
2013	31	0.18 (0.07–0.41)	0.18 (0.07–0.41)	0	42
2014	29	0.34 (0.17–0.64)	0.34 (0.17–0.64)	0	9
All years	61	0.45 (0.28–0.67)	0.41 (0.25–0.62)	0.04 (0.01–0.23)	97

Table 2-2: False transmitter detections on Vemco VR2W receivers after transmitter removal due to fishing mortality. Fish # = unique fish number that is comparable to Piraino and Szedlmayer (2014). Transmitter status: active = transmitter was in the field or not returned by fisher, and off = transmitter was returned by a fisher and turned off. Mortality event: *F* = mortality reported by fishers, and VPS = mortality identified by VPS data. Event date = date of mortality. False det., = the number of false detections post-mortality. VPS site = the reef site of capture. False site(s) = sites where the false detections were observed.

Fish #	Transmitter status	Mortality event	Event date	False det.	VPS site	False site(s)
F44	active	VPS	3 June 2012	13	R2	R1
F35	off	F	3 July 2012	6	R3	R1 & R3
F40	off	F	5 July 2012	4	R3	R1
F14	off	F	10 July 2012	0	R1	
F16	off	F	10 July 2012	0	R1	
F34	off	F	12 July 2012	6	R3	R1 & R3
F3	active	VPS	14 July 2012	0	R1	
F36	active	VPS	15 July 2012	12	R3	R1 & R3
F43	active	VPS	24 October 2012	3	R2	R1 & R3
F96	off	F	7 June 2013	3	R2	R2
F108	active	VPS	7 June 2013	28	R2	R1 & R2
F113	off	F	23 June 2013	27	R3	R2 & R3
F110	active	VPS	23 June 2013	15	R2	R2 & S14
F109	off	F	26 June 2013	7	R2	R2 & R3
F47	off	F	5 June 2014	0	R3	
F146	active	F	5 June 2014	1	R2	R3
F138	active	F	5 June 2014	4	R3	R3
F143	active	VPS	5 June 2014	0	R2	
F89	active	F	6 June 2014	0	R1	
F147	active	F	7 June 2014	0	R1	
F100	active	VPS	7 June 2014	6	R1	S11
F88	off	F	8 June 2014	63	R1	R2 & R3
F82	off	F	9 June 2014	0	R3	

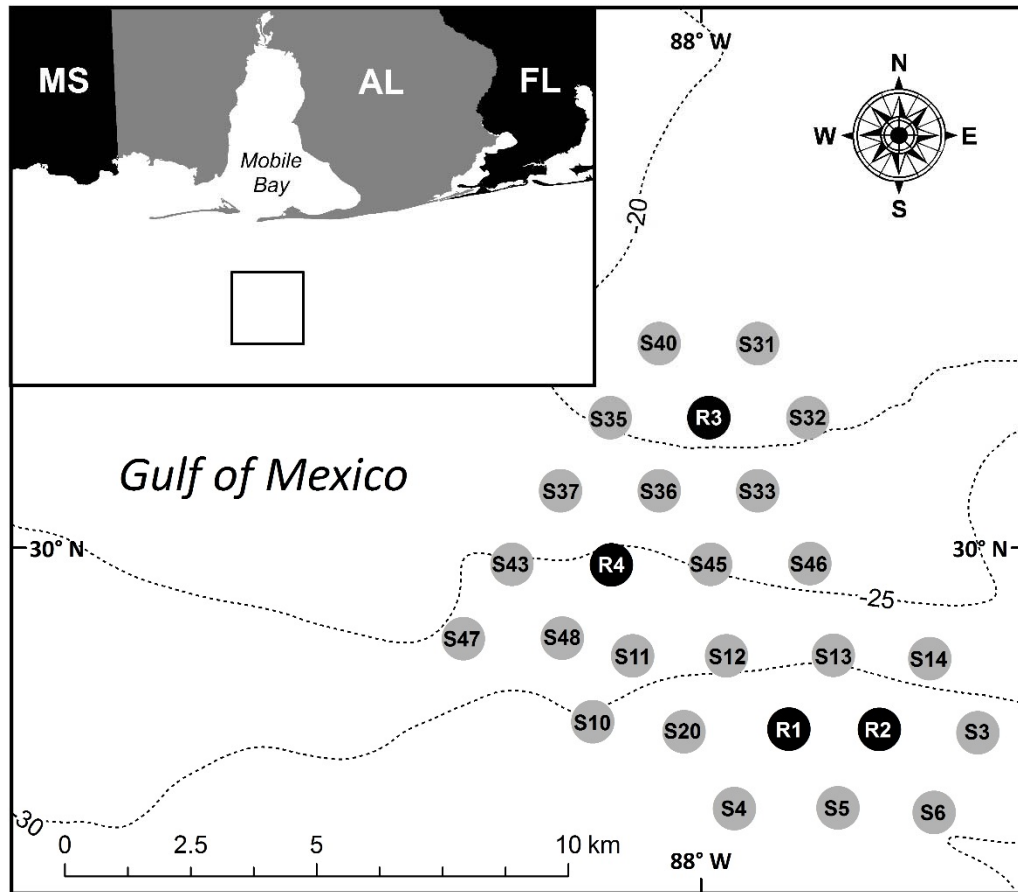


Figure 2-1: Locations of steel cage artificial reef study sites, for tracking the movements of red snapper, *Lutjanus campechanus*, in the northern Gulf of Mexico. Black circles ($n = 4$) were fish release sites (R1, R2, R3, and R4) with VPS receiver arrays. Gray circles ($n = 22$) were surrounding sites with single receivers (S3 – S48, numbering not continuous) that validate emigration and mortality events. Dotted lines are depth contours (5 m).

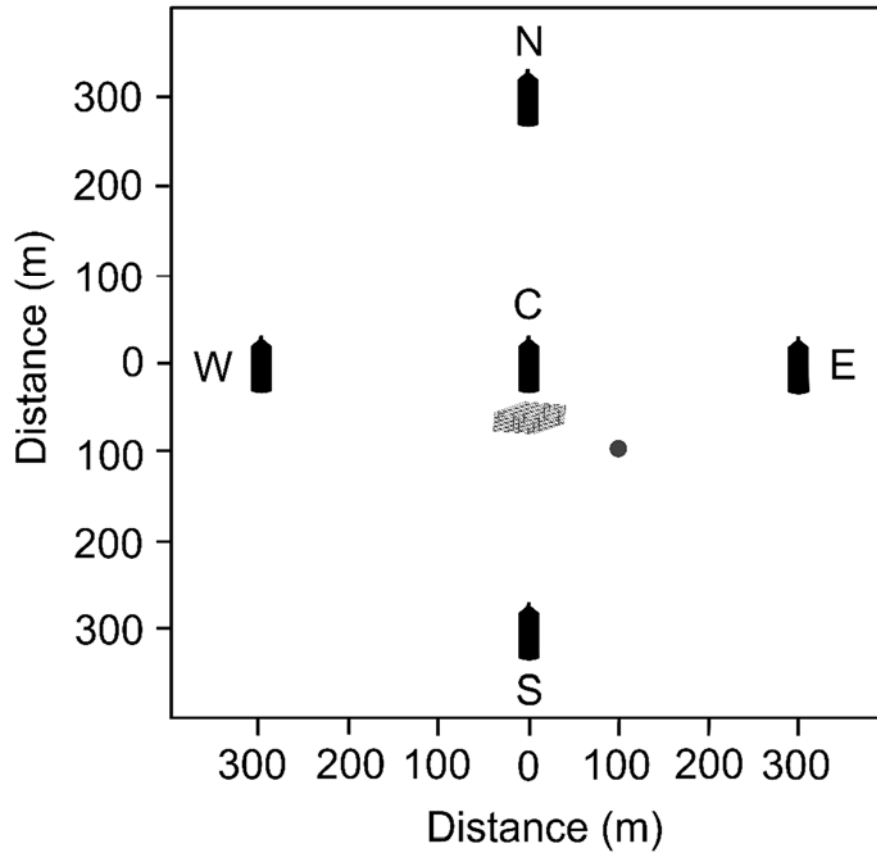


Figure 2-2: Receiver array (VPS) used to examine the fine-scale movements and mortality of red snapper, *Lutjanus campechanus*, around artificial reefs in the northern Gulf of Mexico. The center (C) receiver was positioned 20 m north of the steel cage artificial reef. Additional receivers were placed 300 m north (N), east (E), south (S) and west (W) of the center (C) receiver. A control transmitter was positioned within each array (direction and distance varied by site) for accuracy estimations. Black receiver icons = VEMCO VR2W receivers and synchronization transmitters; gray square = steel cage artificial reef; gray circle = control transmitter.

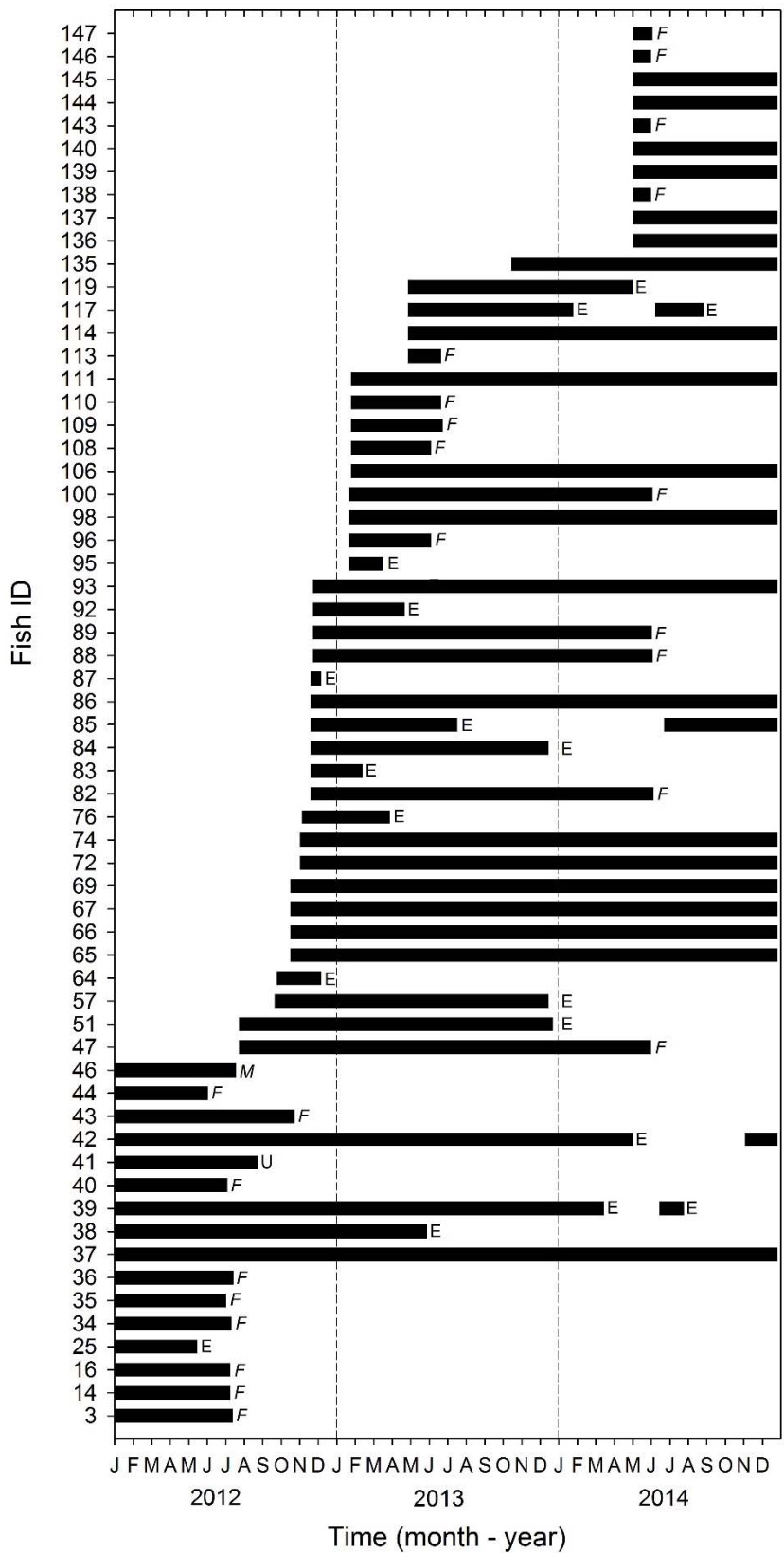


Figure 2-3: Tracking time for transmitter-tagged red snapper, *Lutjanus campechanus*, (n = 61) on VPS-monitored release sites in the northeast Gulf of Mexico. All fish present after the last month of tracking (December 2014) were active and vertical lines separate different study years.

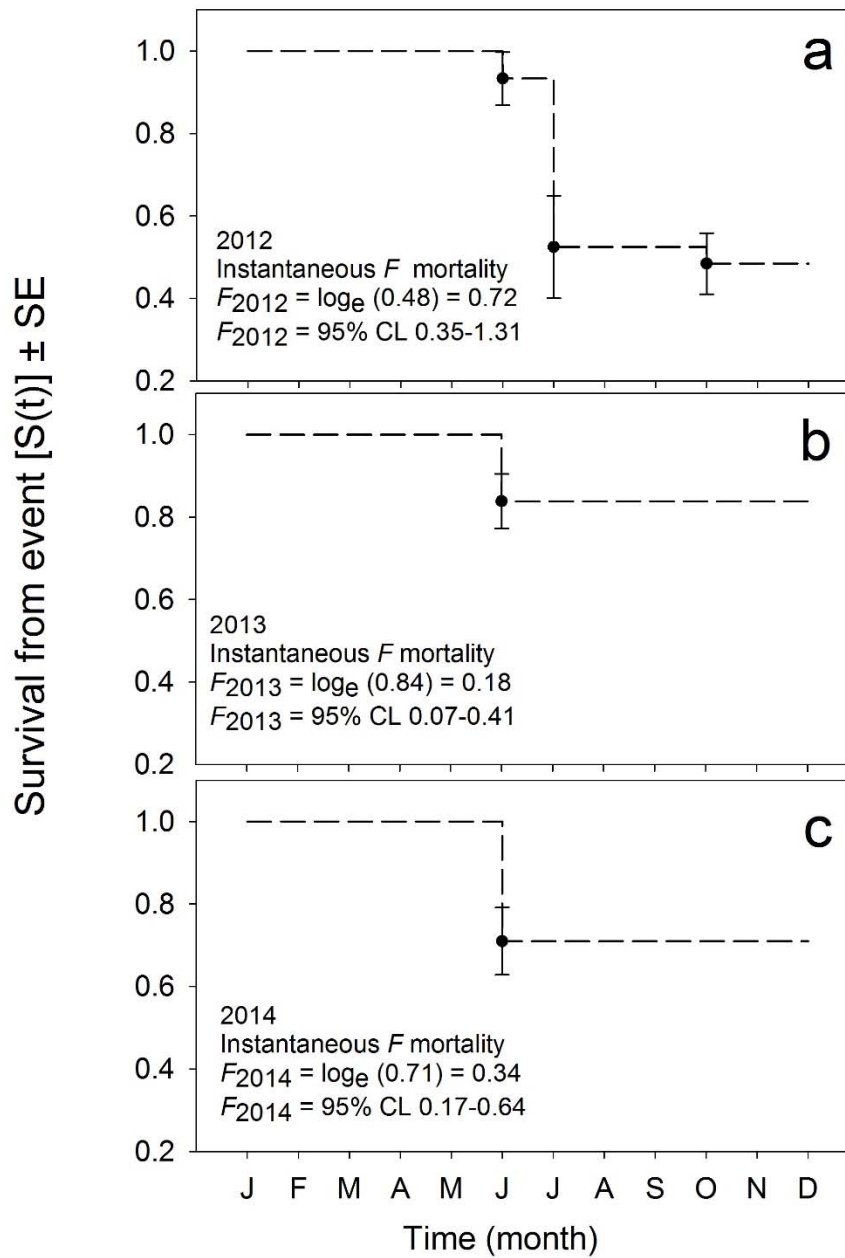


Figure 2-4: Survival (S) of red snapper, *Lutjanus campechanus*, from fishing mortality for years: a) 2012, b) 2013, and c) 2014. Dashed line shows proportion of fish surviving fishing mortality after each monthly interval. Instantaneous fishing mortality rates (F) were calculated from S at 12 months. Points and error bars (SE) were conditional estimates of S for time intervals with an event.

CHAPTER 3:
VIRTUAL POSITIONING AND MOVEMENT PATTERNS OF RED SNAPPER,
***LUTJANUS CAMPECHANUS*, AROUND ARTIFICIAL REEFS**
IN THE NORTHERN GULF OF MEXICO.

Abstract

The present study estimated fine-scale movements of red snapper *Lutjanus campechanus* on 3 artificial reefs with a recently (2011) developed VEMCO Positioning System (VPS), while wider scale (km) movements were estimated with surrounding receivers (n = 23) over a 3 year period (1 November 2011 to 31 October 2014). Red snapper (> 400 mm TL) were internally tagged with transmitters (Vemco V-16; n = 81) and after recovery from anesthesia, released close (< 10 m) to the capture site with a predator protection cage. Most of the tagged fish 76% (59 out of 81) remained near their capture site and were tracked for extended periods (17 to 1,095 d) after accounting for a 7-day post tagging artifact period. Residency (time when 50% of the tagged fish were still present = 34 months) and site fidelity (85% y⁻¹) showed that red snapper maintained a close association to artificial reef structure (mean ± SD distance = 37.4 m ± 58.0 m). Fine-scale movements of red snapper showed that home range (95% kernel density estimates; KDE) and core areas (50% KDE) significantly changed on seasonal, monthly, and diel temporal scales. Seasonal and monthly red snapper movements were positively

correlated with water temperature. In the winter all red snapper showed less movement and remained on their release site 99% of the time. In the summer and fall most (60%; 29 out of 48) red snapper also used secondary reef sites within the VPS array and stayed up to 31% of their time on these other sites. Over diel periods, red snapper showed different movement patterns. On two reef sites they showed significantly greater areas in the day, while at the third site they showed greater areas at night. A large number of tagged red snapper were caught by fishers (39%; $F = 0.49$, 0.01 – 0.89) and 27% emigrated from the VPS tracking areas. The surrounding receiver array validated 94% ($n = 16$) of the VPS determined emigrations. Tagged fish made directed movements. Many (52%; $n = 9$) fish moved short distances (~ 1.5 km) to nearby reefs and then remained on these reef sites for prolonged periods (23 – 336 d). These emigrated red snapper were then subsequently caught by fishers (29%; $n = 5$) or emigrated away from these secondary reef sites (24%; $n = 4$). A few red snapper ($n = 3$) that emigrated from the VPS array returned to their original release site at a later date. The present study suggested some prey-like behaviors in red snapper, *e.g.*, the close association with reef structure over long periods especially at crepuscular time periods, the quick movements over open habitat to nearby reefs (m to km away), and paired emigrations to other reef sites. These behaviors suggested that although red snapper can be a dominant predator, it is also subject to predation pressure by larger apex predators, and as stocks increase under present fishing restrictions such factors will become increasingly more important in future management efforts.

Introduction

Red Snapper, *Lutjanus campechanus*, drive an important commercial and sport fishery in the northern Gulf of Mexico (GOM). The fishery began in the late 1800's in Pensacola, Florida and over time progressively moved further south in Florida and west to Texas by the turn of the century (Camber 1955; Goodyear 1995; Manooch et al. 1998). The fishery was essentially unregulated throughout the 1900's with regulations starting in 1990 (SEDAR 2012). In more recent years, management efforts have resulted in numerous changes in daily and seasonal quotas in attempt to rebuild red snapper stocks (SEDAR 2012). Annual overages in sport fisher catch and different state fishing seasons led to a greatly shortened 9-day sport fishing season in U.S. federal waters in 2014 (NOAA 2014). To improve management efforts it is critical that managers understand red snapper habitat requirements, in particular how these fish use habitat on both small (*e.g.*, daily, seasonally) and large scales (*e.g.*, emigrations).

Previous studies have shown that red snapper were closely tied to structured habitat, both artificial and natural throughout their life span (Moe 1963; Nieland and Wilson 2003; Szedlmayer and Schroepfer 2005; Gallaway et al. 2009; Topping and Szedlmayer 2011a; 2011b; Mudrak and Szedlmayer 2012). The majority of mark-recapture studies are in agreement that red snapper have moderate to high site fidelity in the GOM with 48% to 94% of confirmed recaptured fish remaining on their initial tagging site (Topp 1963; Fable 1980; Szedlmayer and Shipp 1994; Watterson et al. 1998; Patterson et al. 2001; Diamond et al. 2007; Strelcheck et al. 2007). Similarly, long-term (> 1 y) telemetry studies have reported high annual site fidelity > 72% y⁻¹ and high residency for tagged fish up to 1099 d (Szedlmayer 1997; Szedlmayer and Schroepfer

2005; Topping and Szedlmayer 2011a; 2011b; Piraino and Szedlmayer 2014). The close proximity of this species to artificial reefs suggests that these structures provide benefits such as increased prey availability and predator protection (Bohnsack 1989; Ouzts and Szedlmayer 2003; Gallaway et al. 2009). While a strong association with artificial reef structure was clear, the specifics of fine-scale (m) and broad-scale (km) movements greatly vary among previous studies (Topp 1963; Beaumariage 1969; Fable 1980; Szedlmayer and Shipp 1994; Szedlmayer 1997; Watterson et al. 1998; Patterson et al. 2001; Patterson and Cowan 2003; Peabody 2004; Szedlmayer and Schroepfer 2005; Schroepfer and Szedlmayer 2006; Addis et al. 2007; Diamond et al. 2007; McDonough and Cowan 2007; Strelcheck et al. 2007; Topping and Szedlmayer 2011a; 2011b; Piraino and Szedlmayer 2014).

Fine-scale movements of red snapper have been evaluated with telemetry methods (Szedlmayer 1997; Peabody 2004; Szedlmayer and Schroepfer 2005; Schroepfer and Szedlmayer 2006; McDonough and Cowan 2007; Topping and Szedlmayer 2011a; 2011b; Piraino and Szedlmayer 2014). No seasonal differences in habitat use were detected in earlier studies (> 1 y) from presence-absence data collected from a single receiver and telemetry arrays consisting of a series of single receivers with overlapping detection ranges (Szedlmayer 1997; Szedlmayer and Schroepfer 2005; Topping and Szedlmayer 2011b). However, telemetry arrays did show directed and seasonal emigrations by some fish (n = 12; Topping and Szedlmayer 2011b). The most recent study that showed differences in seasonal habitat use by red snapper was based on the development and application of a new and highly accurate telemetry method (1 m accuracy, Vemco Positioning System [VPS], Vemco Ltd, Nova Scotia; Piraino and

Szedlmayer 2014). The VPS data showed that seasonal differences in habitat use (kernel density estimates; KDE) corresponded with water temperature and that home range (95% KDE) and core area use (50% KDE) were significantly smaller during the winter months (Piraino and Szedlmayer 2014). Similarly, earlier data collected from manual and remote tracking telemetry studies indicated that tagged red snapper moved away from reefs at night and stayed closer to the reef during the day (Peabody 2004; Szedlmayer and Schroepfer 2005; McDonough and Cowan 2007; Topping and Szedlmayer 2011a; 2011b). In contrast, red snapper home ranges and core areas were significantly larger during the day than night, and minimum at dawn and dusk based on the VPS method (Piraino and Szedlmayer 2014). It is unclear if this newly reported home range pattern is an accurate reflection of red snapper behavior or simply due to the difference in tracking types (manual versus remote), telemetry resolution (single receiver versus VPS array), study locations (larger reefs and different depths in previous studies), or sample size (VPS study tracked 17 fish; Szedlmayer 1997; Szedlmayer and Schroepfer 2005; Topping and Szedlmayer 2011a; 2011b; Piraino and Szedlmayer 2014).

Greater distance (km) movements of red snapper have primarily been described from conventional mark-recapture studies (Topp 1963; Beaumariage 1969; Fable 1980; Szedlmayer and Shipp 1994; Watterson et al. 1998; Patterson et al. 2001; Addis et al. 2007; Strelcheck et al. 2007). In mark-recapture studies the maximum distance reported by an angler for a recaptured fish ranged from 5 to 352 km (Fable 1980; Patterson et al. 2001). While telemetry studies in the northern GOM have focused on movements around reefs, some studies have shown that red snapper regularly make greater distance movements. For example, Szedlmayer and Schroepfer (2005) used a single stationary

receiver to track fish movements and reported that some of the tagged fish spent more time outside of the receiver range (max = 1.6 km) with one fish in particular making regular trips for over 24 h. Similarly, Topping and Szedlmayer (2011b) showed that some red snapper regularly used multiple reef habitats within their receiver arrays (< 2 km).

Measuring greater distance movements by red snapper to additional reefs located outside of telemetry receivers has been difficult. The distance a fish emigrates can only be measured if the fish moves to another reef with a receiver or if it is captured and reported by a fisher (although fisher reported locations have been unreliable; Szedlmayer and Schroepfer 2005). The detection of tagged red snapper on another reef with a receiver has previously been rare due to the limited number of reef sites monitored with single receivers (max = 12; Szedlmayer and Schroepfer 2005) or telemetry arrays (max = 6; Topping and Szedlmayer 2011b). Thus, our understanding of large-scale movements in both mark-recapture and telemetry studies is largely dependent on fisher reported recapture locations (Topp 1963; Beaumariage 1969; Fable 1980; Szedlmayer and Shipp 1994; Szedlmayer 1997; Watterson et al. 1998; Patterson et al. 2001; Patterson and Cowan 2003; Szedlmayer and Schroepfer 2005; Schroepfer and Szedlmayer 2006; Addis et al. 2007; Diamond et al. 2007; Strelcheck et al. 2007; Topping and Szedlmayer 2011a; 2011b). Most previous tagging studies have focused on either small-scale (*e.g.*, telemetry) or large-scale (*e.g.*, mark-recapture) movements but not simultaneously.

In the present study, red snapper movement patterns from both fine-scale and broad-scale telemetry arrays were examined. In addition, the present study focuses on the movements of large red snapper (> 406 mm TL federal size limit) as few studies have

examined these larger size classes, despite the fact that they are an increasingly important component of the managed fishery (SEDAR 2005; SEDAR 2012; SEDAR 2013). Fine-scale movements were evaluated with the VPS technology over diel, monthly, and seasonal time periods and compared to changes in water temperature. A large-scale (64 km²) receiver array surrounding the VPS sites was used to assess greater distance (up to 12 km) movements to other reefs and assess possible returns or homing behavior. The primary objectives of the present study were to estimate red snapper residency, site fidelity, core and home ranges within the fine scale VPS array (around the release reef site), and estimate greater distance emigration patterns to reef sites outside of the VPS sites. Combined, these data were used to evaluate red snapper movement patterns and habitat use and provide valuable information for managers, fishers, and organizations interested in improving red snapper stocks and their relation to artificial reefs (Bortone 1998; Strelcheck et al. 2007).

Methods

Study Location

The present study sites were located 23 – 35 km south of Mobile Bay, Alabama, USA, in the northeastern Gulf of Mexico. All study sites (n = 26) were at unpublished locations in the Hugh Swingle reef building area. The sites were steel cage artificial reefs (2.5 x 1.3 x 2.4 m) located 1.4 – 1.6 km apart at 20 to 35 m depths (Figure 3-1). There were 3 reef sites with VPS receiver arrays for recording fine-scale movements, and 23 surrounding reef sites with single receivers for recording greater distance movements (Figure 3-2).

Fish Tagging and Release Procedures

Red snapper were tagged and tracked on the VPS sites. Prior to tagging, dissolved oxygen and temperature levels were measured at depth (YSI model 6920, YSI Incorporated, Yellow Springs, Ohio). Fish were tagged and released if dissolved oxygen values were > 2.5 mg/L. If water temperatures at the surface were high ($> 27^{\circ}\text{C}$), temperatures in anesthesia and recovery containers were reduced with ice to more closely match temperatures at depth. All tagged red snapper were larger than the federal commercial (> 330 mm total length; TL) and recreational minimum length limits (> 406 mm TL; SEDAR 2013).

Fish tagging methods followed procedures described by Topping and Szedlmayer (2011a; 2011b; 2013). Red snapper were captured hook-and-line (8/0 circle hook baited with Gulf menhaden, *Brevoortia patronus*), were anesthetized (2 min) in a seawater tank (70 L) with MS-222 (150 mg tricaine methanesulfonate/L seawater), weighed (nearest 0.1 kg) and measured (mm SL, FL, TL) before surgery. A small vertical incision (20 mm) was made above the ventral midline and a uniquely identifiable transmitter (Vemco V16-6x-R64k, transmission delays = 20 – 69 sec) was surgically implanted into the peritoneal cavity. The vertical incision was closed with absorbable, sterile, plain gut surgical sutures (Ethicon 2-0, metric 3). Internal anchor tags (Floy[®]) with unique identification numbers were inserted ~ 3 cm dorsal and posterior of the incision site for visual identification (by SCUBA divers and fishers). Tagged red snapper were moved into a seawater recovery tank (185 L) on the research vessel and were considered recovered when active opercula pumping and fin movements returned.

Tagged fish were returned to depth close (< 10 m) to their VPS site of capture in a wire mesh cage. Prior to November 2012, fish were released in a closed circular cage (height = 40.6 cm, diameter = 60 cm; Piraino and Szedlmayer 2014). Transmitter tagged fish remained in the cage at depth for ≥ 1 h before SCUBA divers visually inspected fish and only released fish in good condition (*i.e.*, sitting upright, regular opercula movements, swimming, responded to diver presence). This cage release method was discontinued after SCUBA divers had frequent encounters with multiple large (≥ 2 m) Carcharhinid shark species.

After discontinuing cage-diver releases all (November 2012 – 2014) tagged red snapper were released with a remotely opening cage (46 x 61 x 61cm; Williams et al. 2015). Recovered fish were placed into the cage at the surface and were observed for 10 – 20 sec, at 1 m depths to verify recovered condition. Fish in good condition were slowly lowered by hand to the bottom (20 – 35 m). Once the cage reached the seafloor the cage door automatically opened and allowed the tagged fish to leave on its own initiative (Williams et al. 2015). Cages were retrieved after ≥ 15 min. If a tagged fish did not exit the cage it was considered in poor condition and was removed from the study.

Fine-scale tracking

From November 2011 through November 2014, fine-scale movements of red snapper were determined on VPS sites ($n = 3$). The VPS study design was first described by Piraino and Szedlmayer (2014). At each VPS site, 5 VR2W receivers were moored ~ 4.5 m above the seafloor. A central receiver was located near the reef (20 m north) and 4 surrounding receivers were positioned 300 m to the north, south, east, and west of the

central receiver (Figure 3-3). Receiver positions within the array allowed for maximum detection (100% detection of transmitters at 400 m; Piraino and Szedlmayer 2014). A synchronization transmitter (sync tags; Vemco V16-6x; 69 kHz; transmission delay: 540 – 720 sec) was attached 1 m above the receiver to standardize the internal receiver clocks. Fish positions with a 1 m accuracy (mean \pm SD; 0.98 m \pm 0.66 m; Piraino and Szedlmayer 2014) were calculated by VEMCO post processing of time differential of signal arrival at 3 to 5 receivers (Vemco Ltd., Nova Scotia). A stationary control transmitter was placed at a known location within each VPS array to confirm the continuous collection of data throughout the study. Receivers were exchanged at 3-month intervals by SCUBA divers, and returned to the laboratory for data retrieval.

Greater distance tracking

Greater-scale movements (km) of tagged red snapper were evaluated on the surrounding steel cage artificial reefs (n = 23; Figure 3-2). These surrounding sites were equipped with a single VR2W receiver (20 m north of each reef) and recorded the presence-absence of transmitter tagged fish. The combination of VPS and surrounding reef sites with receivers allowed for continuous monitoring over a large area (64 km²). This area included steel cage reefs (in the present study) with unpublished locations and several reef sites (concrete pyramids) with published locations.

Water Temperature Monitoring

At each VPS site, two temperature loggers (Onset HOBO[®] U22 Water Temp Pro v2) were attached on the central receiver line. One temperature logger was attached to

the line just above the receiver and a second was attached at the seafloor anchor. Each temperature logger recorded the water temperature (°C) at 1-hour intervals and was downloaded every 3 months.

Residency and Site Fidelity Analyses

The VPS arrays were used to categorize tagged fish as active (continuously swimming), caught (sudden disappearance near reef center, determined independent of fishers), emigrated (tracked for a period of time before progressively moving farther away from the reef center and then disappearance), and deceased (tag becomes stationary; Williams and Szedlmayer In review). Residence time of an active tagged fish was calculated with a known fate model in the “MARK” program (Topping and Szedlmayer 2013). The “MARK” program evaluated the proportion of fish that remained on an artificial reef (S) over time (t) based on the maximum likelihood binomial (MLE; Edwards 1992):

$$\mathcal{L}(\theta|n_i, y_i) = \prod_{i=1}^t S_i^{y_i} (1 - S_i)^{(n_i - y_i)}$$

Median residence time was defined as the time period when 50% of the tagged red snapper were still present over all years, while site fidelity was the percent of tagged fish remaining at their release site 1 year after release (Schroepfer and Szedlmayer 2006; Topping and Szedlmayer 2011b). Both estimates are based on the survival analyses from conditional probabilities of surviving specified events (*e.g.*, emigration). Fish were removed from the analysis (right censored) if they showed other events not under

consideration (*e.g.*, mortality). For example, when estimating residency or site fidelity a fish that emigrated or was caught was removed from subsequent estimates in the following months. The survival function was based on monthly time intervals (θ), the number of individuals at risk of undergoing an emigration (n_i), the number of individuals that did not undergo an emigration (y_i), and the MLE of remaining on a reef during each interval (S_i). Overall annual site fidelity was calculated by converting the total (36 month) estimate to an annual estimate (12 month; Topping and Szedlmayer 2011b).

Fine-scale Tracking Analyses

The distance between artificial reefs and red snapper, the known control transmitter, and the VPS generated control transmitter positions were calculated with the haversine formula (Sinnott 1984). Habitat use patterns (core and home range areas) were based on kernel density analysis (Venables and Ripley 2002; Piraino and Szedlmayer 2014). Kernel density analysis estimates (KDE) the probability of a tagged fish being located in a particular area. Core area = 50% KDE (absent from area 50% of the time) and home range = 95% KDE (absent from area 5%). Kernel density estimates were used instead of mean distance from reef to evaluate habitat use patterns because KDEs are robust to both autocorrelation and outlying positions (Worton 1989; Seaman and Powell 1996). Core and home range areas were examined for each fish by hour, month, and seasonal periods. The effect of time period (diel, month, season) on area use was tested with a one-way, mixed-model repeated measures analysis of variance (rmANOVA; SAS statistical software) with fish as a random factor and time period as a repeated measure (Zar 2010). If significant differences were detected with rmANOVA, specific differences

were shown with Tukey-Kramer multiple comparison tests. The use of a second reef site in the VPS array was analyzed in SAS by site, fish, and month. Fish were considered on the VPS site or a second known reef site within the array if positions occurred < 30 min apart and were located < 77 m from the reef site (*i.e.*, overall mean distance moved \pm 1 SD). If positions were recorded > 77 m from an identified reef site they were assumed to have occurred over the open habitat. Linear regression was used to compare red snapper home range and core area to water temperature and fish total length.

Greater-scale Movements Analysis

The greater-scale movements of red snapper that emigrated from VPS sites were detected by the surrounding receivers. The length of time an emigrated fish remained on a surrounding site was recorded on individual receivers. A false detection analysis was applied to delete false detections from valid fish detections. Transmitter detections were accepted as valid tagged fish if there was at least one short interval (23 min) between detections and more short intervals than long intervals (9h; Pincock 2012; Williams and Szedlmayer In review).

Results

Tagging and Tracking

Transmitter tagged red snapper (n = 81) were tracked on 3 VPS artificial reef sites (R1, R2, and R3) for up to 3 y (Figure 3-2). All tagged fish were above the federal minimum length limits (SEDAR 2013) and ranged in size from 454 to 877 mm TL (604 mm \pm 97 mm; mean TL \pm standard deviation; SD). We analyzed 4.5 million accurate (~

1 m) fish positions for 1,095 d to evaluate red snapper movement patterns. Red snapper that left within a 7-d tagging effect period were categorized as lost and removed from further analyses (n = 22). Among the fish that left within 7-d, most (86%; n = 19) left within 3-d of tagging, while one fish left on each of day 5, 6, and 7 of post-release. The movements of fish (F92) showed the importance of the post-release effect period. This fish immediately left (0 d) the VPS site (R1) where tagged and remained on a surrounding site (S20) for 7 d. On the seventh day this fish returned to R1 where it remained for 152 consecutive days before emigrating. This fish remained at liberty for 40 d before it was caught at an unknown location and returned by a fisher in June 2013. A small portion of the other lost fish (n = 3) were regularly detected on surrounding reef sites (a single fish on S11, S13, and S14) after emigrating from the release site within 7-d. Fish (n = 59) that remained after 7-d were categorized as active, caught, emigrated, or deceased, and used in all subsequent movement analyses.

The fine-scale movements of red snapper (n = 59) were recorded for 17 to 1,095 d. Among these tracked red snapper, 16 emigrated (3 returned), 23 were caught by fishers, 1 suffered natural mortality, 1 had an unknown fate, and 21 remained active at the end of the study (Figure 3-4). Emigration was first observed after 17 d, while the next emigration detected was after 72 d. The longest time between tagging and emigration was 978 d. The mean time before emigration was 351 d (\pm SD 294 d). Similarly, fish were tracked for 29 to 725 d following tagging before being caught by fishers. Most captures were reported by fishers (65%; n = 15) and all fisher reported captures validated the VPS data pattern used to define unreported fisher captures. A total of 4 fish were caught within 1 month (31 d) of tagging validating the survival and quick recovery of

surgery methods. The fate of one fish was unknown, because this fish was lost during the temporary removal of receivers from the field due to the threat of an impending hurricane ($n = 1$). This storm had no detectable effect on receiver arrays (*e.g.*, lost receivers). One fish was identified as a predation mortality based on short time intervals among greater distances (Williams and Szedlmayer In review).

Residency and Site Fidelity

Estimated for each year in separate analyses, annual site fidelity (S) was high (calculated as survival with mortalities right censored). In 2012 $S = 0.94$ with 1 emigration ($n = 20$, $0.66 - 0.99$, 95% CL), in 2013 $S = 0.75$ with 6 emigrations ($n = 32$, $0.55 - 0.88$), and in 2014 $S = 0.77$ with 8 emigrations ($n = 35$, $0.55 - 0.90$). Fishing mortality fluctuated but was also high for each year. In 2012, fishing mortality $F = 0.76$ ($< 0.08 - 0.97$ CL), in 2013 $F = 0.22$ ($< 0.01 - 0.72$) and in 2014 $F = 0.47$ ($< 0.01 - 0.90$). Based on a combined analysis for all 3 years, residence time (50% of tagged fish still present) was 34 months, total survival $S = 0.54$ ($0.36 - 0.71$) and annual site fidelity was $85\% \text{ y}^{-1}$ (Figure 3-5). In the present study, more fish were removed from the VPS reef sites by fishers (39% caught; $F = 0.49$, $0.01 - 0.89$) than through emigration (27%; for further discussion of mortality see Williams and Szedlmayer In review).

Fine-scale Area Use

Over the 3-y study period, control stationary transmitters (480,594 detections) showed that the VPS array detections were continuous (no interruptions in collection of data). The > 4.5 million red snapper positions analyzed showed no significant

differences in core areas (50% KDE) and home ranges (95% KDE) among VPS sites (core area: $F_{2, 580} = 1.42$, $P = 0.24$; home range: $F_{2, 580} = 1.62$, $P = 0.20$). Tagged red snapper maintained a close association with VPS artificial reefs with mean distance from the reef = $37.4 \text{ m} \pm 58.0 \text{ m}$ (mean \pm SD) over all years. Fish total length was positively correlated with core area ($F_{1, 637} = 95.83$, $P < 0.0001$, $r^2 = 0.13$) and home range ($F_{1, 637} = 185.72$, $P < 0.0001$, $r^2 = 0.23$). Larger red snapper ($> 700 \text{ mm TL}$) had significantly larger core areas ($< 600 \text{ mm TL}$; $F_{4, 580} = 5.29$, $P = 0.0003$) and home ranges ($< 699 \text{ mm TL}$; $F_{4, 580} = 12.10$, $P < 0.0001$) than smaller red snapper.

Red snapper movement patterns varied significantly by season, month, and water temperature. Summer (June – August) and fall (September – November) movements were significantly greater compared to winter (December – February) and spring months (March – May; core area: $F_{3, 577} = 42.97$, $P < 0.0001$; home range: $F_{3, 577} = 37.77$, $P < 0.0001$; Figure 3-6). Monthly movements followed seasonal movements and were significantly positively correlated with water temperature (core area: $F_{11, 623} = 116.211$, $P < 0.0001$, $r^2 = 0.16$; home range: $F_{11, 623} = 78.43$, $P < 0.0001$, $r^2 = 0.11$; Figure 3-7).

In the winter, most red snapper (90%; 35 out of 39) showed a home range centered around a single reef, *i.e.*, their original release site. During the summer most 60% (29 out of 48) red snapper showed home ranges that included two or more reef sites (original release site and secondary reef sites with the VPS array; Figure 3-8). The fish that used multiple reef sites in the summer continued to use these sites through the fall months.

For all years (2011 – 2014), the percentage of time spent on the VPS site, a second known reef site area, and open habitat was evaluated for all red snapper that had

monthly fish positions ($n = 56$). Over the entire study (all months), 75% of tagged fish showed the use of a secondary reef site spending $< 1\%$ to 31% of time on this second site and $< 1\%$ to 8% of time over open habitat (transiting between sites) depending on the VPS site and month. On R1, 46% (6 of 13) tagged fish had positions around a second site identified as a steel cage reef located ~ 200 m directly north of R1. For all years, fish spent $< 1\%$ ($0.1\% \pm 0.2\%$; mean \pm SD) of the time on the secondary reef site, $3\% \pm 3\%$ of time over open habitat, and most $97\% \pm 3\%$ of their time on the original release site (R1). Most time on the VPS site occurred in February ($> 99\%$) and slightly less time in June (91%). During June fish spent 1% of time on the secondary reef site and 8% of time over open habitat. On R2, 67% (12 of 18) tagged fish spent $98\% \pm 2\%$ of time on the VPS site, $1\% \pm 1\%$ around the second reef site identified as a concrete pyramid reef located ~ 250 m to the southwest of the VPS site, and $1\% \pm 1\%$ of time over open habitat. Time on the VPS reef site was greatest in February ($> 99\%$) and least in November (95%) spending more time on the secondary reef site (2%) or open habitat (3%) during that month. On R3, a secondary steel cage reef site located ~ 150 m northeast of the VPS site was visited by almost all fish (96%; 24 of 25). Red snapper spent most time on the VPS site ($83\% \pm 10\%$) however, fish spent comparatively larger amounts of time ($15\% \pm 9\%$) on the secondary reef site and little time over open habitat ($2\% \pm 1\%$). Greatest time on the VPS site occurred in January (95%, 4% on secondary reef site), while in October fish spent 66% of their time on the VPS site, 31% of their time on the secondary reef site and 3% of time over open habitat. Overall transit times between reef sites was short, with fish spending 1% to 3% of time over open habitat.

Red snapper showed significantly different core area and home ranges around VPS reefs over diel periods by reef site (core area $F_{46, 13E3} = 12.83$, $P < 0.0001$ and home range $F_{46, 13E3} = 14.48$, $P < 0.0001$). Sites R1 and R2 were both located in deeper water (31 m), had silt substrate, and showed a lower abundance of red snapper compared to R3. Reef site R3 was located in shallower water (19 m) with sand substrate. On R1 and R2, the largest movements occurred during day hours (0600 to 1600 h) while smaller movements were observed during night hours (2000 to 0200 h). The smallest KDE areas were observed during the early morning (0300 to 0400 h) and evening hours (1800 to 1900 h). In contrast, red snapper on R3 showed the largest movements at night (2300 h) and smallest movements in the day (1300 h; Figure 3-9).

Emigrations and greater-scale patterns

Our surrounding receiver array and recapture data were used to confirm emigrations. Most (94%, 15 out of 16) of the VPS detected emigrations, were also detected and validated on surrounding reef sites. Many (52%; $n = 9$) remained on surrounding sites for prolonged periods of time (23 – 336 d) before being caught by sport fishers (29%; $n = 5$) or emigrating away from these second reef sites (24%; $n = 4$).

Sport fishers reported catching tagged red snapper on surrounding reef sites 23 – 177 d after they had emigrated from their VPS release sites. For example, fish F38 remained on VPS site R1 for 643 d, then emigrated to a surrounding site (S13). This fish was detected on S13 for 23 d before it was captured by a fisher. Another red snapper (F64) stayed on site R3 for 72 d after release, then emigrated and was detected on two

surrounding sites (S33 and S36) for 177 d before it was captured by a fisher (Figure 3-10).

Additional movements to different reefs were also detected for some tagged red snapper ($n = 4$). One fish (F42) remained on a surrounding site for 50 d, then emigrated outside of the receiver array. Homing behavior (emigration followed by return to original VPS site of tagging) was detected in three red snapper that used surrounding sites for prolonged periods (160 – 336 d). For example, red snapper F85 resided on R3 for 240 d, then emigrated to a surrounding site (S32) and stayed for 336 d, then returned to R3 and stayed for 124 d until the end of the study (Figure 3-10). The other two red snapper (F39 and F117) used multiple surrounding reef sites. Red snapper F39 was detected on two surrounding reef sites (S12 and S13) and the VPS site (R1) for shorter periods of time (< 1 to 58 d) over a 5 month period (160 d; 3 March to 13 August 2014) before remaining on the VPS site (R1) until the end of the study (Figure 3-11). Movements were direct with detections ceasing at one site and starting at the new site quickly (minimum < 1 minute). Movements from R1 to S13 were sometimes briefly detected by west and north receivers of the R2 VPS array. Red snapper F39 was 565 mm TL when tagged, then emigrated after 931 d and most likely had increased in size to > 800 mm TL, when it started using multiple reef sites. Fish F117 was a large (808 mm TL) red snapper when tagged and made multiple movements to surrounding sites ($n = 4$) and moved outside the receiver array for varying periods of time (< 1 to 67 d). Red snapper F117 was tracked on R1 for 34 d post-tagging before temporarily emigrating to two nearby (1.5 km) surrounding reef sites S12 and S13 for ~ 12 d in June 2013. This fish then returned to R1 and remained for 169 d before emigrating (30 November 2013). Fish F117 proceeded to

make 21 detectable movements within (max > 2 km) and outside of the surrounding receiver array before returning to R1 on 13 June 2014 (after ~ 6 m or 195 d; Figure 3-12) and remained until the end of the study.

A smaller portion of red snapper ($n = 7$) that emigrated were detected but did not remain (< 1 d) on a surrounding reef site before exiting our receiver array. Most ($n = 6$) had multiple valid detections while passing by or briefly stopping (< 1 d) at up to 4 surrounding reef sites following emigration. All of these fish made similar movements away from the center of the reef after staying at their release site for 14 – 447 d. Following emigration these fish moved ~ 2 – 3.5 km to exit the surrounding receiver array. The exact distances that these fish traveled remains unknown and any further information was dependent on fisher recaptures. For example, one fish (F84) was tracked for 338 d on R3 before emigrating outside of our receiver array. This fish remained at liberty for 528 d before it was caught by a fisher. The reported recapture location for this fish was located 4.2 km away from its original VPS site. Only one red snapper (F57) that emigrated was not detected on a surrounding reef site. This fish stayed on its VPS (R3) release site for 447 d after release, then emigrated and was only detected on the R3 south receiver for 3 d before its disappearance. Overall, 12% (7 out of 59) of the tagged red snapper made these larger directed emigrations away from the receiver array.

Emigration rates varied by season with most emigrations occurring during the winter ($n = 7$) and spring ($n = 8$) months. No emigrations were observed in the fall and one emigration occurred during the summer (July). Paired emigrations were observed on two occasions when two tagged fish emigrated on the same day and from the same site. Both of these paired emigrations occurred at the shallowest VPS site (R3) at the

beginning of winter. These fish were tagged within 2 months of each other (September – November 2012) and were smaller red snapper (497 to 542 mm TL). The first two emigrated on 7 December 2012 (final detections = 8 min apart) and the second two fish emigrated 1 year later on 18 December 2013 (final detections = 3 min apart). In both years fish were then detected on surrounding reef site S33 for short periods (1 to 3 d) before making a second emigration. Temperature data showed that the paired emigrations occurred when the water temperature was 19°C in both years. In addition, two tagged red snapper emigrated in the spring on the same day (6 May 2014) but from different VPS sites (F42 from R3 and F119 from R1). We tagged additional fish on both R1 and R3 on 6 May 2014. During tagging efforts on 6 May 2014 fish F119 was recaptured after being tracked for 1 year. This fish appeared in excellent condition with no visible signs of tagging, was re-released in the predator protection cage, and was detected multiple times before emigration. The second red snapper (F42) that emigrated on 6 May 2014 was tracked for 978 d on R3 and was not recaptured. This fish was larger when tagged (662 mm TL) and made larger movements within the VPS array prior to emigration and temporarily remained on a surrounding reef site (50 d) before exiting our surrounding receiver array.

Discussion

The fine-scale and greater-scale movement patterns of red snapper around artificial reefs in the northern GOM were successfully estimated for 3 years. The present

study (1,095 d; n = 59) considerably expanded on a previous study that validated the feasibility of VPS telemetry methods with red snapper (694 d; n = 17; Piraino and Szedlmayer 2014). The present study increased red snapper locations to 4.5 million accurate positions over short time intervals (mean detection time < 5 min) continuously for up to 1,095 days, for unprecedented evaluation of fine-scale movement patterns in this species. In addition, all tracked fish (mean TL \pm SD; 604 mm \pm 97 mm) were above the federal minimum size limits (> 406 mm TL), thus providing detailed emigration, mortality, and movement patterns of red snapper that were fully recruited to the sport and commercial fishery.

Residency and Site Fidelity

Present estimates of red snapper median residency was 34 months and annual site fidelity was 85% y^{-1} , both of which were higher than most previous telemetry studies in the same region in the northern GOM (Szedlmayer 1997; Szedlmayer and Schroepfer 2005; Peabody and Wilson 2006; Topping and Szedlmayer 2011b; Piraino and Szedlmayer 2014). One other study reported similar high red snapper site fidelity to be 88% after 10 months based on VPS methods (Piraino and Szedlmayer 2014), while another study reported a slightly lower red snapper site fidelity at 72% y^{-1} over > 3 years based on frequency of tag detections (Topping and Szedlmayer 2011b). Similar to other red snapper telemetry studies (Szedlmayer and Schroepfer 2005; Topping and Szedlmayer 2011b; Piraino and Szedlmayer 2014), the site fidelity in the present study was higher than previous mark-recapture studies (Patterson et al. 2001; Patterson and Cowan 2003; Addis et al. 2007; Diamond et al. 2007; Strelcheck et al. 2007). For

example, Strelcheck et al. (2007) estimated 51.5% y^{-1} site fidelity for red snapper in the northern GOM. These differences between telemetry and conventional tagging mark-recapture studies are typical and likely due to the methods used to calculate site fidelity estimates. Mark-recapture studies have used an estimated instantaneous emigration, an estimated decline of recapture rate, and a fixed mortality rate (*e.g.*, Patterson and Cowan 2003; Strelcheck et al. 2007) or estimated site fidelity based on the number of recaptures reported by anglers on, versus away from the original tagging site (*e.g.*, Addis et al. 2007; Diamond et al. 2007). For example, Strelcheck et al. (2007) used an instantaneous decline in recapture rate D calculated from an instantaneous rate of emigration ($E = 0.72 y^{-1}$) and an assumed natural mortality rate $M = 0.1$, while fishing mortality was not considered ($F = 0$).

In the present study, site fidelity was estimated from known events (*i.e.*, emigration and mortality) based on accurate positions and movement patterns from the VPS array following a post-tagging release period (7 d). Importantly, emigrations and fishing mortalities were not dependent on fisher reports (for further discussion of fishing mortality see Williams and Szedlmayer In review). The greatly increased accuracy provided by telemetry methods has led to increased site fidelity estimates in the present study as well as previous studies.

Red snapper in the present study were tracked over long periods (up to 1,095 d) and showed some of the highest residencies and site fidelities of any previous study. However, present residency and site fidelity estimates are known underestimates, because fish were already resident on the tagging reef site for unknown additional time periods prior to tagging and release. In support of even greater residencies and site fidelities was

the correlation of mean age of red snapper with the age of the artificial reef from a previous study on the same reef sites used in the present study, suggesting that some of the tagged red snapper in the present study may have been resident for several years prior to tagging (Syc and Szedlmayer 2012).

Diel Movements

In the GOM, fishes typically forage during the day or night hours splitting time between foraging and avoiding predation (Helfman 1986). In the present study, when reef sites were analyzed together, no pattern was detected in red snapper core areas and home ranges over diel periods. However, different patterns were observed when diel movements were examined separated by reef site.

Red snapper on reef sites R1 and R2 showed largest movements during day hours, smaller movements during night hours, and smallest movements at dawn and dusk. These results agree with the first VPS tracking study that suggested red snapper behaved more like a prey fish species having significantly larger home ranges during day, less movement at night, but the smallest home ranges during dawn and dusk (Piraino and Szedlmayer 2014). As described in other species from previous studies (Collette and Talbot 1972; Hobson 1972; Helfman 1986; Hixon 1991) and suggested for red snapper (Piraino and Szedlmayer 2014) prey species enter a quiet period during dusk and dawn to avoid predation when larger predators are most efficient. In our study area in the northern GOM (10 – 40 m depth) many larger shark species are common including, blacktip shark, *Carcharhinus limbatus*, bull shark, *C. leucas*, sandbar shark, *C. plumbeus*, spinner shark, *C. brevipinna*, scalloped hammerhead, *Sphyrna lewini*, and tiger shark,

Galeocerdo cuvier (Drymon et al. 2010). In addition, we frequently (about 1 out of 3 SCUBA dives) encounter larger (> 2 m) carcharhinid shark species during quarterly change out of VR2W receivers.

Red snapper on artificial reef site R3 showed the opposite diel movement pattern, with the largest areas used during night hours. The areas used gradually decreased to minimal areas at midday hours (no changes during dusk and dawn). The movements of red snapper on R3 agree with earlier studies that suggested this species forages farther away from reefs at night to access additional prey (Peabody 2004; Szedlmayer and Schroepfer 2005; McDonough and Cowan 2007; Topping and Szedlmayer 2011a; 2011b).

Thus, in the present study, diel movement patterns agree with both of these contrasting patterns. The movement patterns are likely a result from the need to forage, balanced by the need to avoid predation (Werner et al. 1983), but these functions may have differed among reef sites. Sites R1 and R2 were located 1.5 km apart in deeper water (30 m) with silt substrate, while R3 was located 6.5 km north from R1 and R2 at shallower depths (19 m), with sand substrate. It is possible that the different movement patterns observed could be due to diel differences in prey availability between the different depths due to substrate types. Abele (1974) showed that decapod crustacean species abundance was closely related to substrate type and species commonly found in sand habitats had specialized morphological adaptations to allow for quick burrowing. Other burrowing species such as conger eels, *Conger oceanicus*, have been shown to burrow in sand substrate and forage during night hours (Levy et al. 1988). Prey species that burrow in the sand may become more available at night for red snapper on R3. Red

snapper are generalist predators and consume available prey types from reef, sand, and pelagic habitats (Ouzts and Szedlmayer 2003; Szedlmayer and Lee 2004; McCawley and Cowan 2007; Wells et al. 2008). Movements could also be related to water clarity or light at depth. The location of R3 in shallower water with sandy substrate may have increased visibility for foraging during night hours compared to the deeper reef sites. Several of the previous telemetry studies that detected movements away from the reef at night were at shallower depths similar to R3 in the present study (Schroepfer and Szedlmayer 2006; Topping and Szedlmayer 2011a; 2011b). Diel differences among sites could also be related to different reef fish density, *e.g.*, as reef fish density increases, competition for food may increase forcing resident fish to increase foraging (Gallaway et al. 2009; Jaxion-Harm and Szedlmayer 2015). Red snapper and gray triggerfish, *Balistes capriscus*, were consistently at greater densities on R3 compared to R1 and R2 over the present study period. In addition, higher fish density on R3 may have provided increased protection from predators (safety in numbers) during night, dawn, and dusk hours when movements were smallest on the other VPS reef sites with lower fish abundances.

Seasonal Movements

Seasonal movements (home range and core areas) were significantly larger during the summer and fall months and significantly correlated with water temperature supporting previous fine-scale red snapper movement patterns. Piraino and Szedlmayer (2014) showed significantly smaller movements during the winter season when water temperatures were lowest. Seasonal differences in area use and the number of sites visited by red snapper within the VPS arrays is likely due to foraging behaviors. Less

foraging is known to occur when water temperatures are cooler due to decreased metabolic rates (Helfman 1986; Hidalgo et al. 1987; Johnston and Dunn 1987).

In the present study, comparisons of time on the VPS reef site, secondary sites and open habitat showed that most (75%) red snapper spent at least some time on a secondary reef site within the VPS array. Time spent on secondary sites varied by season and was lowest during winter months and highest during summer and fall months. Maximum time spent on a secondary reef site varied by site with fish on R1 only using secondary sites 1% of the time, while fish on R3 would use secondary sites up to 31% of time. The closer location (~ 150 m) of the secondary reef site to R3 or different habitat (sand bottom and more shallow) may explain these differences. Red snapper on R1 spent the most amount of time over the open habitat (up to 8%). Multiple fish that were away from R1 and the secondary reef site, were concentrated over open habitat > 300 m away to the northwest suggesting that a third reef site may be present within the VPS array. Thus, time over open habitat may be overestimated for R1. For all years and sites combined, red snapper spent the majority of time on the VPS sites (93%), and little time on secondary sites (5%) and over open habitat (2%). Piraino and Szedlmayer (2014) described the use of multiple reef sites in the VPS array as homing behavior and suggested that red snapper know their habitat as indicated by the long periods of time on secondary sites with returns to the VPS site. In the present study the regular use of known sites varied by season suggesting that nearby habitat may be especially important for seasonal foraging and spawning behaviors.

Large Scale Movements

The present study successfully estimated red snapper movement patterns and emigration distances over a large area (64 km²) independent of the fishery. Among red snapper that emigrated from their VPS site (n = 16; 27%), additional movements were successfully detected for 94% of these fish by the surrounding receiver array. Most (56%) remained on a nearby reef site (1.5 km away from VPS site) for extended periods of time (up to 336 d) before capture or subsequent emigration. The consistent use of nearby surrounding reef sites for prolonged periods prior to capture (min 23 d) or subsequent emigration (min 90 d) supports several concepts: 1) validates that red snapper emigrated from the VPS arrays and were not predation events; 2) directed quick movement (*i.e.*, little time over open habitat) to a nearby reef site confirms the high association of red snapper to artificial reefs; 3) indicated a reef hopping behavior where red snapper move larger distances by making prolonged stops at different reef sites (~ 1.5 km) before further emigration.

Emigrations were observed in other published studies based on VPS telemetry methods. Many of these studies observed emigrations during shorter tracking times including flatback turtle hatchlings, *Natator depressus* (mean < 30 min; Thums et al. 2013), lingcod, *Ophiodon elongatus* (27 d; Andrews et al. 2011), southern flounder, *Paralichthys lethostigma* (~ 1 m; Furey et al. 2013), American lobsters, *Homarus americanus* (~ 1 m; McMahan et al. 2013), Atlantic cod, *Gadus morhua* (max 101 d; Dean et al. 2014), Burbot, *Lota lota* (3 m; Cott et al. 2015), white croaker, *Genyonemus lineatus* (max 150 d; Wolfe and Lowe 2015), gray smoothhound, *Mustelus californicus* (max 153 d; Espinoza et al. 2011), bonefish, *Albula vulpes*, permit, *Trachinotus falcatus*,

and great barracuda, *Sphyraena barracuda* (~ 6 m; Finn et al. 2014), and red snapper (max 694 d; Piraino and Szedlmayer 2014). Emigrations were identified when transmitter tagged individuals displayed normal behaviors when exiting the VPS array. In a few studies, emigrations were confirmed when fish immigrated back into the VPS array (Dean et al. 2014; Finn et al. 2014; Wolfe and Lowe 2015). For example, Atlantic cod (n = 17 out of 43) returned to the monitored spawning grounds one year after emigration (Dean et al. 2014). In the present study we were able to use a combination of a VPS array and surrounding receiver array to confirm 94% of the VPS identified emigrations, and large-scale homing behavior (km distances) for three red snapper.

Some previous mark-recapture studies that relied on fisher returns to calculate distances moved reported similar low numbers of tagged red snapper making large-scale movements. For example, 56% of tagged red snapper remained on their release site and 76% remained within 2 km of their tagging location (Szedlmayer and Shipp 1994). Similarly, 65% of tagged red snapper were recaptured at their tagging site, 86% remained within 2 km, and 94.6% remained within 5 km (Strelcheck et al. 2007). Higher rates of emigrations have been shown on natural reefs with as high as 93% of fish tagged emigrating (Diamond et al. 2007), and the maximum distance reported for an individual fish ranged from 5 km (Fable 1980) to 352 km (Patterson et al. 2001). Fishery dependent data collected in the present study suggested a maximum distance moved to be 16 km, however this reported recapture location by a private fisher was invalidated, as the VPS data showed that this fish was present on the VPS reef site at the time of capture. The discrepancy between the fisher reporting site (16 km away) and where the fish was actually caught has previously been recognized with fishery dependent recaptures

(Szedlmayer and Schroepfer 2005). However, most fisher dependent mark-recapture studies are in agreement with the present study, showing that red snapper have high site fidelity in the GOM with 55% to 94% of recaptured fish remaining on their initial tagging site (Topp 1963; Fable 1980; Szedlmayer and Shipp 1994; Watterson et al. 1998; Patterson et al. 2001; Addis et al. 2007; Diamond et al. 2007; Strelcheck et al. 2007).

Understanding Larger Movements

Fish emigrations have been related to foraging, spawning, and environmental factors. Artificial reefs support high densities of fish most likely due to increased prey availability and predator protection (Bohnsack 1989; Ouzts and Szedlmayer 2003; Gallaway et al. 2009) however, if prey resources become depleted fish will move to higher quality habitat (*e.g.*, Chapman and Bjornn 1969; Wilzbach 1985; Matthews 1990; Olsson et al. 2006). For example, brown trout, *Salmo trutta*, showed greater movement with high fish density and low prey availability, and less movement with low fish density and high prey availability (Olsson et al. 2006). Similar to previous studies, larger red snapper appear to show lower residency to original release sites, make greater movements, and show an increased use of other reef sites (Szedlmayer and Schroepfer 2005; Topping and Szedlmayer 2011a; Piraino and Szedlmayer 2014).

Several species of the Lutjanidae have shown movements that are also related to spawning (Wicklund 1969; Carter and Perrine 1994; Domeier and Colin 1997). In the Gulf of Mexico, life history studies on red snapper showed early maturation (earliest ~ 2 years), spawning from May to September, and increased fecundity and spawning in older fish (Szedlmayer and Shipp 1994; Goodyear 1995; Collins et al. 2001; Woods et al.

2003). In the present study, we did not detect coordinated movements or aggregations away from reef sites that might be considered spawning groups, but red snapper have been observed by SCUBA divers spawning directly over resident reef sites (unpublished data Szedlmayer, S.T.). However, seasonal differences in emigration rates were detected. The majority of red snapper emigrated during the winter (44%) and spring (50%) months. No significant patterns between fish size and emigration were detected, however, emigrations during the spring months were made by larger red snapper (mean TL 594 mm \pm 89 mm), many of which had been tracked over long periods (57 – 978 d; mean 449 d) prior to emigration. The extended time at liberty, combined with the known size at release for most fish prior to emigration would suggest that many of these red snapper were > 6 y (Szedlmayer and Shipp 1994; Wilson and Nieland 2001). Older (\geq 6 y) red snapper have been reported to spawn at a 50% greater frequency compared to younger red snapper (\leq 5 y; Collins et al. 2001). Thus, increased emigrations by larger red snapper during the spring months may be related to spawning. For example, in the present study two of the largest tagged fish (F39 and F117; > 800 mm TL) regularly used multiple surrounding reef sites (n = 3) during the spring months before returning to their original VPS site in the summer.

Seasonal differences in emigration may also be attributed to the lower temperatures observed during these seasons. For example, seasonal movements of red snapper due to the passage of cold fronts has been reported (Topping and Szedlmayer 2011b). Many other species of coastal marine fish are known to annually make inshore and offshore migrations due to changing water temperatures. These fish regularly overwinter farther offshore in relatively higher water temperatures (Stokes 1977; Pittman

and McAlpine 2003). Topping and Szedlmayer (2011b) reported different seasonal emigration rates than the present study with the highest emigration during the summer months (37%) followed by fall (29%), winter (26%), and spring (8%). However, more than half of the emigrations during the summer and fall months occurred during seasonal hurricanes (Topping and Szedlmayer 2011b). No major storm events occurred during the present study.

Paired Emigrations

Four fish emigrated from our shallowest VPS site (R3) in the beginning of winter when the water temperature decreased to 19°C in 2012 and 2013. The day of emigration was not the first day that water temperatures fell below 20°C in either year, and it was not the lowest temperature observed during the winter season which occurred during February (2012 = 13.2°C and 2013 = 14.9°C). The VPS data showed movements to be significantly smaller during the winter and spring months but emigration rates were the highest. The paired movements of two red snapper during the same month (December) one year apart may suggest that an environmental factor, such as photoperiod or temperature could be the cause. However, if temperature at the VPS site was outside the physiological range of red snapper we might expect more emigrations of tagged fish rather than just a few. Although the cause of these movements is unknown, it does provide evidence that red snapper may choose to emigrate in groups. Emigrating together or as an organized school of fish could increase foraging success or predator-avoidance (Pitcher 1983; Pitcher 1986; Parrish and Edelman-Keshet 1999; Soria et al. 2007). It is possible that the paired emigrations that we observed were fish increasing

protection from predators by forming a loose school while making movements away from the VPS reef site. However while group emigrations may occur more often in the wild, detections of paired emigrations may have been reduced due to the low number of tagged fish per reef ($n \leq 10$).

Two additional emigrations occurred on the same day (6 May 2014) but from different reef sites (R1 & R3). These emigrations could have been induced by capture and release in the present study. We tagged additional red snapper on both sites on 6 May 2014 and recaptured one of the tagged fish (F119). Immediate emigration following red snapper tagging has been attributed to capture stress and considered a tagging artifact. Tagging studies, including the present study, have applied a tag effect period to account for post-release emigration (Szedlmayer 1997; Szedlmayer and Schroepfer 2005; Topping and Szedlmayer 2011a; 2011b; Piraino and Szedlmayer 2014). The tagged red snapper that was recaptured and re-released by the present study and emigrated on its recapture date (6 May 2014) may be similar to private fisher capture and releases, suggesting that fisher recaptures could also increase emigrations.

Conclusions

The 4.5 million fish positions used in the present study showed that red snapper were closely associated with artificial reef structures over long periods of time ($> 1,095$ d). The present study confirmed previous long-term (> 1 y) telemetry studies that showed red snapper had high residency and site fidelity. Similarly, fish size positively

correlated with area used, and seasonal and monthly movements positively correlated with water temperature where tagged red snapper stayed close to the VPS site (99%) during winter months. The use of a second reef site was shown for most red snapper (75%) and time spent on the second site was greatest in the summer and fall months. This study showed that red snapper had different diel patterns at different reef sites. These different patterns may be related to prey availability, reef depth, water clarity, and fish abundance. The surrounding receiver array (outside VPS arrays) showed that red snapper mostly made short distant emigrations (~ 1.5 km) compared to greater distance emigrations (> 3 km) and remained on nearby sites for prolonged periods before making additional movements or being caught by fishers. Some tagged red snapper (n = 4) showed paired emigrations (n = 2). These paired emigrations most likely reduced predation as fish travelled over open unsheltered habitat. Movements to new reef sites for additional foraging, for spawning, environmental factors, or fisher capture effects, indicates that the quantity and arrangement of artificial reefs are important factors for red snapper ecology and survival, and need to be considered when planning new reef deployments and in management efforts to increase stock abundance.

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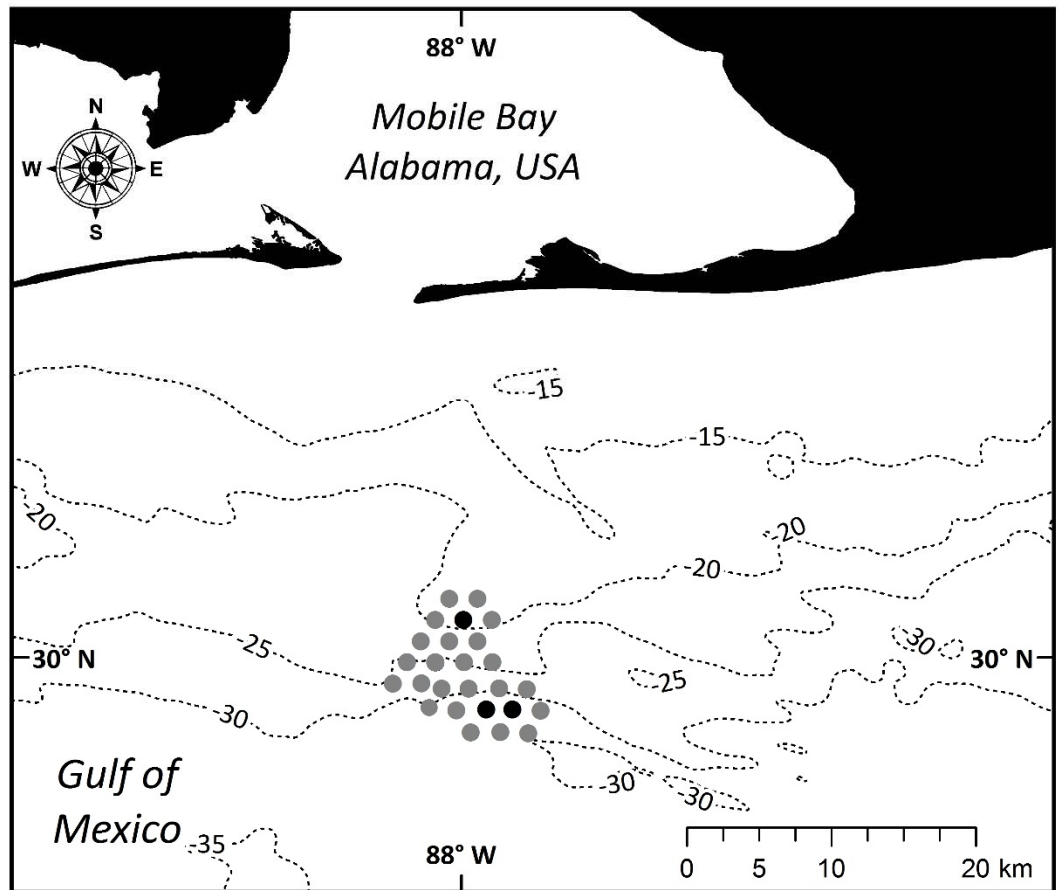


Figure 3-1: Locations of steel cage artificial reef sites used to track movement patterns of red snapper, *Lutjanus campechanus*, off the coast of Alabama in the northern Gulf of Mexico. Black circles (n = 3) are Vemco VPS reefs that record fine-scale movements and gray circles (n = 23) represent surrounding sites with VR2W receivers that monitor emigrations and greater scale movements.

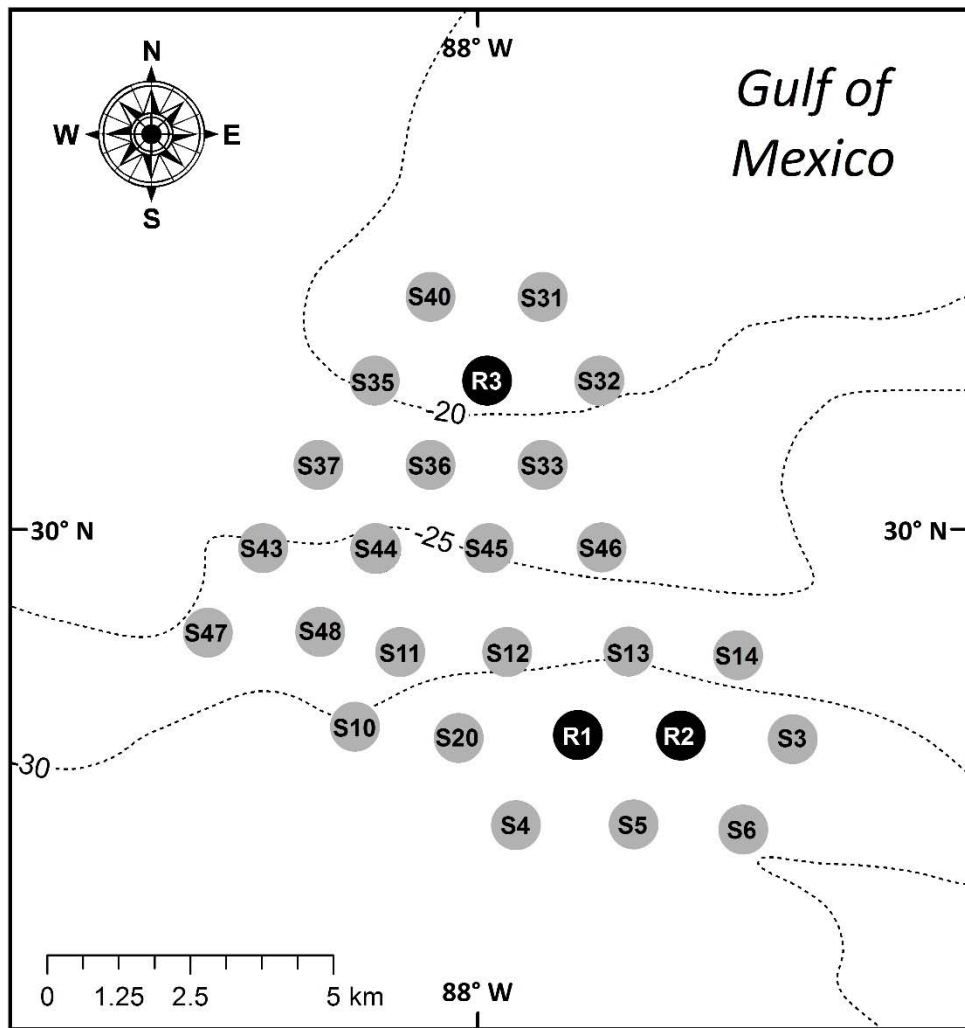


Figure 3-2: Artificial reef sites ($n = 26$) used to track movement patterns of red snapper, *Lutjanus campechanus*, in the northern Gulf of Mexico. Black circles ($n = 3$) were Vemco VPS receiver arrays (R1, R2, and R3) that measured fine-scale movements and gray circles ($n = 23$) represent surrounding sites with single receivers (S3 – S48) that measured greater scale movements.

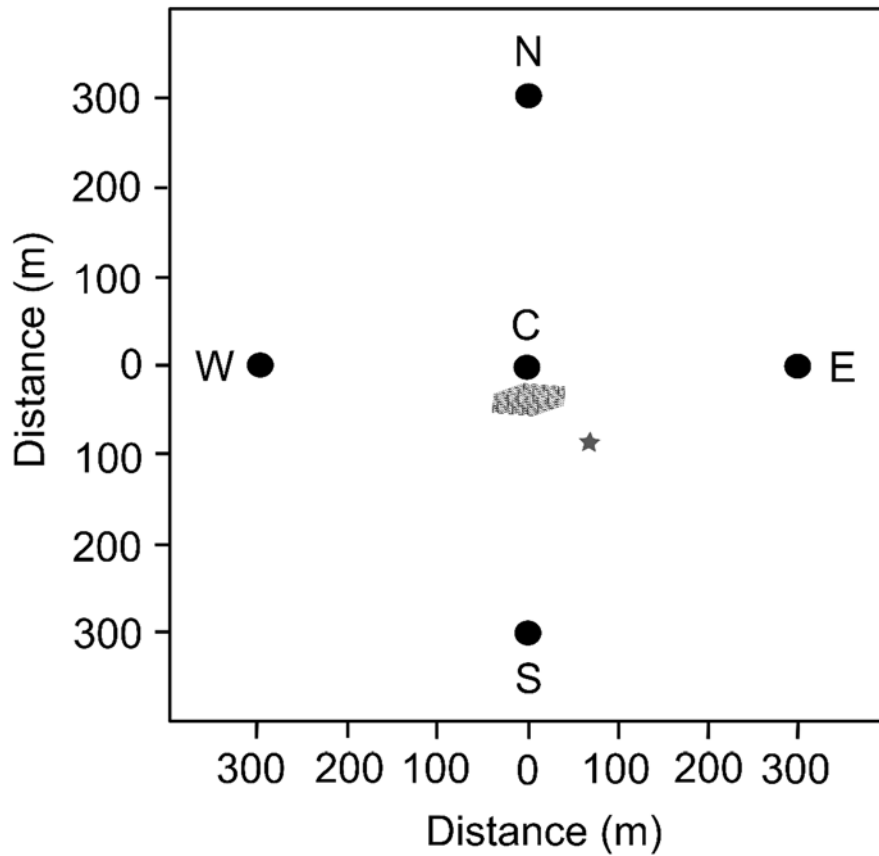


Figure 3-3: Receiver array (VPS) used to examine fine-scale movements of red snapper, *Lutjanus campechanus*, on artificial reefs in the northern Gulf of Mexico. The center (C) receiver was positioned 20 m north of the steel cage artificial reef (reef not to scale). Additional receivers were placed 300 m north (N), east (E), south (S) and west (W) of the center (C) receiver. A control transmitter was positioned within each array to determine the accuracy of the VPS positions. Black circles = VEMCO VR2W receivers and synchronization transmitters; gray square = steel cage artificial reef; gray star = control transmitter.

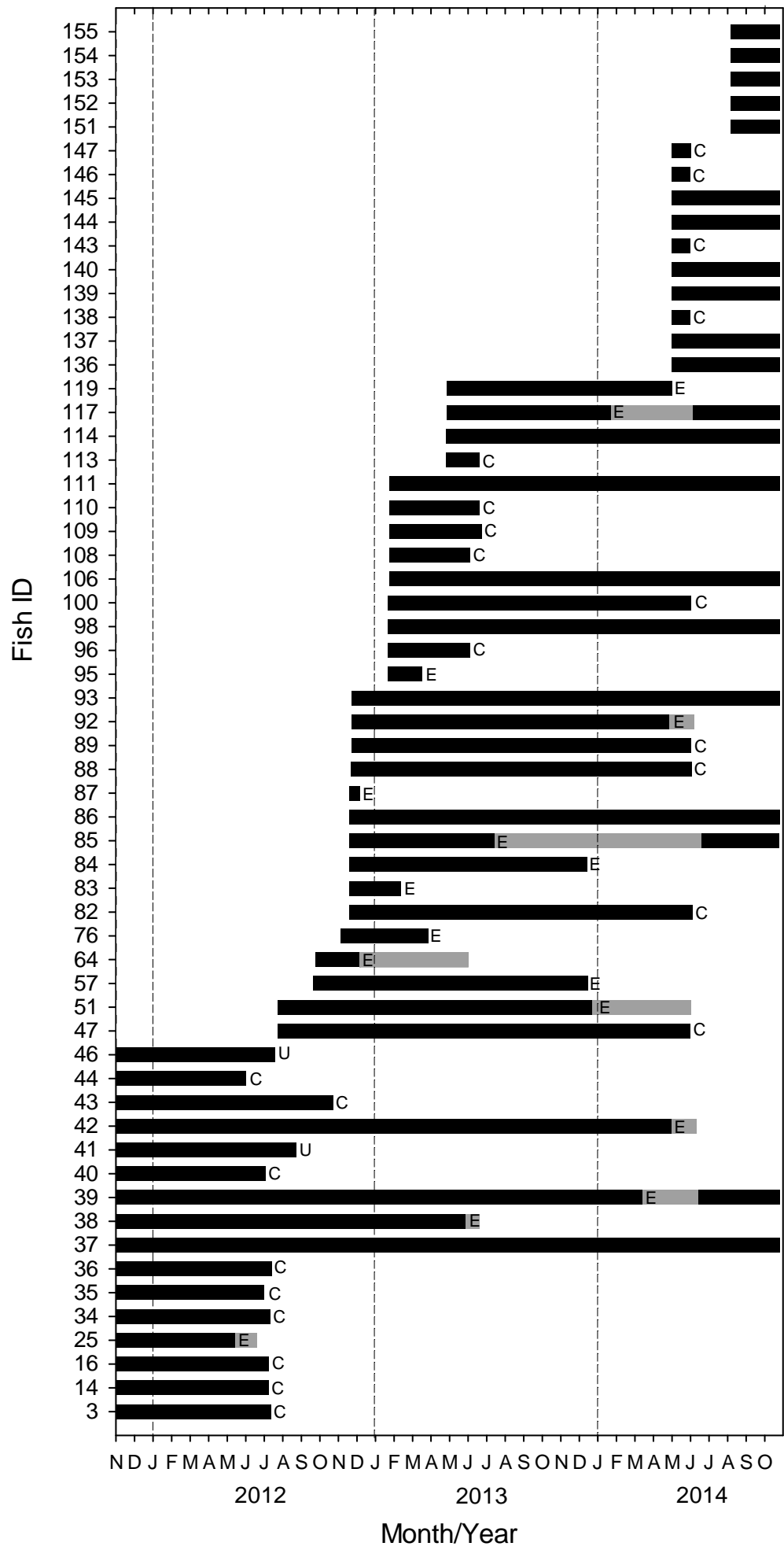


Figure 3-4: Tracking periods for transmitter-tagged (n = 59) red snapper, *Lutjanus campechanus*, on VPS sites and on surrounding reef sites, after a 7 d post tagging recovery period. Fish still present after the last month of tracking (31 October 2014) were all active. Black bars = active on VPS site; gray bars = active on surrounding receiver site; and letters denote fate for fish on VPS site, C = caught, E = emigration, and U = unknown.

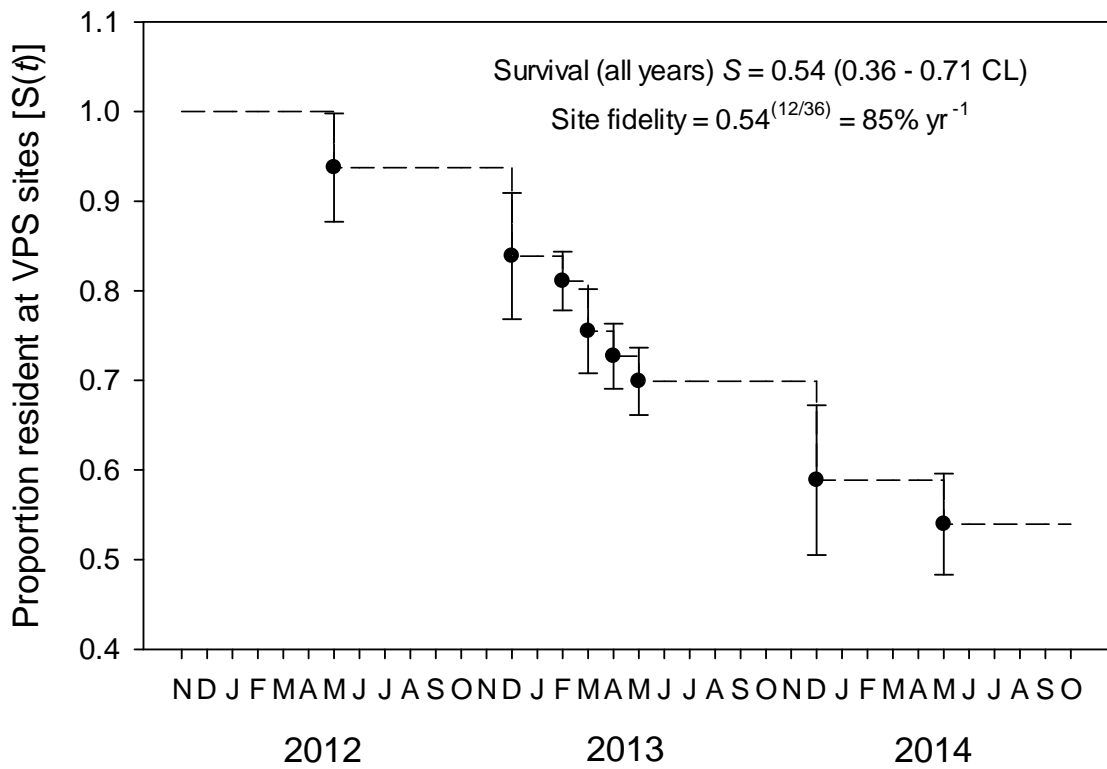


Figure 3-5: Survival (S) of red snapper *Lutjanus campechanus* at their artificial reef site of capture and fine-scale Vemco VPS tracking. Dashed line shows proportion of fish that remain residents (did not emigrate) after each monthly interval. Points and error bars (SE) are conditional estimates of S for time intervals at each emigration.

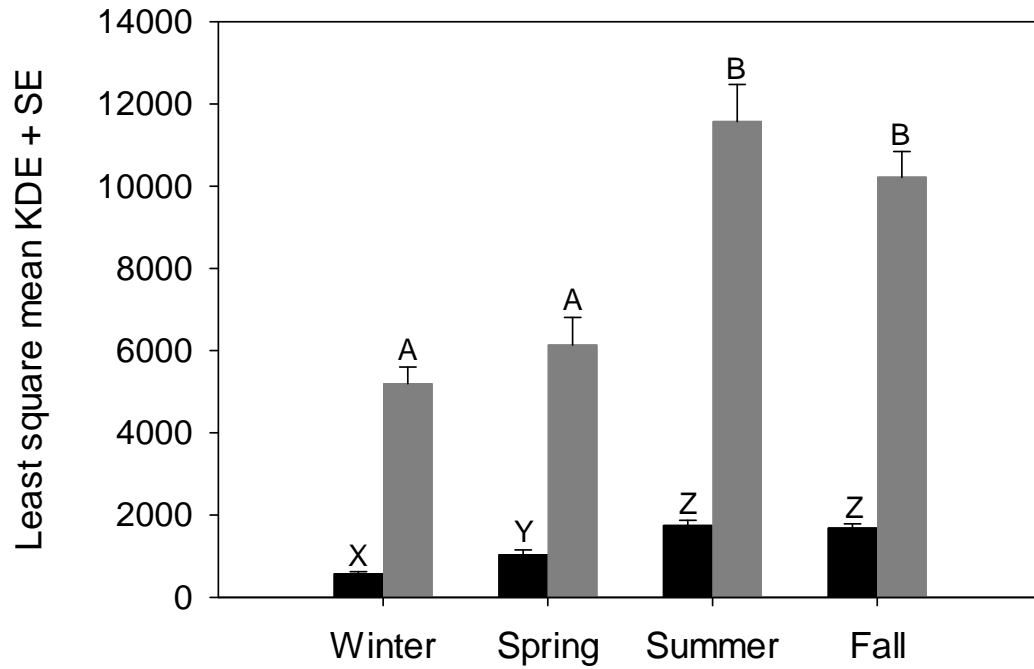


Figure 3-6: Seasonal differences in core area and home range of tagged red snapper, *Lutjanus campechanus*, on artificial reefs in the northern Gulf of Mexico. Black bars = core area (50% KDE); gray bars = home range (95% KDE); error bars = SE. Different letters denote significant differences ($p \leq 0.05$).

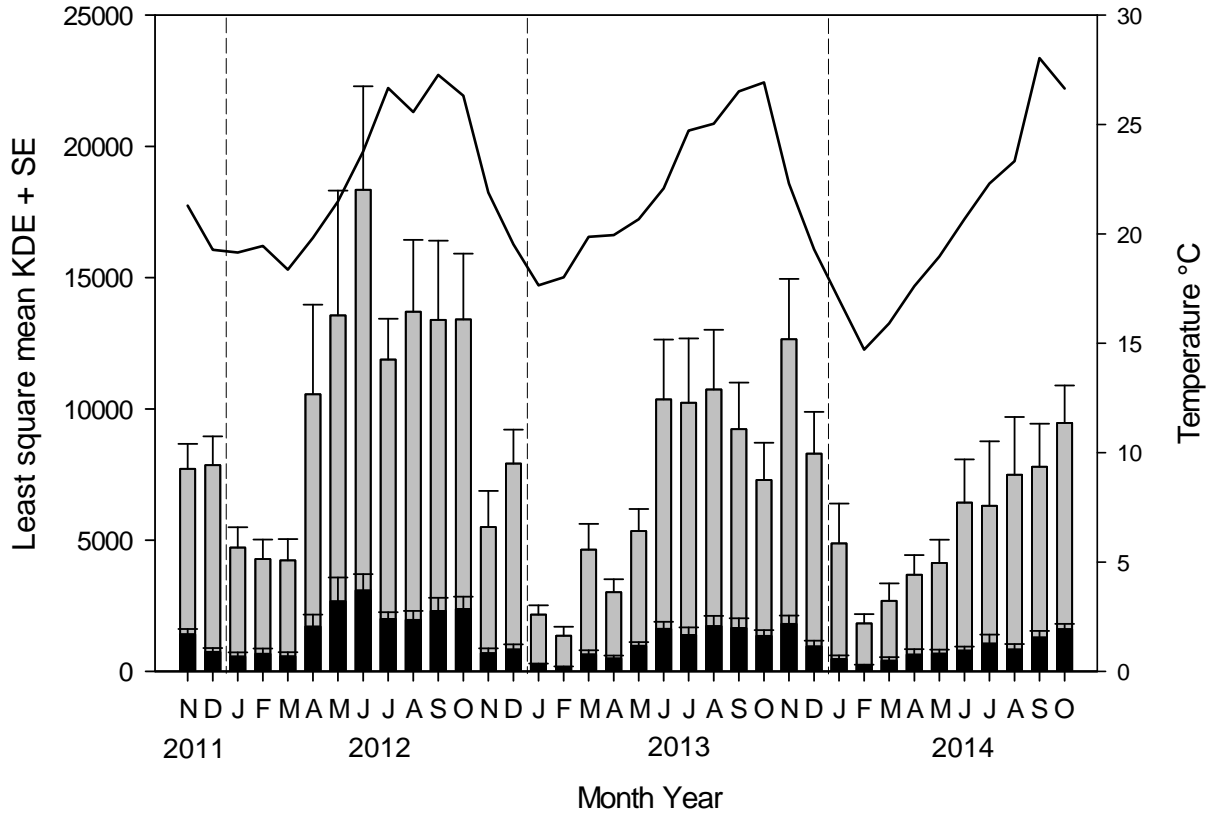


Figure 3-7: Comparison of water temperature and mean monthly home ranges (95% KDE) and core areas (50% KDE) of red snapper, *Lutjanus campechanus*, around artificial reefs in the northern Gulf of Mexico over 3 years (1 November 2011 to 31 October 2014). Black bars = core area (50% KDE); gray bars = home range (95% KDE); and error bars = SE. Black line = water temperature at depth.

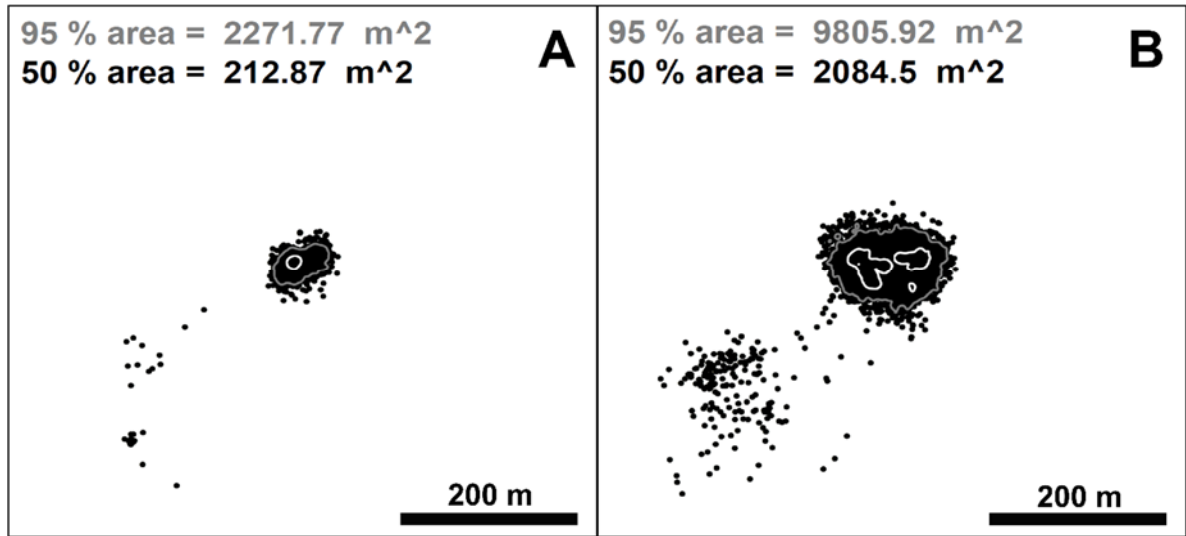


Figure 3-8: Red snapper, *Lutjanus campechanus*, home range (95% KDE) and core area (50% KDE) comparison between February and June for fish F47 from artificial reef site R2 in the northern Gulf of Mexico. Black dots = individual VPS calculated fish positions; gray line = home range (95% area); white = core area (50% area). Density plot = 3D perspective of the density of recorded positions within the VPS array (large peak = many points on VPS site).

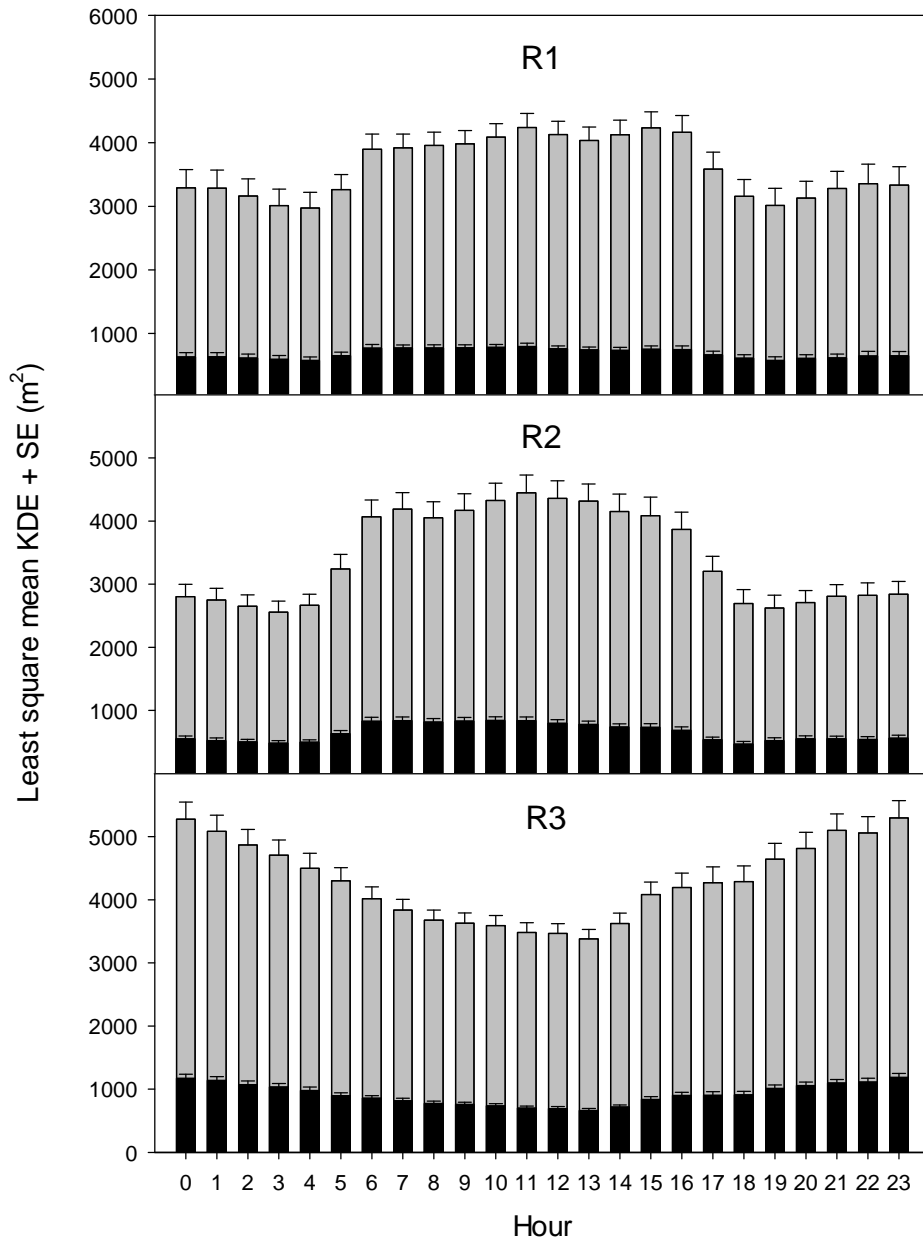


Figure 3-9: Mean hourly area use by red snapper, *Lutjanus campechanus*, on artificial reefs in the northern Gulf of Mexico. Hours begin at midnight (0 hour = 00:00 – 00:59 h) and continue for a 24-h period. Larger movements occurred during daytime hours on site R1 and R2 and night hours on R3. Home range (95% KDE) = gray bars and core area (50% KDE) = black bars.

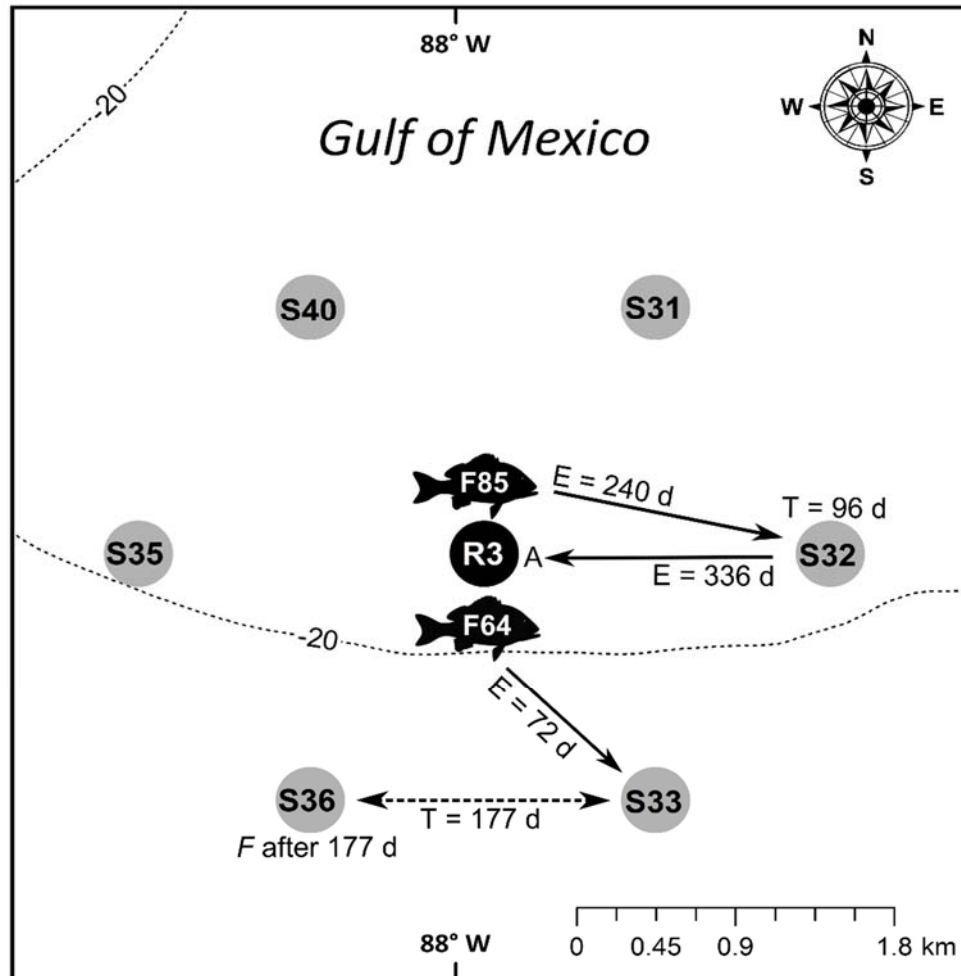


Figure 3-10: Larger (~ 1.5 km) movements made by red snapper, *Lutjanus campechanus*, from VPS artificial reef of release to surrounding reef site(s) in the northern Gulf of Mexico. Figure shows the movements of two fish (F64 and F85) from a VPS reef site R3 (black circle); gray circles = surrounding reef sites with a single VR2W receiver; E = day of emigration from site; T = number of days tracked on surrounding site(s); A = fish was active on the original release site at the end of the study; F = fishing mortality following days after emigration (total tracking time on VPS and surrounding site = E 72 d + T 177 d = 249 d).

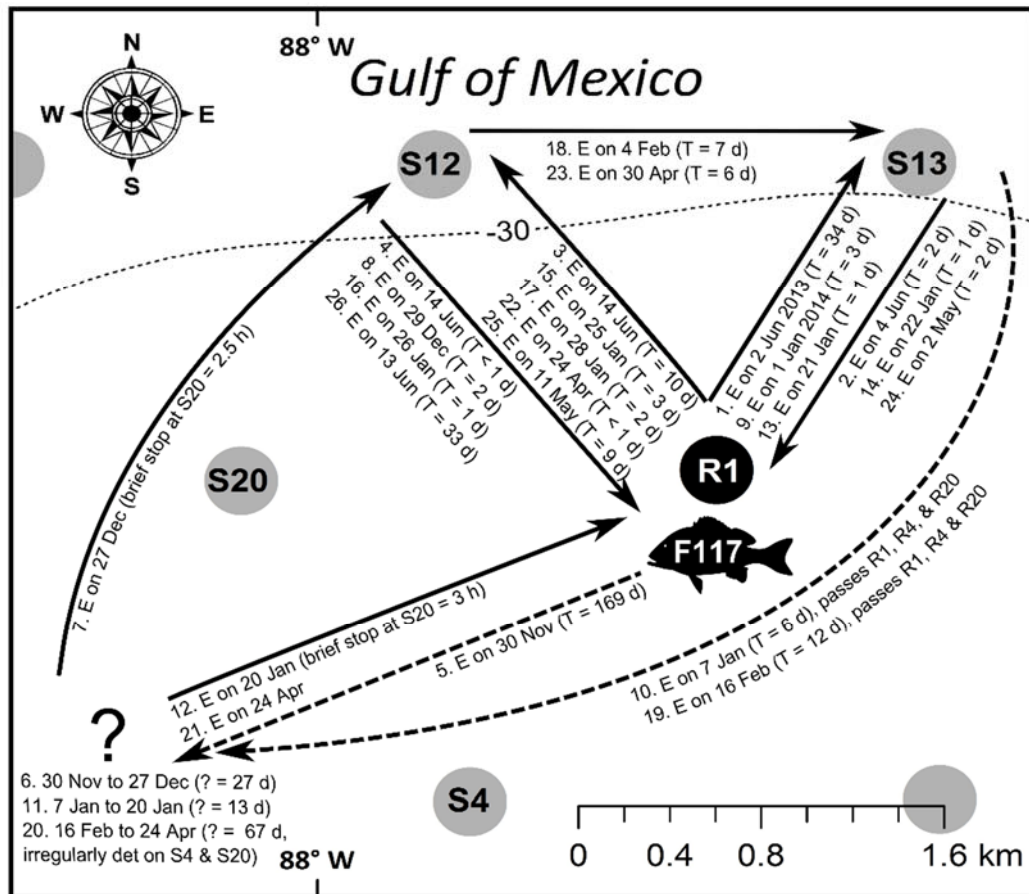


Figure 3-12: Movements of a transmitter-tagged red snapper (F117) from VPS release site to surrounding reef site(s) from 2 June 2013 to 31 October 2014 (end of study). Arrows with solid lines indicate movement directions and arrows with dashed lines indicate suspected movement (based on pattern of last detections). Movement numbers (1 to 26) are listed below each arrow. Black circle = VPS reef; gray circles = surrounding reef sites with a single VR2W receiver; ? = movement outside of receiver array; E = date of emigration from site; T = number of days tracked prior to emigration.

CHAPTER 4:
DEPTH PREFERENCES AND THREE-DIMENSIONAL MOVEMENTS OF
RED SNAPPER, *LUTJANUS CAMPECHANUS*, ON AN ARTIFICIAL REEF
IN THE NORTHERN GULF OF MEXICO

Abstract

Several studies have examined the horizontal or two-dimensional (2D) movements of red snapper, *Lutjanus campechanus*, but none have described the long-term depth preferences of this economically important fish species. Red snapper were tagged ($n = 11$) with depth transmitters on an artificial reef site 28 km south of Dauphin Island, Alabama in the northern Gulf of Mexico and movements were tracked for 2 years (VR2W Positioning System, Vemco Ltd, Nova Scotia). More than 3.5 million accurate positions (~ 1 m) were obtained and used to assess red snapper depth patterns over seasonal, monthly and hourly time periods. In addition, three-dimensional (3D) patterns of red snapper volume use (m^3) were determined based on depth and location (latitude, longitude) from $> 700,000$ 3D positions. Red snapper depth preferences and volume use varied over time periods. Diel depth patterns and volume use both showed that red snapper remained closer to the reef during night (1900 – 0400 h) compared to day (0600 – 1700 h; $F_{23, 3.5E6} = 3312$, $P < 0.0001$). Seasonal volume use patterns showed a significant positive correlation with water temperature with smaller volumes used during

the winter and larger volumes used during the fall (core 50% KDE, $F_{1,23} = 21.43$, $P < 0.0001$, $r^2 = 0.48$; home range 95% KDE, $F_{1,23} = 33.28$, $P < 0.0001$, $r^2 = 0.59$). Red snapper tended to stay at deeper depths during the winter months (< 3 m from seafloor), and move up in the water column more frequently in the late spring and summer months ($F_{3,3.5E6} = 340979$, $P < 0.0001$). These changing patterns were most likely related to spawning patterns and prey availability over both diel and seasonal time periods, but future research is needed to compare possible correlations. However, the present habitat use patterns were surprising, because for the most part red snapper was previously considered a demersal reef species, yet in the present study consistently used the entire water column.

Introduction

The determination of depth use patterns has mainly focused on highly mobile fish species of high economic value (*e.g.*, family Scombridae, Istiophoridae, Xiphiidae, Carcharhinidae, Lamnidae). In these species, long-term depth data has been used to describe movement patterns during large-scale migrations over various habitats (*e.g.*, Block et al. 1992; Holland et al. 1992; Brill et al. 1999; Lutcavage et al. 1999; Brill and Lutcavage 2001; Marcinek et al. 2001; Boustany et al. 2002; Block et al. 2005; Wilson et al. 2005; Teo et al. 2007; Weng et al. 2009; Stevens et al. 2010; Fenton et al. 2015). Depth data has also been used to describe short-term movements often related to specific events (*i.e.*, spawning, foraging, or nursery grounds) associated with unique behaviors

(*e.g.*, Josse et al. 1998; Goldman and Anderson 1999; Dewar et al. 2004; Seitz et al. 2005; Semmens et al. 2006; Starr et al. 2007; Witteveen et al. 2008; Whitney et al. 2010). For example, acoustic telemetry depth tags have been used to describe vertical foraging behaviors of humpback whales, *Megaptera novaeangliae*, off the coast of Alaska, USA (Witteveen et al. 2008) and vertical movement behaviors of spawning aggregations by Nassau grouper, *Epinephelus striatus* in the Caribbean (Semmens et al. 2006; Starr et al. 2007). In more recent years, the use of depth tags has expanded and used to show movement patterns of exploited species (*e.g.*, Erickson and Hightower 2007; Stevens et al. 2008; Currey et al. 2014), deep water species (*e.g.*, Starr et al. 2002; Hulbert et al. 2006; Andrews et al. 2009), and reef-associated species (*e.g.*, Luo et al. 2009; O'Toole et al. 2011; Bryars et al. 2012).

Most previous studies have analyzed depth patterns independently from location (latitude, longitude). Depth patterns were then compared to two-dimensional (2D) locations to make inferences about habitat use (Simpfendorfer et al. 2012). Few studies have examined three-dimensional (3D) patterns for fishes even though their environment is 3D. To date, the analysis of 3D movements has been examined in captive goldfish, *Carassius auratus* and zebrafish, *Danio rerio* (Zhu and Weng 2007; Maaswinkel et al. 2013), coastal habitat use of European eels, *Anguilla anguilla*, in Norway (Simpfendorfer et al. 2012), movement of barred sand bass, *Paralabrax nebulifer*, and spawning season in California (McKinzie et al. 2014), and long-term movement patterns of grey reef sharks, *Carcharhinus amblyrhynchos*, to environmental conditions on the Great Barrier Reef (Heupel and Simpfendorfer 2014; Heupel and Simpfendorfer 2015).

Red snapper have been extensively studied due to their broad distribution in both shallow and deeper waters (~ 10 – 350 m), close association to reef structures (artificial and natural), and economic importance to both commercial and recreational fisheries (Gallaway et al. 2009; Dance et al. 2011; SEDAR31 2013). Tagging studies have used both conventional and transmitter tags to determine the horizontal movements of red snapper (*e.g.*, Szedlmayer 1997; Patterson et al. 2001; Szedlmayer and Schroepfer 2005; Addis et al. 2007; Diamond et al. 2007; Strelcheck et al. 2007; Topping and Szedlmayer 2011b; Piraino and Szedlmayer 2014). For the most part these studies have shown high residency and site fidelity to artificial reef structure. More recently telemetry studies have examined fine-scale (m accuracy, Vemco VPS) 2D movements of red snapper around artificial reefs (Piraino and Szedlmayer 2014; Williams and Szedlmayer In prep). These fine-scale movement studies showed that red snapper made smaller movements during dusk and dawn hours and larger movements during months with warmer water temperatures (Piraino and Szedlmayer 2014; Williams and Szedlmayer In prep), but little is known regarding the vertical movement or water column use patterns of red snapper. The objectives of the present study were to evaluate long-term (two year) red snapper vertical movement patterns and 3D volume use patterns over seasonal and diel time periods.

Methods

Study Site

The present study site was a steel cage artificial reef (n =1; 2.5 x 1.3 x 2.4 m), at 28 m depth, located 28 km south of Dauphin Island, Alabama, USA in the northern Gulf

of Mexico (Figure 4-1). A Vemco VPS array was deployed at the reef site that included a central VR2W receiver located 20 m north of the reef and four surrounding receivers located 300 m to the north, south, east, and west of the central receiver (reef site). This receiver array design permitted maximum (100%) detection of transmitter tagged red snapper (Piraino and Szedlmayer 2014). Receivers were positioned ~ 4.5 m above the seafloor and synchronization transmitters were attached 1 m above each receiver (Vemco V16-6x; 69 kHz; transmission delay: 540 – 720 sec). A stationary control transmitter was positioned at a known location within the VPS array to validate the accuracy of Vemco calculated fish positions (Vemco Ltd, Nova Scotia). Additional steel cage artificial reefs were positioned 1.4 – 1.6 km away from the VPS reef. These surrounding reef sites (n = 25) had a single VR2W receiver to verify emigrations from the VPS array (Figure 4-1). Receivers (VPS) were exchanged every three months and surrounding receivers were exchanged every six months by SCUBA divers and were downloaded in the laboratory.

Fish Tagging and Release Procedures

Red snapper were tagged and released on 17 October and 2 November 2012 (n = 10) and 17 October 2013 (n = 1) and VPS positions determined up to 31 October 2014 (Table 4-1). All tagged red snapper were larger than the recreational minimum length limits (> 406 mm TL; SEDAR31 2013). Dissolved oxygen (DO) and temperature were measured at depth prior to fish release (YSI model 6920, YSI Inc., Yellow Springs, Ohio). Tagged fish were only released if DO was > 2.5 mg/L at depth, to minimize additional stress from reduced DO.

Fish tagging methods followed Topping and Szedlmayer (2011a; 2011b; 2013). We caught red snapper by hook-and-line (8/0 circle hook baited with Gulf menhaden, *Brevoortia patronus*). Fish were immediately anesthetized (~ 2 min) with MS-222 (150 mg tricaine methanesulfonate/L seawater) in a seawater tank (70 L) onboard the research vessel. Anesthetized red snapper were weighed (kg) and measured (mm SL, FL, TL). Individually coded depth transmitters (Vemco V16P-6x-R64k, transmission delays = 20 – 69 sec) were inserted into the peritoneal cavity of the red snapper through a small vertical incision (20 mm). The incision site was closed with absorbable, sterile, plain gut surgical sutures (Ethicon 2-0, metric 3). Red snapper were also tagged with anchor tags (Floy[®]) with unique identification numbers for external identification by SCUBA divers and fishers. Post-surgery tagged red snapper were held in a recovery tank (185 L) until regular opercula and fin movements were observed before release (< 5 min).

In late October 2012 transmitter tagged fish (n = 4) were returned to depth in a closed wire mesh cage (height = 40.6 cm, diameter = 60 cm; Piraino and Szedlmayer 2014) within 10 m of their capture site. After ≥ 1 h SCUBA divers visually inspected these fish at depth and released fish in good condition (*i.e.*, regular opercula movements, upright and capable of swimming). During the SCUBA release large (≥ 2 m) sandbar shark *Carcharhinus plumbeus* and bull shark *C. leucas* displayed aggressive behaviors towards divers and diver releases were discontinued due to safety considerations.

In November 2012 (n = 6) and October 2013 (n = 1) red snapper were released using a remotely opening cage (46 x 61 x 61cm; Williams et al. 2015). Recovered fish were placed into the cage at the surface and fish condition was observed for 10 – 20 sec at ~ 1 m depth. Red snapper in good condition were lowered to the seafloor (28 m)

where the cage door automatically opened and the recovered fish left on their own initiative (Williams et al. 2015). Cages were retrieved after ≥ 15 min and if a tagged fish had not left the cage on its own initiative it was considered in poor condition and not released.

Environmental Parameter Monitoring

For the duration of the study, two temperature loggers (Onset HOBO[®] U22 Water Temp Pro v2) were attached on the central receiver line at the VPS reef site. One temperature logger was attached slightly above the receiver and the second logger was attached at the seafloor. Temperature loggers recorded the water temperature (°C) at one-hour intervals and were downloaded every three months.

Residency Analysis

Red snapper positions were calculated by Vemco based on time differential of signal arrival at three or more receivers. Fish positions were used to categorize the status of tagged fish as active, emigrated, or deceased within the VPS array area. Active fish made continuous movements around the reef, emigrated fish made progressive movements away from the reef center before exiting the VPS array, and deceased fish became stationary (natural mortality) or were suddenly absent near the reef (fishing mortality; Williams and Szedlmayer In review). Residence and mortality were calculated with a known fate model in the “MARK” program (Topping and Szedlmayer 2013; Williams and Szedlmayer In prep).

Depth Preferences

Depth data was exported from Vue software (Vemco Ltd., Nova Scotia) and statistical analyses were completed with SAS statistical software (SAS Institute Inc., Cary, NC, USA). All depth analyses used Central Standard Time (CST). Depth preferences were evaluated over seasonal, monthly and diel time periods. The effect of time period on depth use was tested with a one-way, mixed-model repeated measures analysis of variance (rmANOVA) with fish as a random factor and time period as a repeated measure (Zar 2010). We reported depth positions as mean \pm standard deviation (SD). Sea floor depth was assumed to be uniform (28 m) throughout the receiver array.

3D Kernel Density Estimations

All horizontal positions (latitude and longitude) were converted to Universal Transverse Mercator projection (m) for comparison to depths (m). Red snapper VPS locations were used to estimate core volumes or 50% kernel density estimates (KDE) and home ranges or 95% KDE (Piraino and Szedlmayer 2014). For example, red snapper were located 50% of the time within the core volume. Three-dimensional (3D) KDEs or 3D activity space were calculated in the R statistical environment with the “ks” package (Duong 2007; Simpfendorfer et al. 2012; RCoreTeam 2014). The effects of season, month, and diel time periods on volume use were tested with a one-way, mixed-model repeated measures analysis of variance (rmANOVA; SAS statistical software) with fish as a random factor and time period as a repeated measure (Zar 2010). If significant differences were detected with the rmANOVA, a Tukey-Kramer test was applied to show specific differences in volume use over time intervals.

Results

Tagging and Residency

Depth and 3D fine-scale movements of red snapper were recorded for up to two years (November 2012 to October 2014). Sizes of tagged fish ranged from 489 to 702 mm TL (595 mm \pm 69 mm; mean TL \pm SD). A total of 11 red snapper were released with depth transmitters. After release, four fish left within a two-day tagging recovery period and seven fish were tracked for extended periods of time (379 – 729 d). All seven fish that remained after the two-day recovery period stayed on the reef site for the duration of the study. Thus, residency time exceeded the duration of the study, *i.e.*, no fish emigrated after they were tagged, and site fidelity was 100% for one-year periods (Table 4-1). In addition, no fishing or natural mortalities were observed for these tagged red snapper (total survival $S = 1.0$ and total instantaneous mortality $Z = 0.0$) during this study, however, three fishing mortalities were reported from 2 to 8 July in 2015 after tracking ended (31 October 2014).

Additional movements were observed for the three fish that left the VPS site during the 2-d tagging recovery period. Fish F71 emigrated 1.5 km away to a surrounding artificial reef site with a single receiver on the day of tagging (2 November 2012). This fish remained at this second site for 599 d until 24 June 2014 then was lost. Fish F75 emigrated from the VPS site one day after tagging (3 November 2012), was detected on 9 November 2013 at a surrounding reef site 1.5 km away, and remained at the second reef site for 204 d until a fisher recapture in June 2013. Fish F73 moved south of the VPS receiver array on the day of tagging (2 November 2012) and was intermittingly detected by only the south receiver for the duration of the study (no detections on other

receivers). Fish F73 continued to produce depth tag data (> 40,000 detections) on the south receiver that showed changing depths, verifying its survival outside the receiver array.

Depth Preferences

Over 3.5 million depth positions were collected from the seven tracked red snapper (~ 500,000 positions per fish) over the two-year study period. Mean \pm SD depth was 21.8 m \pm 6.0 m and fish used the entire water column from the seafloor (28 m) to the water surface (0 m). No significant correlation was observed between fish total length and depth used ($F_{1,6} = 1.97$, $P = 0.23$, $r^2 = 0.33$).

Red snapper depth use significantly varied by season ($F_{3,3.5E6} = 340979$, $P < 0.0001$). The greatest depth was recorded during the winter season (December – February; mean \pm SD depth = 25.9 m \pm 3.0 m). Fish were higher in the water column in the spring (March – May; 23.0 m \pm 5.8 m) and fall (September – November; 22.6 m \pm 4.8 m), and were highest in the water column during the summer (June – August; 18.3 m \pm 5.9 m; Figure 4-2). Similarly, mean depths used by red snapper were significantly different for all months ($F_{11,3.5E6} = 140033$, $P < 0.0001$). Monthly mean depths were greatest in the winter months (February 2013 = 27.5 m \pm 2.2 m and 2014 = 25.1 m \pm 3.0 m), and shallowest in spring (May 2013 = 17.5 m \pm 8.4 m) and summer months (July 2014 = 14.1 m \pm 5.5 m). Red snapper mean monthly depth use was positively correlated with water temperature ($F_{1,23} = 4.53$, $P = 0.04$, $r^2 = 0.17$; Figure 4-3). Red snapper showed significant differences in diel depth patterns and used deeper depths at night

(2100 – 0200 h) compared to day periods (0900 – 1300 h; $F_{23, 3.5E6} = 3312$, $P < 0.0001$; Figure 4-4).

3D Kernel Density Estimations

The present study recorded > 700,000 red snapper positions (latitude, longitude, and depth) to evaluate fine-scale 3D movements. A control transmitter showed a mean horizontal (latitude and longitude) accuracy of $2.4 \text{ m} \pm 1.5 \text{ m}$ (mean \pm SD) and vertical (depth) position accuracy $< 1 \text{ m}$. No significant correlation was observed between fish total length and core volume m^3 (50% KDE; $F_{1, 6} = 0.08$, $P = 0.79$, $r^2 = 0.02$) or home range volume (95% KDE; $F_{1, 6} = 0.89$, $P = 0.39$, $r^2 = 0.15$).

Red snapper 3D movement patterns varied significantly by season and month. Seasonal core volumes (50% KDE) significantly changed from the smallest volume in the winter (mean \pm SE = $2404 \text{ m}^3 \pm 391 \text{ m}^3$) to largest volumes in the fall ($19705 \text{ m}^3 \pm 2541 \text{ m}^3$; $F_{3, 160} = 19.2$, $P < 0.0001$), and home range volumes (95% KDE) significantly changed from the smallest volume in winter ($33972 \text{ m}^3 \pm 5049 \text{ m}^3$) to the largest volume in the fall ($207442 \text{ m}^3 \pm 18920 \text{ m}^3$; $F_{3, 160} = 38.8$, $P < 0.0001$; Figure 4-5). Similarly, significant differences in monthly core volumes ($F_{11, 1998} = 86.0$, $P < 0.0001$) and home range volumes ($F_{11, 1998} = 44.56$, $P < 0.0001$) were observed (Figure 4-6 to 4-10). For both years, February showed the smallest monthly core volume (2013 = $253 \text{ m}^3 \pm 66 \text{ m}^3$; 2014 = $251 \text{ m}^3 \pm 282 \text{ m}^3$) and home range volume (2013 = $4664 \text{ m}^3 \pm 522 \text{ m}^3$; 2014 = $16890 \text{ m}^3 \pm 1620 \text{ m}^3$; Figure 4-10). The largest core and home range volumes were observed in August 2013 (core = $35679 \text{ m}^3 \pm 11311 \text{ m}^3$; home range = $271468 \text{ m}^3 \pm 56523 \text{ m}^3$; Figure 4-9) and October 2014 (core = $43866 \text{ m}^3 \pm 8799 \text{ m}^3$; home range =

354332 m³ ± 48822 m³). Temperature was positively correlated to monthly core volume ($F_{1,23} = 21.43, P < 0.0001, r^2 = 0.48$) and home range volume ($F_{1,23} = 33.28, P < 0.0001, r^2 = 0.59$).

Significant diel changes were detected in red snapper 3D pattern use (core volume $F_{23,1722} = 8.64, P < 0.0001$; home range volume $F_{23,1722} = 10.65, P < 0.0001$; Figure 4-11). Red snapper made smaller movements during the night (1700 – 0500 h) and larger movements during the day (0600 – 1600 h). The smallest core and home range volumes occurred near dawn (0300 – 0400 h) and dusk (1900 h), while the largest core and home range volumes occurred in the late morning (1000 h) and early afternoon (1300 – 1500 h).

Discussion

Seasonal Vertical Movement Patterns

Due to recent advances in technology, the present study was able to determine red snapper depth patterns over long time periods (2 years). Red snapper moved higher in the water column in summer months, used intermediate depths during spring and fall, and moved closest to the bottom during the winter months (Figure 4-2). Core and home range volumes showed similar patterns with red snapper using larger volumes in summer and fall, and smaller volumes in winter and spring (Figure 4-5 to 4-9). Two previous studies also showed reduced area use (2D) by red snapper in winter (Piraino and Szedlmayer 2014).

Few studies have examined the 3D movements of fish species. Similar to the present study, European eels, *Anguilla anguilla*, from Norwegian coastal waters showed

reduced 3D movements in winter and greater movements in summer (Simpfendorfer et al. 2012). In contrast, no clear patterns were detected in redthroat emperor, *Lethrinus miniatus*, on Australian coral reefs (Currey et al. 2014). Other studies also did not detect clear temporal patterns but did show a correlation of increased 3D KDE with spawning activities (Heupel and Simpfendorfer 2014; McKinzie et al. 2014). In the present study, larger volumes were observed during the red snapper spawning season (April to October; Collins et al. 2001) and increased monthly 3D movements were correlated with water temperature. Most likely greater volume use in warmer months and reduced volume use in cooler months were driven by red snapper metabolic rates and foraging behaviors (Hidalgo et al. 1987) or spawning activity.

In the present study, red snapper used smallest volumes (core and home range) and stayed closer to the bottom in February (2013 and 2014) when water temperatures were lower. In contrast, the greatest monthly volume use (August 2013 and October 2014) occurred when water temperatures were warmest (fall months). However, fish used more of the water column (shallower depths) in late spring and summer (May 2013 and July 2014) before water temperatures peaked. In addition, during warmer months, shallower depths and greater variation in vertical movements were observed compared to colder months (Figure 4-3).

There are several possible factors that could contribute to the observed vertical movement patterns. For example, in the northern Gulf of Mexico, red snapper spawning peaks from May to July (Woods et al. 2003). In the present study, the shallowest monthly depth use corresponded with the peak spawning season period (May 2013 and June 2014). Spawning behaviors in some Lutjanidae have been observed and in those

species (lane snapper, *Lutjanus synagris*, dog snapper, *L. jocu*, and cubera snapper, *L. cyanopterus*) rapid vertical ascents (2 – 40 m) were made followed by the release of gametes higher in the water column (in some cases < 10 m from the surface; Wicklund 1969; Carter and Perrine 1994; Heyman et al. 2005). At present, red snapper spawning behaviors have not been reported, but SCUBA divers have observed red snapper making vertical ascents during spawning (unpublished data Szedlmayer, S.T.).

Sport fishing activity is another factor that may contribute to vertical red snapper movement patterns. Marine sport fishing is economically important in the northern Gulf of Mexico and within the past 50 years additions of many artificial reefs in this region has led to the establishment of a large red snapper fishery off the coast of Alabama (Shipp 1999; Adams et al. 2004; Shipp and Bortone 2009). Fishing activity off the coast of Alabama substantially increases during the summer months during open sport fish seasons and as fishing boats move over reef habitat, red snapper tend to rise up from the bottom attracted by the vessel activity (unpublished data Szedlmayer, S.T.).

Another potentially important factor that could contribute to red snapper vertical movements is dissolved oxygen (Rabalais 1992; Chesney et al. 2000). Seasonal (summer) hypoxia has been observed off coastal Alabama, and fish either leave horizontally or vertically during such events (Vinyard and O'Brien 1976; Kramer 1987; Chesney et al. 2000; Huenemann et al. 2012; Szedlmayer and Mudrak 2014). In fall 2012 (25 September 2012), we measured very low dissolved oxygen (< 1 mg/L) at depth on our VPS reef site. SCUBA divers visually inspected the reef site and observed no fish around the reef structure, however, many red snapper were observed higher in the water column (> 10 m above the seafloor) above the reef structure. Whether or not DO

concentrations regularly contribute to red snapper vertical movement patterns will need further study.

Diel Movement Patterns

Red snapper showed significantly different depth and volume use between night and day hours. Red snapper were closer to the bottom at night (1900 – 0400 h) and core and home range volume use were smaller at night (1700 – 0500 h). In contrast, fish moved up in the water column and volume use was greater during the day (0600 – 1600 h). Few studies have examined red snapper diel depth patterns. In one study to date, hourly depth use for red snapper around oil platforms off the coast of Louisiana in the northern Gulf of Mexico was examined and no differences in diel depth patterns were detected (McDonough 2009). The lack of a diel movement pattern could be due to the limited sampling period (four weeks) or due to artificial lighting common on oil platforms during the night hours, which has been shown to alter the behaviors of marine bird and fish species (Wiese et al. 2001; Longcore and Rich 2004; Keenan et al. 2007). For example, light levels adequately enhanced foraging during the night hours allowing fishes to readily locate and capture prey (Keenan et al. 2007). In the present study, we assessed hourly movements of red snapper on an artificial reef type that did not have artificial lighting and red snapper were significantly deeper during night hours.

Earlier 2D telemetry studies (manual and remote tracking) reported that red snapper moved farther away from reefs during night hours. These studies suggested that these movements were driven by foraging behaviors allowing red snapper to access additional prey sources during night hours (Peabody 2004; Szedlmayer and Schroepfer

2005; McDonough and Cowan 2007; Topping and Szedlmayer 2011a; 2011b). In contrast, the first VPS tracking study showed that red snapper had significantly smaller 2D area use during night hours and made larger movements during day hours (Piraino and Szedlmayer 2014). Hourly 3D movement patterns (m^3) in the present study were similar to the previous 2D fine-scale movements (m^2) that showed greater areas in the day (Piraino and Szedlmayer 2014). The use of shallower waters and greater volume (m^3) during the day suggests that red snapper largely rely on their vision for activities such as foraging or escaping predation. Laboratory studies have suggested that red snapper are a visual species. Parsons et al. (2012) assessed the ability of juvenile red snapper to exit a test chamber in the laboratory, and a bycatch reduction device attached to a shrimp trawl in the field. In both cases, red snapper more frequently made the appropriate escape movements in the presence of illumination. The use of deeper depths and smaller volume during the night has also been observed in other common reef-associated fish species. For example, western blue groper, *Achoerodus gouldii*, tagged with depth transmitters showed clear diurnal movement and depth patterns. During night hours western blue groper moved to deeper waters and remained relatively stationary suggesting that this species may seek refuge in caves and crevices (Bryars et al. 2012). Similarly, short-term tracks of white trevally, *Pseudocaranx dentex*, tagged with depth transmitters showed that this species remained close to the substrate during night and during dawn and dusk periods (Afonso et al. 2009).

In the present study, fish stayed closer to the bottom at night from 1900 to 0600 h the next day. The smallest movements (m^3) were also observed just before dawn (0300 – 0400 h) and at dusk (1900 h). Similar crepuscular patterns were reported for red snapper

in an earlier telemetry study (Piraino and Szedlmayer 2014). As previously suggested the movements of red snapper during the crepuscular periods resemble prey-like behaviors. Several studies have shown that prey species reduce movements, whereas apex predators increase foraging during crepuscular periods (Hobson 1972; Hobson 1975; Helfman 1986). For example, reef-associated apex predators tagged with depth transmitters, such as Caribbean reef shark, *Carcharhinus perezi*, and whitetip reef shark, *Triaenodon obesus*, showed increased movements and shallower depth use during night hours (Chapman et al. 2007; Whitney et al. 2007; Fitzpatrick et al. 2011). In the northern Gulf of Mexico there are several larger shark species that are potential predators on red snapper and common in our study area (10 – 40 m depth), for example, blacktip shark, *Carcharhinus limbatus*, bull shark, *C. leucas*, sandbar shark, *C. plumbeus*, spinner shark, *C. brevipinna*, scalloped hammerhead, *Sphyrna lewini*, and tiger shark, *Galeocerdo cuvier* (Drymon et al. 2010).

Additional Comments

Simpfendorfer et al. (2012) and Zhu and Weng (2007) were the first to evaluate 3D fish movements in detail. These studies suggested that an advantage to assessing 3D movements was the ability to separate fish that vertically differed that might otherwise be considered in the same habitat based on 2D comparisons. However, in the present study we observed 3D volumes that were similar to previous 2D estimates (Piraino and Szedlmayer 2014). These similarities were most likely due to many similarities between the studies, including the same reef type (small, isolated artificial reef), similar size classes and same geographical locations of red snapper.

Conclusions

This study provided the first detailed depth patterns and 3D movements for red snapper showing that this previously considered demersal reef species consistently used the entire water column. Over two years we evaluated over 3.5 million depth positions and 700,000 3D fish positions. The 3D volume use was significantly correlated with temperature and increased 3D movements in the fall were likely linked to elevated metabolism and foraging during those months. Depth patterns showed the use of significantly shallower waters during the summer months and deeper waters during the winter months. Future research is needed to better define the driving functions that cause changes in seasonal and diel water column use by red snapper. In addition, the further use of depth tags on different size classes of red snapper could provide improved understanding of changing habitat preferences for this long-lived species.

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Table 4-1: Red snapper, *Lutjanus campechanus*, that were tagged with depth transmitters on an artificial reef in the northern Gulf of Mexico. Lost fish (n = 4) left the VPS array within 2-d of release, subsequently seven fish were actively tracked for extended time periods. All seven fish were still active after the last month of tracking (October 2014).

Fish ID	TL (mm)	Weight (kg)	Date Tagged	Days VPS Tracked	VPS Status	Surrounding Site	Distance (km)	Days Tracked	Surrounding Site Status
F65	566	2.6	17 October 2012	744	Active				
F66	563	2.1	17 October 2012	744	Active				
F67	612	3.3	17 October 2012	744	Active				
F69	594	2.8	17 October 2012	744	Active				
F70	497	1.6	2 November 2012	1	Lost	No			
F71	702	5.2	2 November 2012	0	Lost	Yes	1.5	592	Emigrated
F72	576	2.4	2 November 2012	729	Active				
F73	693	4.2	2 November 2012	0	Lost	No			
F74	657	4.0	2 November 2012	729	Active				
F75	595	3.0	2 November 2012	1	Lost	Yes	1.5	202	Caught
F135	489	1.7	17 October 2013	379	Active				

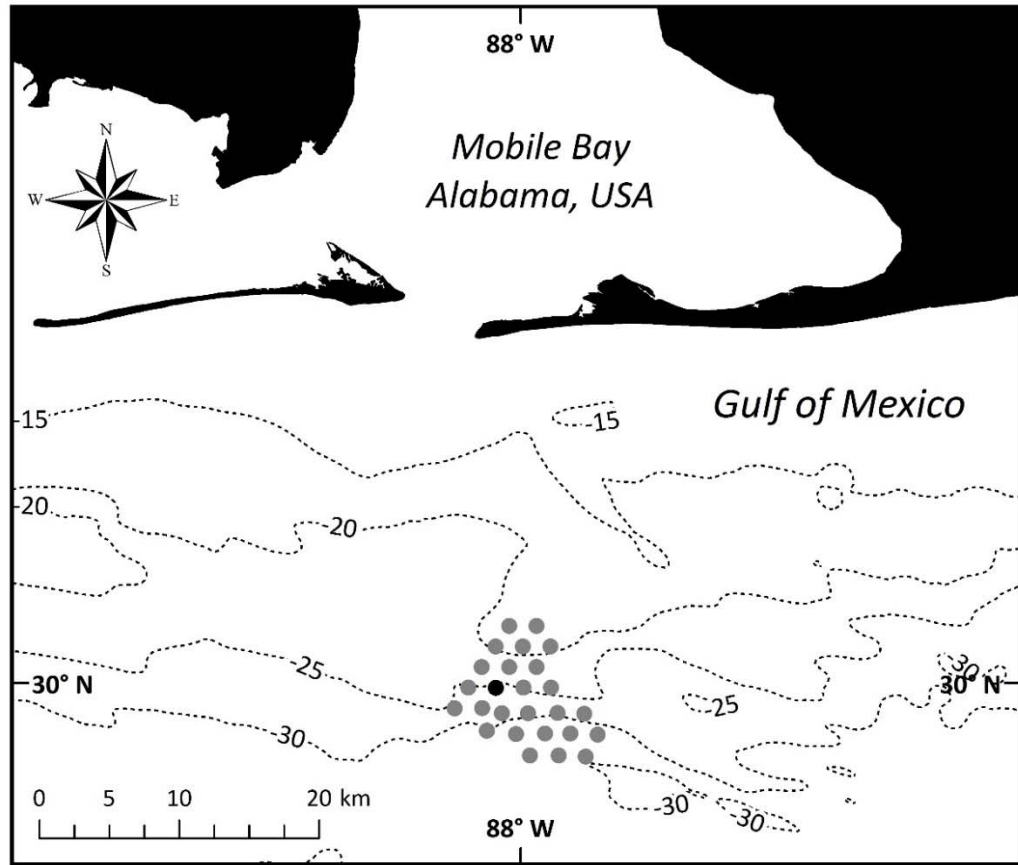


Figure 4-1: Steel cage artificial reef locations in the northern Gulf of Mexico. Black circle (n = 1) is the Vemco VPS reef site tracking the 3D movements of red snapper, *Lutjanus campechanus*. Gray circles (n = 25) are other sites with single VR2W receivers that detected emigrated fish that left the VPS array during the 2-day tagging recovery period.

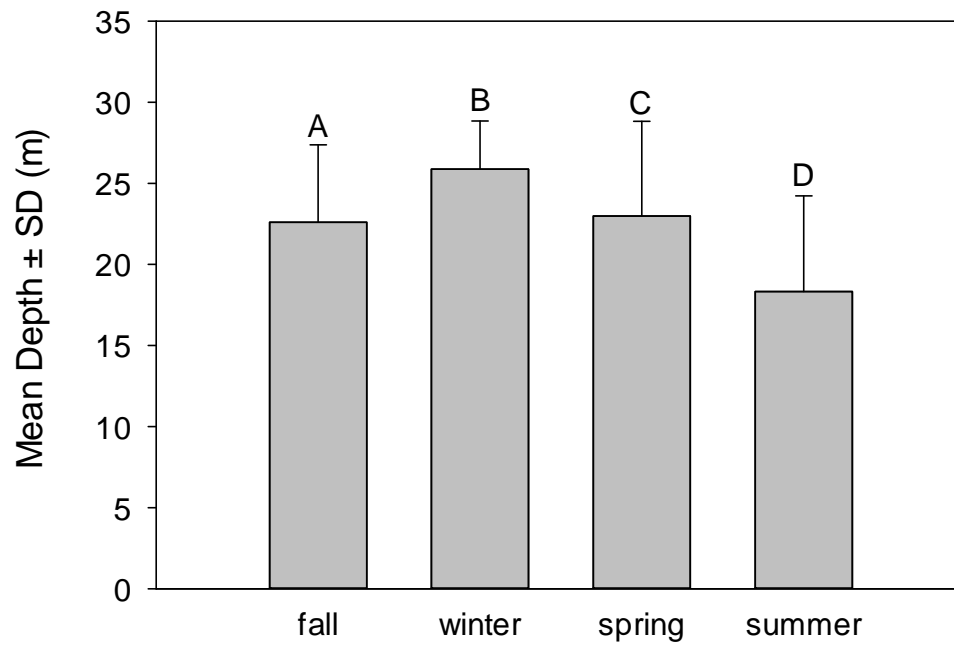


Figure 4-2: Seasonal differences in depth used by tagged red snapper, *Lutjanus campechanus*, on an artificial reef in the northern Gulf of Mexico. Different letters denote significant differences.

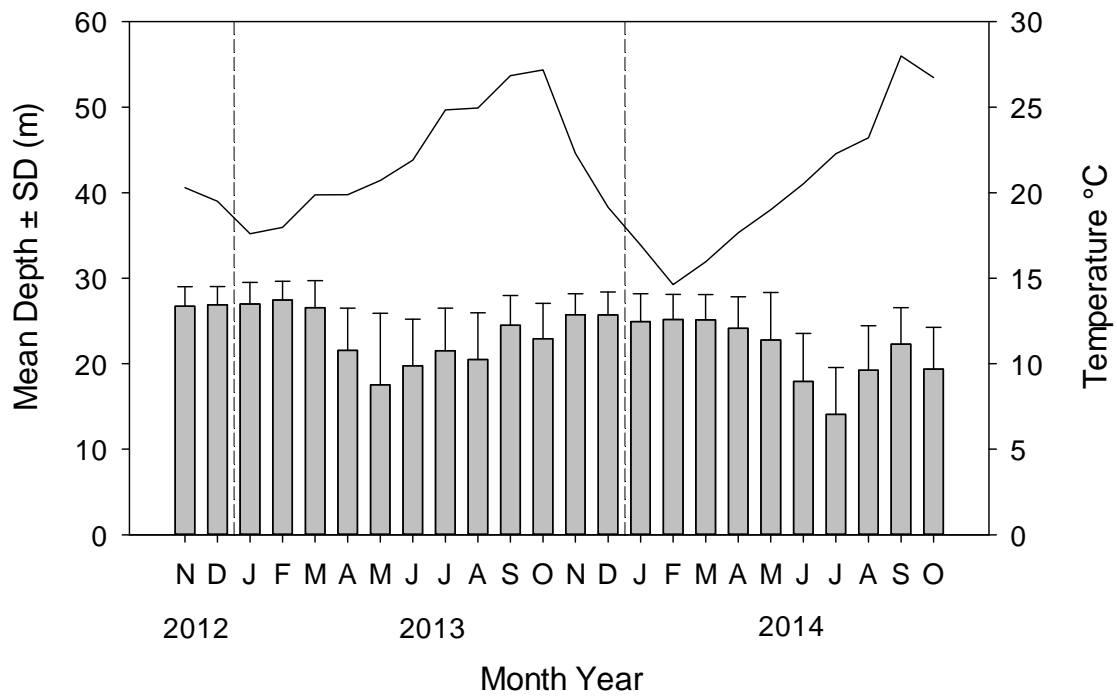


Figure 4-3: Temperature and mean monthly depth used by red snapper, *Lutjanus campechanus*, in the northern Gulf of Mexico from November 2012 to October 2014.

Primary axis: Gray bars = depth and SD. Line = water temperature at depth.

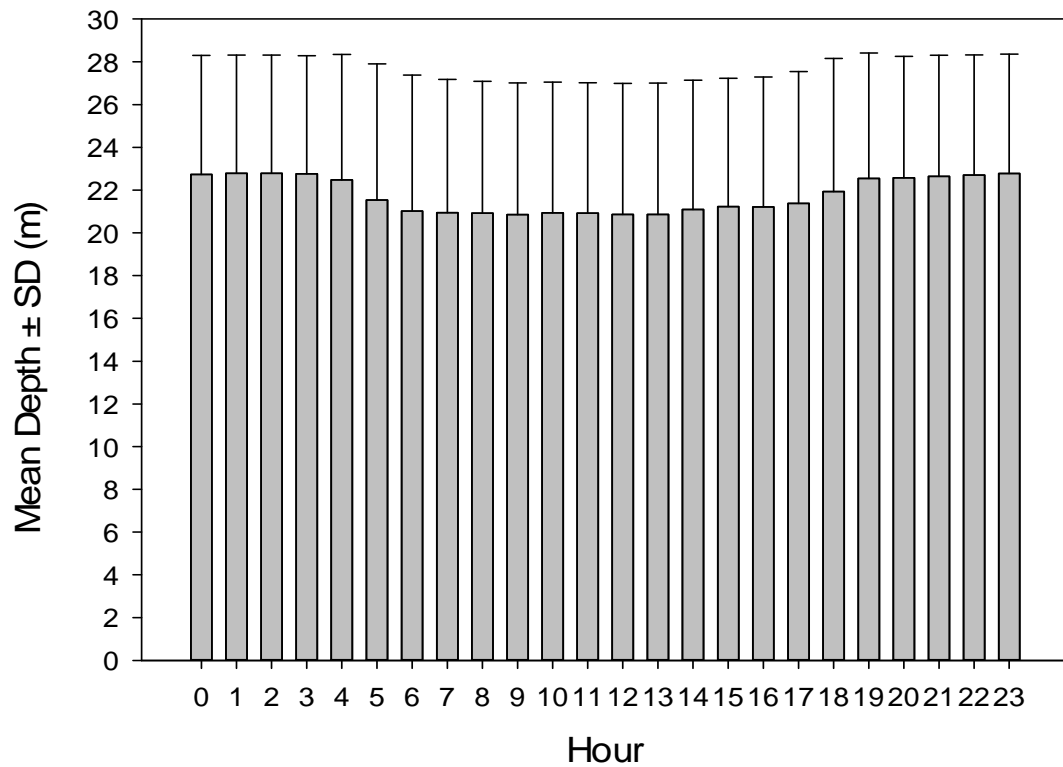


Figure 4-4: Diel depth use (mean \pm SD hour) by red snapper, *Lutjanus campechanus*, on an artificial reef in the northern Gulf of Mexico. Hours begin at midnight (0 hour = 00:00 – 00:59 h) and continue for a 24-h period. Fish stayed closer to the bottom at night (1900 to 0400).

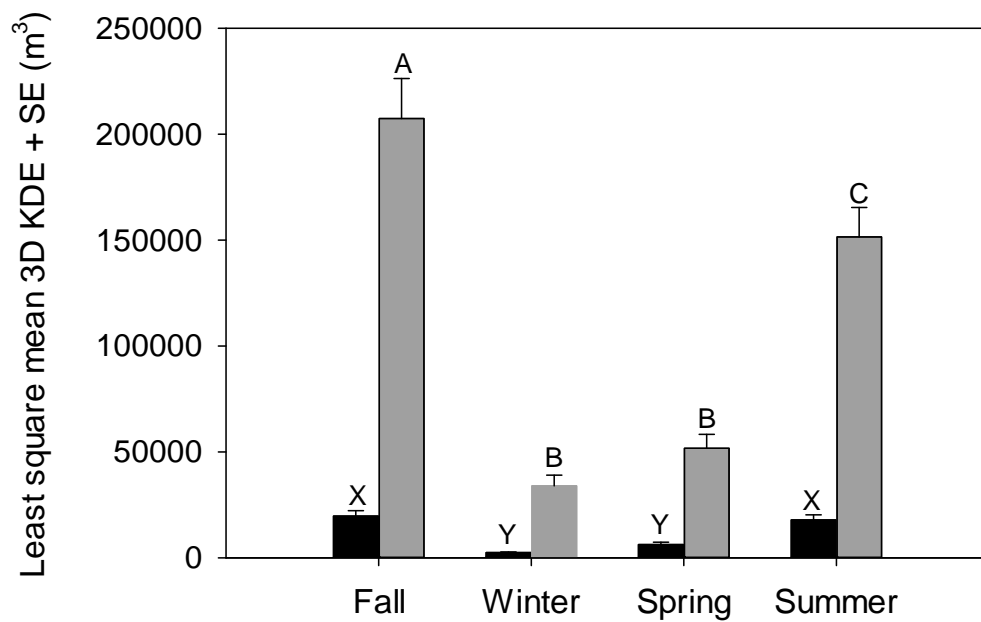


Figure 4-5: Seasonal patterns in 3D volume use (m³) for tagged red snapper, *Lutjanus campechanus*, around an artificial reef in the northern Gulf of Mexico. Black bars = core volume (50% KDE), gray bars = home range volume (95% KDE), error bars = SE, and different letters denote significant differences ($p \leq 0.05$).

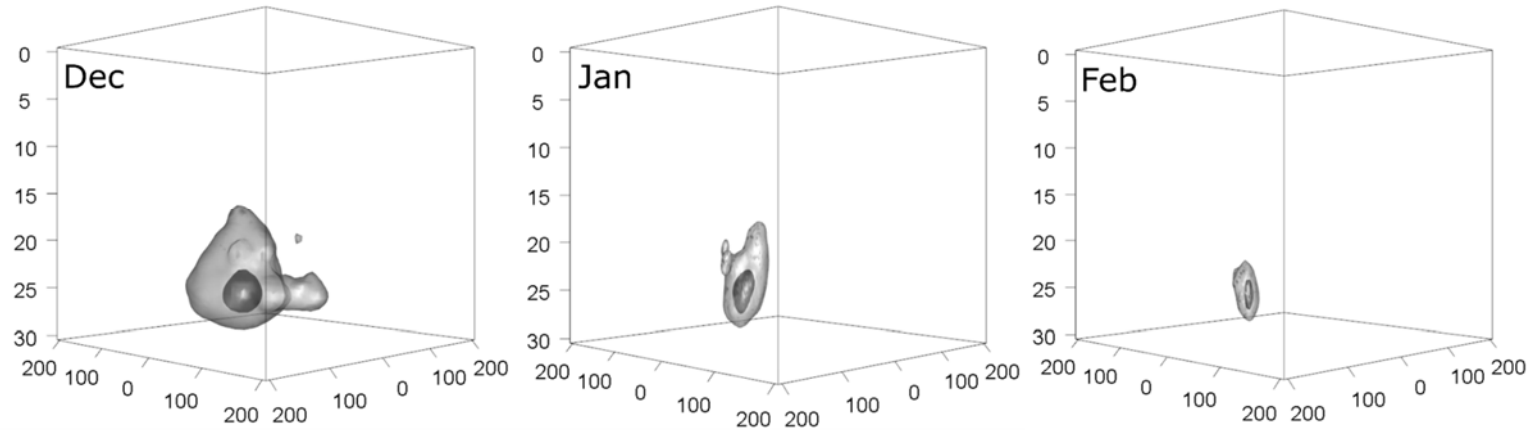


Figure 4-6: Three-dimensional volume (m^3) use for an individual tagged red snapper (F72) around an artificial reef during winter months in 2013. Core volume (50% KDE) = dark gray; home range volume (95% KDE) = light gray; horizontal position (latitude and longitude) = range of 400 m (0 m at reef to 200 m away); and vertical position (depth) = 0 – 30 m.

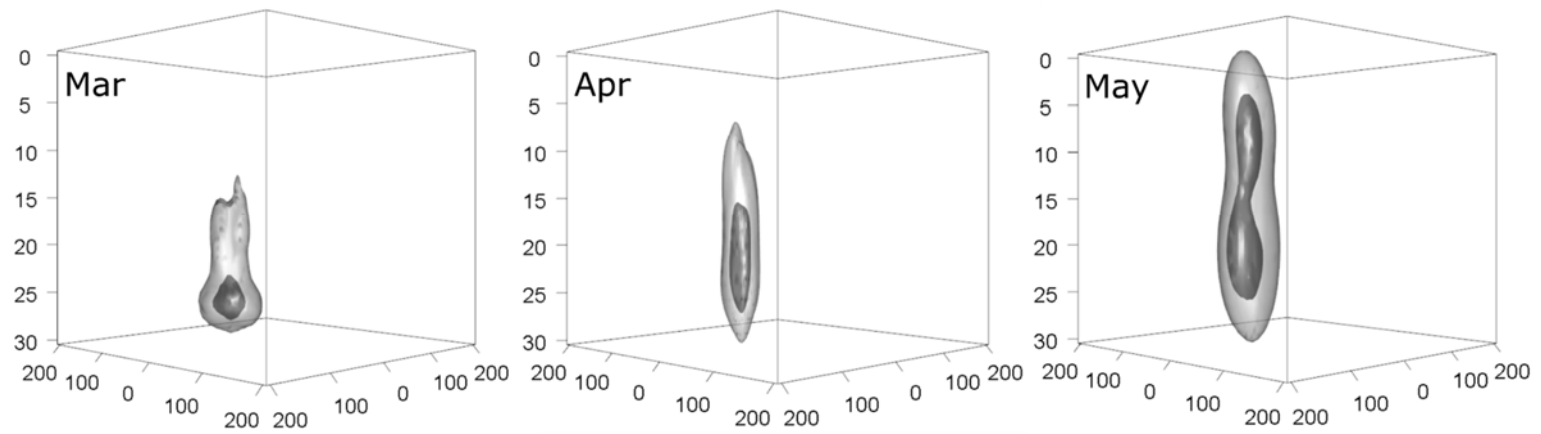


Figure 4-7: Three-dimensional volume (m^3) use for an individual tagged red snapper (F72) around an artificial reef during spring months in 2013. Core volume (50% KDE) = dark gray; home range volume (95% KDE) = light gray; horizontal position (latitude and longitude) = range of 400 m (0 m at reef to 200 m away); and vertical position (depth) = 0 – 30 m.

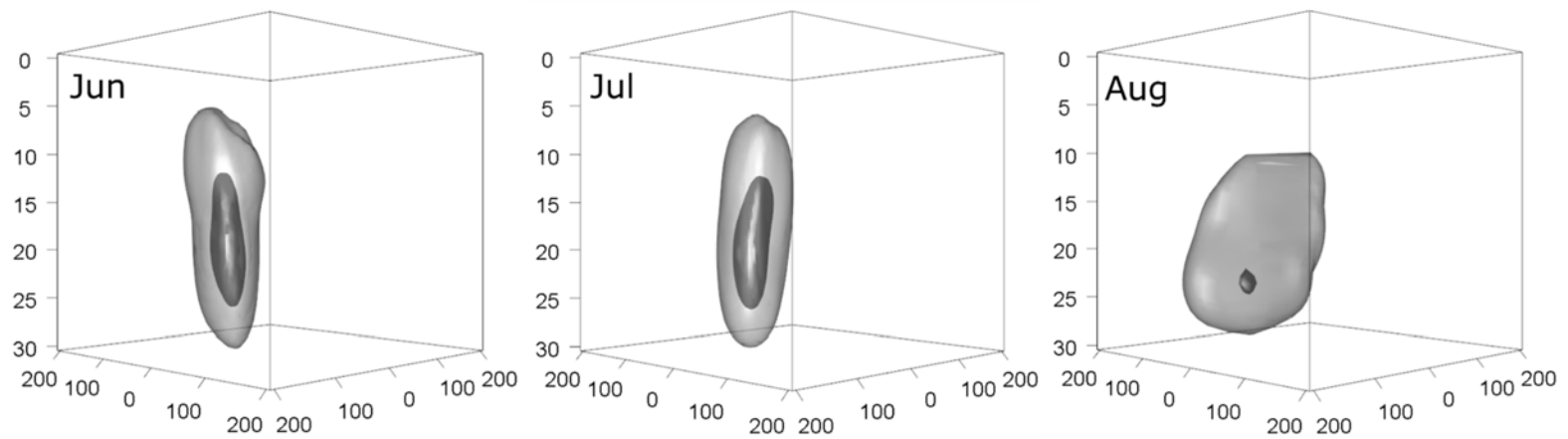


Figure 4-8: Three-dimensional volume (m^3) use for an individual tagged red snapper (F72) around an artificial reef during summer months in 2013. Core volume (50% KDE) = dark gray; home range volume (95% KDE) = light gray; horizontal position (latitude and longitude) = range of 400 m (0 m at reef to 200 m away); and vertical position (depth) = 0 – 30 m.

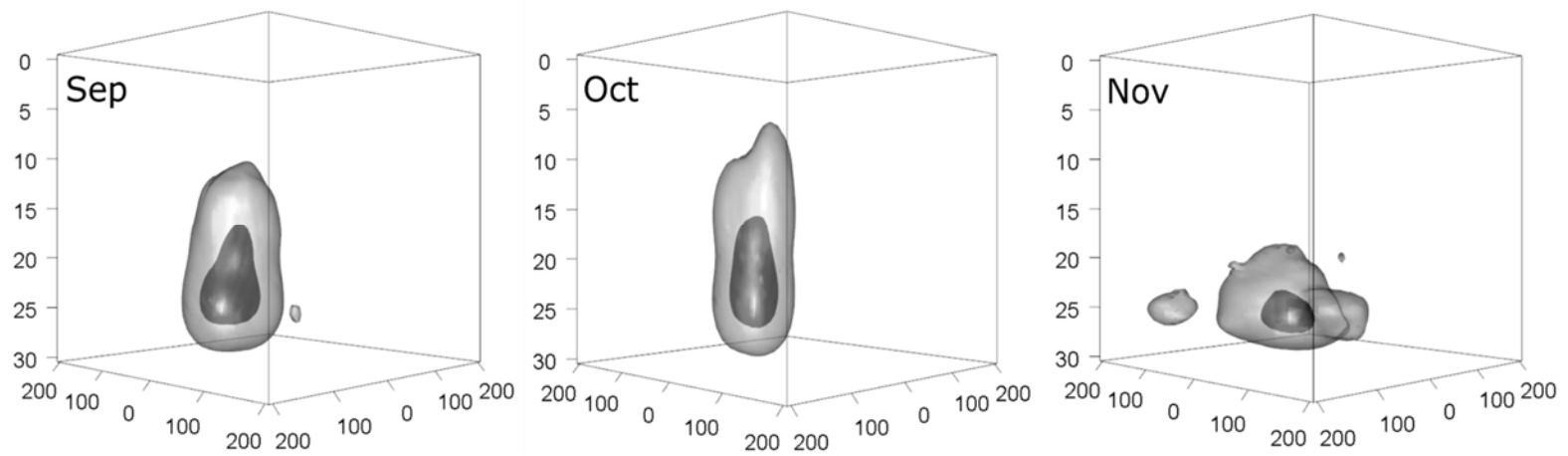


Figure 4-9: Three-dimensional volume (m^3) use for an individual tagged red snapper (F72) around an artificial reef during fall months in 2013. Core volume (50% KDE) = dark gray; home range volume (95% KDE) = light gray; horizontal position (latitude and longitude) = range of 400 m (0 m at reef to 200 m away); and vertical position (depth) = 0 – 30 m.

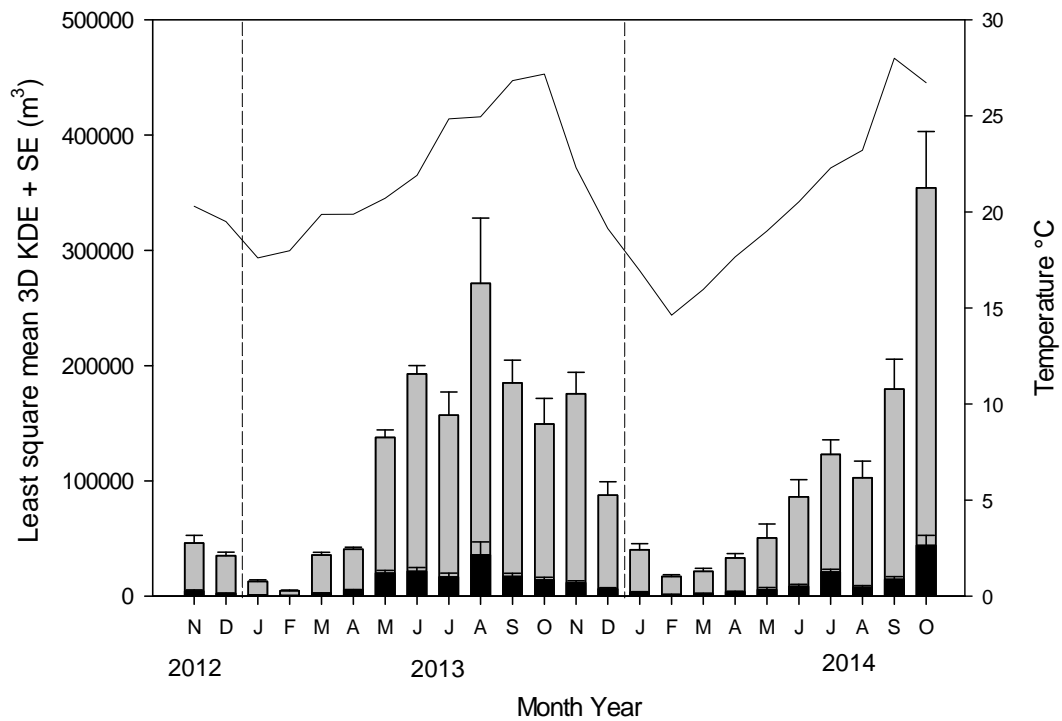


Figure 4-10: Comparison of water temperature and mean monthly core volume (50% KDE, m³) and home range volume (95% KDE, m³) for red snapper around artificial reefs in the northern Gulf of Mexico.

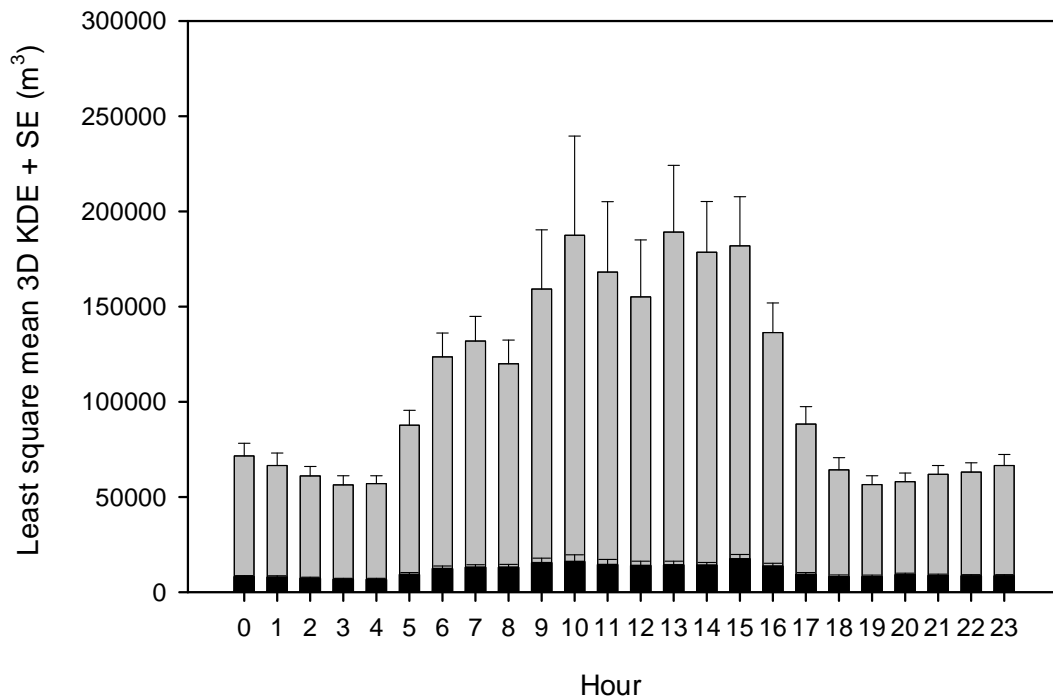


Figure 4-11: Diel volume use (m³) by red snapper, *Lutjanus campechanus*, on an artificial reef in the northern Gulf of Mexico. Hours begin at midnight (0 hour = 00:00 – 00:59 h) and continue for a 24-h period. Black bars = core volume (50% KDE); gray bars = home range volume (95% KDE); and error bars = SE.