

Acoustic positioning and movement patterns of red snapper, *Lutjanus campechanus*, around artificial reefs in the northern Gulf of Mexico

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ABSTRACT: Over a 3 yr period fine-scale (m) movements of red snapper *Lutjanus campechanus* were estimated with the Vemco VR2W Positioning System (VPS) on 3 artificial reefs, and wider scale (km) movements were estimated with surrounding receivers (n = 23). Tagged red snapper (n = 56) were tracked for extended periods (17–1096 d). Residency (23 mo) and site fidelity (82 % yr⁻¹) showed that red snapper maintained a close association with the artificial reef structure (34.5 ± 44.0 m). Fine-scale monthly home range (95 % kernel density estimates [KDE]) and core areas (50 % KDE) were positively correlated with water temperature. In the winter, all red snapper showed less movement, and during the warmer months most (63 %, 29 out of 46) fish used a secondary reef site. Over diel periods, fish showed significantly greater movements during day hours on 2 reef sites and during night hours on 1 reef site. The surrounding receiver array validated 88 % (15 of 17 fish) of the VPS-determined emigrations. Many (53 %, n = 9) fish moved short distances (~1.5 km) to nearby reefs, and some red snappers (n = 3) that emigrated returned to their original release site. Red snapper showed some prey-like behaviors, e.g. close association with reef structure, quick movements over open habitat, and paired emigrations to nearby sites. These behaviors suggested that red snapper are subject to predation by larger apex predators, and as stocks increase, such factors will become increasingly more important for future management.

KEY WORDS: Telemetry · Residency · Site fidelity · Emigrations

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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 1800s 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 1900s, with regulations starting in 1990 (SEDAR 2012). In more recent years, management efforts have resulted in numerous changes in daily and seasonal quotas in an 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 d 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, monthly) and large scales (e.g. emigrations).

Previous studies have shown that red snapper are closely associated with structured habitat, both artificial and natural, throughout their life span (Szedlmayer & Schroepfer 2005, Gallaway et al. 2009, Topping & Szedlmayer 2011a,b, Mudrak & Szedlmayer 2012). The majority of mark-recapture studies are in

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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 & Shipp 1994, Patterson et al. 2001, Diamond et al. 2007, Strelcheck et al. 2007). Similarly, long-term (>1 yr) telemetry studies have reported high annual site fidelity >72 % yr⁻¹ and high residency for tagged fish up to 1099 d (Szedlmayer 1997, Szedlmayer & Schroepfer 2005, Topping & Szedlmayer 2011a,b, Piraino & 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 & Szedlmayer 2003, Gallaway et al. 2009). While a strong association with artificial reef structure was clear, the specifics of fine-scale (m) and large-scale (km) movements greatly vary among previous studies (Szedlmayer & Shipp 1994, Patterson et al. 2001, Schroepfer & Szedlmayer 2006, Strelcheck et al. 2007, Topping & Szedlmayer 2011a,b).

Fine-scale movements of red snapper have been evaluated with telemetry methods (Schroepfer & Szedlmayer 2006, Topping & Szedlmayer 2011a,b, Piraino & Szedlmayer 2014). No seasonal differences in habitat use were detected in earlier studies that lasted >1 yr, 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 & Schroepfer 2005, Topping & Szedlmayer 2011b). However, telemetry arrays did show directed and seasonal emigrations by some fish (n = 12; Topping & Szedlmayer 2011b). The most recent study that showed differences in monthly habitat use by red snapper was based on the development and application of a new and highly accurate acoustic telemetry method (1 m accuracy, Vemco Positioning System [VPS], Vemco Ltd, Nova Scotia; Piraino & Szedlmayer 2014). The VPS data showed that monthly 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 colder months as compared to warmer months (Piraino & 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 & Schroepfer 2005, Topping & Szedlmayer 2011a,b). In contrast, red snapper home ranges and core areas were significantly larger during the day than at night, and were

minimum at dawn and dusk based on the VPS method (Piraino & 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 (Szedlmayer 1997, Szedlmayer & Schroepfer 2005, Topping & Szedlmayer 2011a,b, Piraino & Szedlmayer 2014).

Greater distance (km) movements of red snapper have primarily been described from conventional mark-recapture studies (Szedlmayer & 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 & Schroepfer (2005) used a single stationary receiver to monitor fish presence, and reported that some of the tagged fish spent more time outside than inside the receiver range (maximum = 1.6 km), with 1 fish in particular making regular trips for over 24 h. Similarly, Topping & Szedlmayer (2011b) showed that some red snapper regularly used multiple reef habitats within their receiver arrays (detection area ≈ 3.6 km²).

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 & 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 (maximum = 12; Szedlmayer & Schroepfer 2005) or telemetry arrays (maximum = 6; Topping & Szedlmayer 2011b). Thus, our understanding of large-scale movements in both mark-recapture and telemetry studies is largely dependent on fisher-reported recapture locations (Szedlmayer & Shipp 1994, Watterson et al. 1998, Patterson et al. 2001, Diamond et al. 2007, Topping & Szedlmayer 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 large-scale telemetry

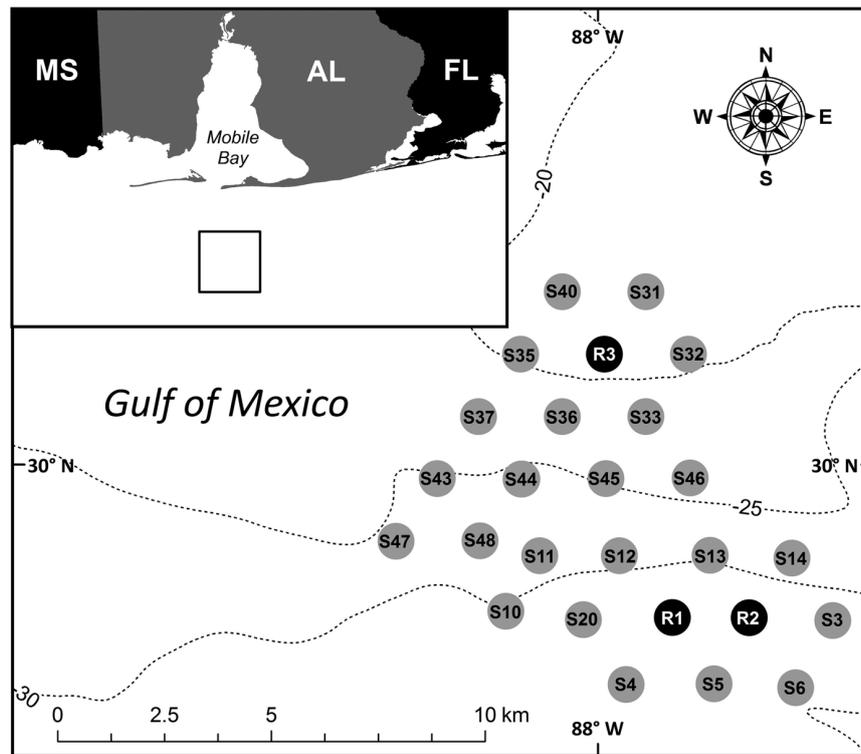


Fig. 1. Locations of steel cage artificial reef sites ($n = 26$) used to track movement patterns of red snapper *Lutjanus campechanus* off the coast of Alabama (AL) in the northern Gulf of Mexico. Black circles ($n = 3$) were Vemco VR2W Positioning System (VPS) acoustic receiver arrays (R1, R2, and R3) that measured fine-scale movements; gray circles ($n = 23$) represent surrounding sites with single receivers (S3–S48) that measured greater scale movements. Dotted lines are depth contours (5 m)

arrays were examined. In addition, the present study focuses on the movements of large red snapper (>406 mm total length [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, 2012, 2013). Fine-scale movements were evaluated with the VPS technology (vemco.com/products/vps/) over diel and monthly time periods and compared to changes in water temperature. A large-scale (64 km^2) 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, and core and home ranges within the fine-scale VPS array (around the release reef site) and to estimate greater distance emigration patterns to reef sites outside the VPS sites. Combined, these data were used to evaluate red snapper movement patterns and habitat use and to 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).

MATERIALS AND METHODS

Study location

The present study sites ($n = 26$) were at unpublished locations, 23–35 km south of Mobile Bay, Alabama, USA, in the northeastern Gulf of Mexico. The sites were steel cage artificial reefs ($2.5 \times 1.3 \times 2.4$ m) located 1.4–1.9 km apart at 20–35 m depths (Fig. 1). There were 3 reef sites with VPS receiver arrays for recording fine-scale movements with 90% detection rates within 0.32 km^2 areas (90% detection at 400 m; Topping & Szedlmayer 2011b), and 23 surrounding reef sites with single receivers for recording greater distance movements (Fig. 1). The single receivers were placed 1.4–1.9 km away from the VPS sites and other surrounding receivers, to provide high detection rates of transmitters over the greatest area. This design left a 1200 m portion of perimeter (six 200 m sections or 14%) between surrounding receivers with detection rates of 40–60% (Topping & Szedlmayer 2011b), but a 8400 m portion of perimeter (six 1400 m sections or 86%) with higher detection rates ($>60\%$ detection rate at 700 m; Topping & Szedlmayer 2011b). Thus, we ex-

pected near 100% detection of emigrating tagged red snapper on surrounding receivers as they emigrated from the VPS sites, because they only had a 14% chance of emigrating through the lower detection perimeters, and, even if they did, they would still be detected due to the high frequency of emitted signals (<60 s). Within each VPS array there was a second artificial reef site (without a receiver), and these were located 154–250 m away from the VPS reef.

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 throughout the water column and at depth (YSI Model 6920, YSI Incorporated). Fish were tagged and released if dissolved oxygen values were $>2.5 \text{ mg l}^{-1}$. 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 ($>330 \text{ mm TL}$) and recreational minimum length limits ($>406 \text{ mm TL}$; SEDAR 2013). To reduce signal collisions, the number of red snapper tagged in the present study was limited to <10 per VPS site. With <10 fish we obtained frequent ($<10 \text{ min}$) and accurate (m) fish positions (Topping & Szedlmayer 2011b, Piraino & Szedlmayer 2014).

Fish tagging methods followed procedures described by Topping & Szedlmayer (2011a,b, 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^{-1} seawater), weighed (nearest 0.1 kg), and measured (mm SL, FL, and TL [standard, fork, and total length]) 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 s, battery life $> 6 \text{ yr}$, power = 152 dB) 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 $\sim 3 \text{ cm}$ 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 the seafloor close ($<10 \text{ m}$) 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 & Szedlmayer 2014). Transmitter-tagged fish remained in the cage at depth for $\geq 1 \text{ h}$ before SCUBA divers visually inspected fish and only released fish in good condition (i.e. oriented upright, regular opercula movements, swimming, responded to diver presence). This cage release method was discontinued due to safety concerns after SCUBA divers had frequent aggressive encounters with multiple large ($\geq 2 \text{ m}$) Carcharhinidae sharks.

After discontinuing cage-diver releases all (November 2012–2014) tagged red snapper were released with a remotely opening cage (46 × 61 × 61 cm; Williams et al. 2015). Recovered fish were placed into the cage at the surface and were observed for 10–20 s at 1 m depth to verify recovered condition. All fish showed adequate recovery at the surface and were slowly lowered by hand to the seafloor (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 $\geq 15 \text{ min}$. 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 & Szedlmayer (2014). At each VPS site, 5 VR2W receivers were moored $\sim 4.5 \text{ m}$ 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 (Fig. 2). Receiver positions within the array allowed for maximum detection (100% detection of transmitters at 400 m; Piraino & Szedlmayer 2014). A synchronization transmitter (sync tags, Vemco V16-6x, 69 kHz, transmission delay: 540–720 s) was attached 1 m above the receiver to standardize the internal receiver clocks. Fish positions with a 1 m accuracy (mean \pm SD, $0.98 \pm 0.66 \text{ m}$; Piraino & Szedlmayer 2014) were calculated by VEMCO post-processing of the time differential of signal arrivals at 3–5 receivers (Vemco Ltd.). A stationary control transmitter was placed at a known location within each VPS array to confirm the continuous collection of data throughout

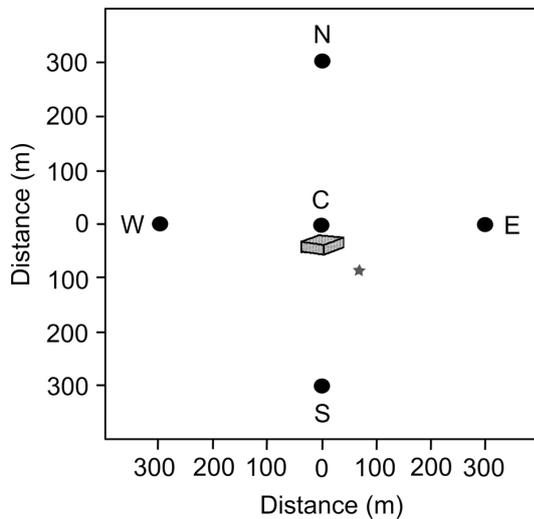


Fig. 2. Receiver array (VPS) used to examine fine-scale movements of red snapper *Lutjanus campechanus* on artificial reefs in the northern Gulf of Mexico. The center (C) receiver was positioned 20 m north of the steel cage artificial reef (shown in gray, not to scale). Additional receivers were placed 300 m north (N), east (E), south (S), and west (W) of C. A control transmitter (gray star) was positioned within each array to determine the accuracy of the VPS positions. Black circles: VEMCO VR2W receivers and synchronization transmitters

the study. Receivers were exchanged at 3 mo 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 ($n = 23$; Fig. 1). 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 km^2). 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, 2 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 ($^{\circ}\text{C}$) at 1 h intervals and was downloaded every 3 mo.

Residency and site fidelity analyses

The VPS arrays were used to categorize tagged fish as active (continuously swimming), caught (sudden disappearance near reef center, fishing mortality), emigrated (tracked for a period of time before progressively moving farther away from the reef center and then disappearing), and deceased (tag becomes stationary; Williams-Grove & Szedlmayer in press). Residence time of an active tagged fish was calculated assuming fish were released on the same day with a known fate model in the 'MARK' program (Topping & 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):

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

This survival equation 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). Median residence time was defined as the time period when 50% of the active tagged red snapper were still present over all years ($S = 0.5$), while site fidelity was the percent of tagged fish remaining at their release site 1 yr after release (Schroepfer & Szedlmayer 2006, Topping & 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.

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 &

Ripley 2002, Piraino & Szedlmayer 2014). Kernel density analysis estimates the probability of a tagged fish being located in a particular area. Core area shows 50 % KDE (absent from area 50% of the time) and home range shows 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 & Powell 1996, De Solla et al. 1999). Core and home range areas were examined for each fish by hour and month. The effect of time period (diel and month) on area use was tested with a 1-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 <73 m from the reef site. This 73 m distance was based on the average radius of all 95 % KDE areas plus the average SD from all 95 % KDE calculations for all fish for each month ($n = 726$, for 95 % KDE areas). We then use this as the distance (73 m) limit for defining that a tagged fish was residing on that reef. If fish positions were recorded >73 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.

Large-scale movements analysis

The greater scale movements (outside the VPS detection areas) 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. A short interval time was set at 23 min (30 times the average transmitter delay: 20–69 s, mean = 45 s) and a long interval was set at 9 h (720 times the mean = 45 s transmitter delay; Pincock 2012). Transmitter detections were accepted as valid tagged fish if there was at least 1 short interval (23 min) between detections and more short intervals than long intervals (9 h; Pincock 2012, Williams-Grove & Szedlmayer in press).

RESULTS

Tagging and tracking

Transmitter-tagged red snapper ($n = 82$) were tracked on 3 VPS artificial reef sites (R1, R2, and R3) for up to 3 yr (Fig. 1). At the beginning of the study, 16 fish were present on the VPS sites (Piraino & Szedlmayer 2014). All tagged fish were above the federal minimum length limits (SEDAR 2013) and ranged in size from 454 to 877 mm TL (mean TL \pm standard deviation [SD]: 605 ± 97 mm). We analyzed 4.1 million accurate (~ 1 m) fish positions for 1096 d to evaluate red snapper movement patterns. The number of detections by fish ranged from 25 to 289 526. Lower detections or positions (25 and 30) for 2 fish were used in percent time on reef estimations, but not used for KDE area calculations. All other fish had high detections, 1000–10 000 (14%), 10 000–20 000 (11%), 20 000–100 000 (45%), and 100 000–289 526 (25%). Some fish emigrated just after tagging (within 7 d); such movements were considered post-release tagging effects (lost) and were removed from further analyses ($n = 26$). Among the fish that left within 7 d, most (88%, $n = 23$) left within 3 d of tagging, while on Days 5, 6, and 7 of post-release 1 fish left on each day. For example, Fish 92 showed such post-release tagging behavior within the first 7 d after release; it immediately left (0 d) the VPS tagging site (R1) and remained on a surrounding site (S20) for 7 d. On the seventh day this fish returned to R1 and stayed for 152 d, then emigrated and was removed from the analyses. Fish 92 remained at liberty for another 40 d before it was caught at an unknown location and returned by a fisher in June 2013. Three other lost fish were regularly detected on surrounding reef sites (a single fish at S11, S13, and S14) after emigrating from the release site within 7 d. Fish ($n = 56$) 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 56 red snapper were recorded over periods ranging from 17 to 1096 d. Among these tracked red snapper, 17 emigrated (3 returned), 24 were caught by fishers, 1 suffered natural mortality, 1 had an unknown fate, and 14 remained active at the end of the study (Fig. 3). Emigration was first observed after 17 d, while the next emigration did not occur until after 72 d. The longest time between tagging and emigration was 978 d. The mean (\pm SD) time before emigration was 368 d (± 285 d). Similarly, fish were tracked for 29–725 d following tagging before being caught by fishers.

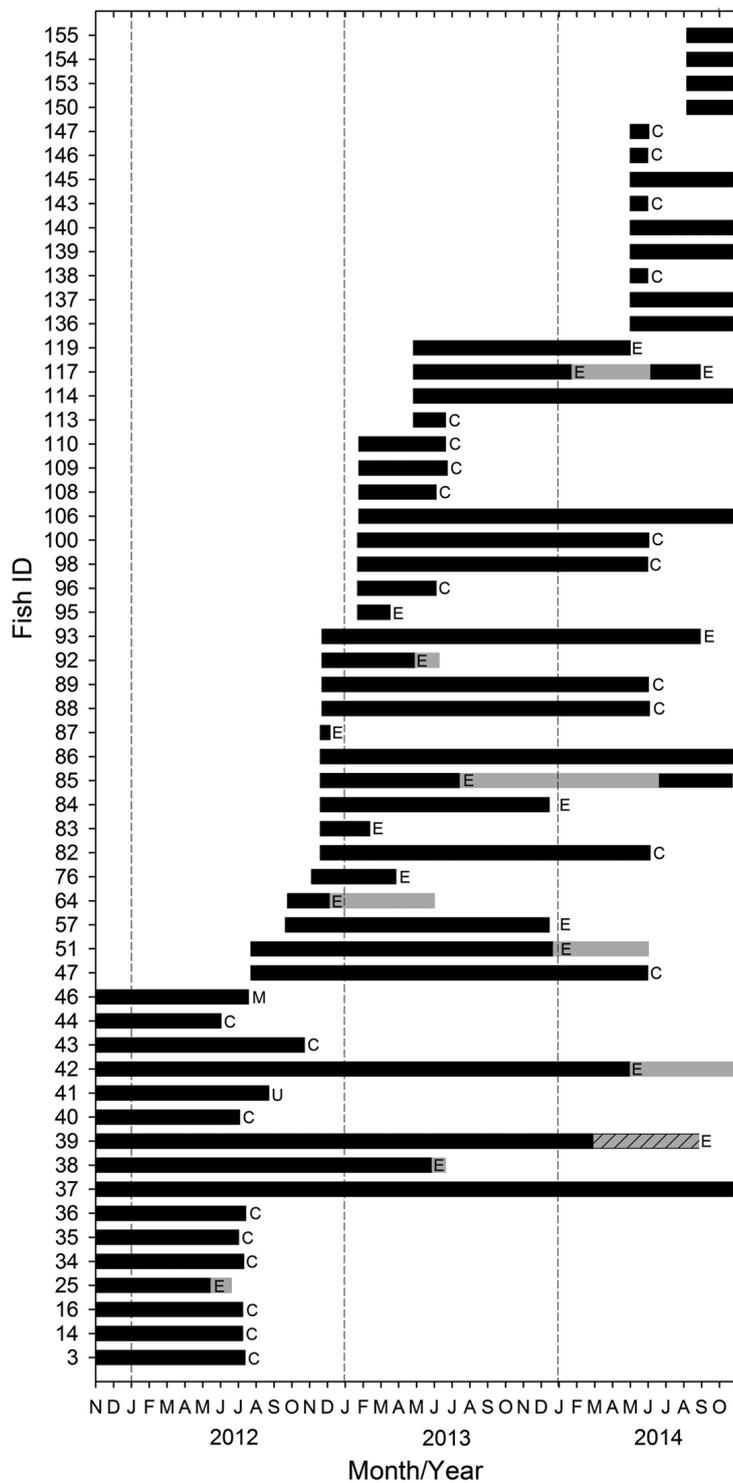


Fig. 3. Tracking periods for transmitter-tagged ($n = 56$) red snapper *Lutjanus campechanus* on VPS sites and surrounding reef sites, after a 7 d post-tagging recovery period. Fish still present after the last month of tracking (31 October 2014) were all active. Black bars: active on VPS site; gray bars: active on surrounding receiver site; gray bars with diagonal black bars: regularly active on surrounding site and VPS site; vertical dashed bars: separate calendar years; letters denote fate of fish on VPS site — C: caught; E: emigration; M: mortality (predation); U: unknown

Most captures were reported by fishers (63%, $n = 15$), 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 mo (31 d) of tagging, validating the survival and quick recovery of surgery methods. The fate of 1 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 ($n = 1$). One fish was identified as a predation mortality based on short time intervals among long distances (Williams-Grove & Szedlmayer in press).

Residency and site fidelity

Based on a combined analysis for all 3 years, residence time (50% of tagged fish still present) was 23 mo, total survival $S = 0.12$ (0.01–0.57) and annual site fidelity was 82% yr^{-1} (Fig. 4). In the present study, more fish were removed from the VPS reef sites by fishers (43% caught) than through emigration (30%, for further discussion of fishing mortality see Williams-Grove & Szedlmayer in press).

Fine-scale area use

Over the 3 yr study period, control stationary transmitters (480 594 detections) showed that the VPS array detections were continuous (no interruptions in collection of data). The >4.1 million red snapper positions analyzed showed no significant differences in core areas (50% KDE) or home ranges (95% KDE) among VPS sites (core area: $F_{2, 556} = 0.97$, $p = 0.38$; home range: $F_{2, 556} = 0.26$, $p = 0.28$). Tagged red snapper maintained a close association with VPS artificial reefs, with a mean (\pm SD) distance from the reef of 34.5 m (± 44.0 m) over all years. Fish total length was positively correlated with core area ($F_{1, 12E3} = 1638.50$, $p < 0.0001$, $r^2 = 0.11$) and home range ($F_{1, 12E3} = 2161.86$, $p < 0.0001$, $r^2 = 0.15$). Larger red snapper (>700 mm TL) had significantly larger core areas (<599 mm TL, $F_{4, 556} = 4.17$, $p = 0.0004$) and home ranges (<699 mm TL, $F_{4, 556} = 11.07$, $p < 0.0001$) than smaller red snapper.

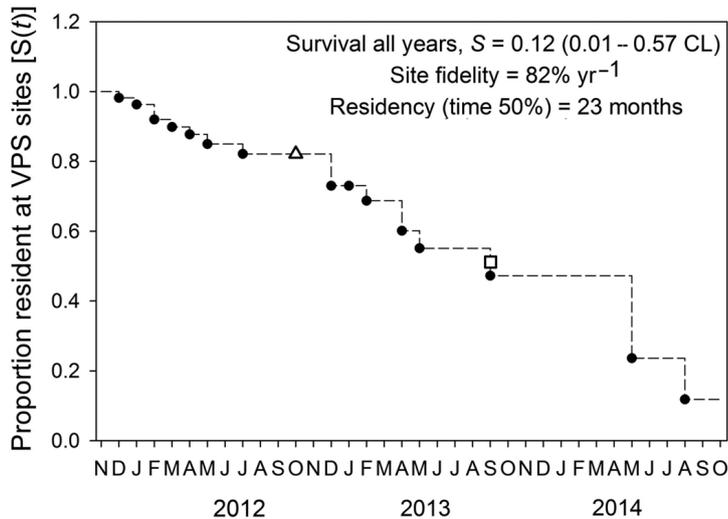


Fig. 4. Survival (S) of red snapper *Lutjanus campechanus* at their artificial reef site of capture, and fine-scale Vemco VPS tracking. Dashed line: proportion of fish that remain residents (did not emigrate) after each monthly interval; black circles: emigration; white triangle: site fidelity (percent of tagged fish remaining at their release site 1 yr after release); white square: median residency time when 50% of active tagged red snapper were still present ($S = 0.5$). CL: 95% confidence limits

Red snapper movement patterns significantly varied by month (core area: $F_{11, 545} = 16.05$, $p < 0.0001$; home range: $F_{11, 545} = 15.15$, $p < 0.0001$) and monthly movement patterns were significantly positively correlated with water temperature (core area: $F_{11, 541} = 202.28$, $p < 0.0001$, $r^2 = 0.27$; home range: $F_{11, 623} = 155.96$, $p < 0.0001$, $r^2 = 0.22$; Fig. 5). In the colder winter months (December to February) 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 warmer summer months (June to August) most (63%, 29 out of 46) red snapper showed home ranges that included 2 or more reef sites (original release site and secondary reef sites within the VPS array; Fig. 6). The fish that used multiple reef sites in the summer continued to use these sites through the warmer fall months (September to October).

For all years (2011–2014), 77% of all tagged and tracked red snapper ($n = 56$) showed the use of secondary reef sites within the VPS detection areas. These secondary reefs were not

known to exist at the start of the present study, but fish use showed concentrated detection patterns at specific locations away from the VPS reef site within the VPS detection areas (Fig. 6). These secondary sites were then identified as reef sites by SCUBA visual observations (2 steel cages and 1 concrete pyramid). At Sites R1 and R2, fish spent most time near (≤ 73 m) the VPS reef (mean $> 96\%$) and little time on other reefs or over open habitat within the VPS detection areas (mean $< 4\%$). Fish at R3 showed more use of the second reef (mean = 15%), but still mostly resided on the VPS site (mean = 83%; Table 1). Similar patterns were shown by month, where fish spent the most time on the VPS reef sites, the exception being the summer and fall months at VPS R3, where fish showed greater use of the second reef site (16–31%; Table 1).

Red snapper showed significantly different core area and home ranges around VPS reefs over diel periods by reef site (core area: $F_{23, 12E3} = 3.63$, $p < 0.0001$ and home range: $F_{23, 12E3} = 3.29$, $p < 0.0001$). 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 (06:00–16:00 h),

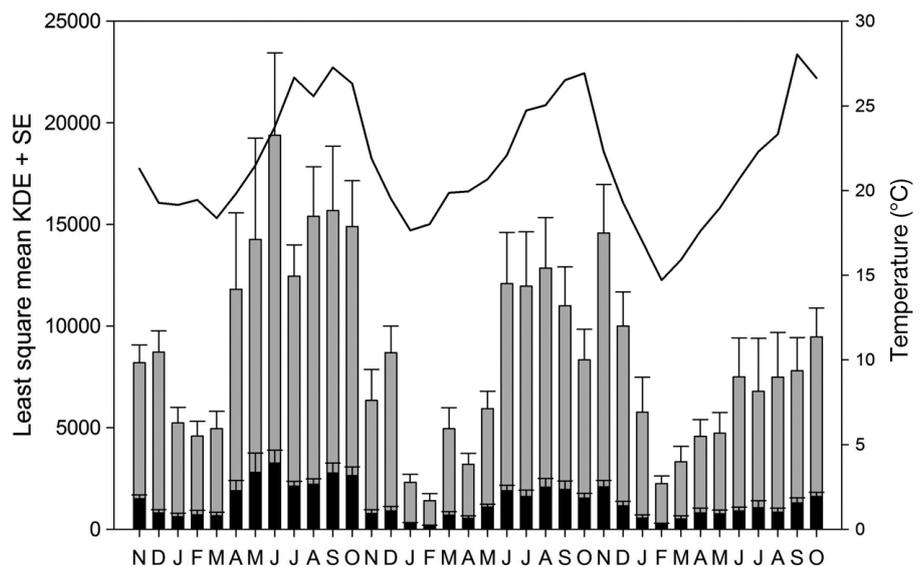


Fig. 5. Comparison of water temperature and mean monthly home ranges (95% KDE) and core areas (50% KDE) of red snapper *Lutjanus campechanus* around artificial reefs in the northern Gulf of Mexico over 3 yr (1 November 2011–31 October 2014). Black bars: core area (50% KDE); gray bars: home range (95% KDE); error bars: SE; black line: water temperature at depth

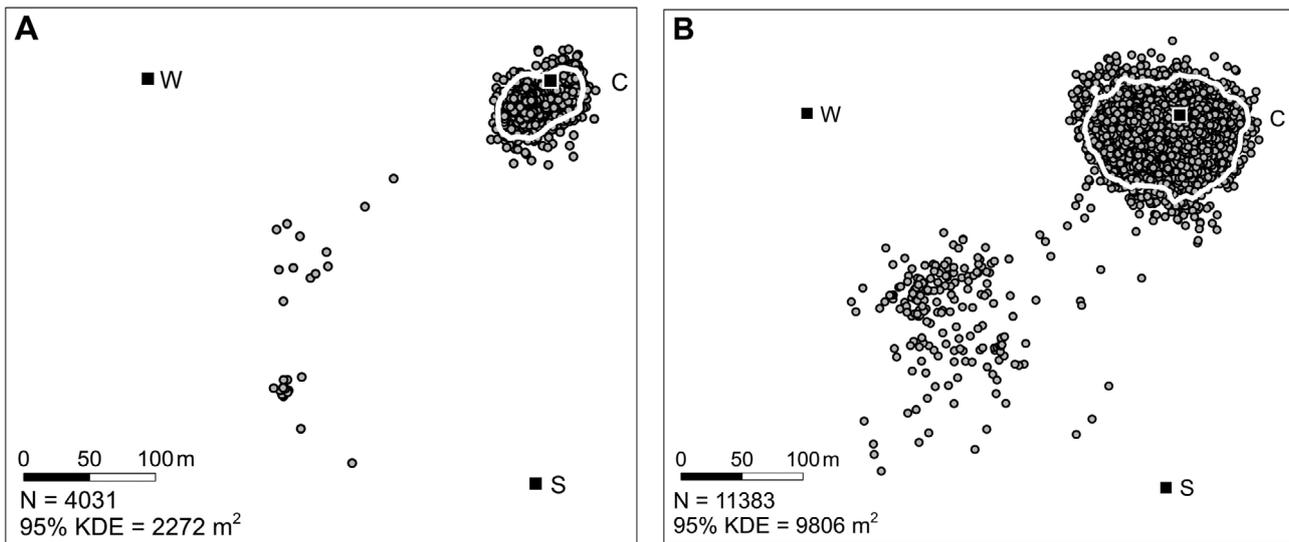


Fig. 6. Red snapper *Lutjanus campechanus* home range (95 % KDE) comparison between (A) February and (B) June for Fish 47 from artificial reef site R2 in the northern Gulf of Mexico. Gray points: individual VPS-calculated fish positions; white line: home range (95 % KDE area); black squares: receivers

while smaller movements were observed during night hours (20:00–02:00 h). The smallest KDE areas were observed during the early morning (03:00–04:00 h) and evening hours (18:00–19:00 h). In contrast, red snapper on R3 showed the largest movements at night (23:00–00:00 h) and smallest movements in the day (12:00–13:00 h; Fig. 7).

Emigrations and large-scale patterns

Our surrounding receiver array and recapture data were used to confirm emigrations. Most fish (88%, 15 out of 17) with VPS-detected emigrations were also detected and validated on surrounding reef sites. Many (53%, $n = 9$) 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 secondary 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 38 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 2 surrounding sites (S33 and S36) for 177 d before it was captured by a fisher (Fig. 8).

Homing behavior (emigration followed by return to the original VPS site of tagging) was detected in 3 red snapper that used surrounding sites for prolonged periods (160–336 d; Table 2). 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 (Fig. 8). The other 2 red snapper (F39 and

Table 1. Percent time by month that red snapper *Lutjanus campechanus* resided on the VPS reefs (R1, R2, or R3), secondary reefs, or open habitat within the VPS detection area, based on detections within 73 m of the reef and time between consecutive detections ≤ 30 min

Month	R1			R2			R3		
	VPS reef	2 nd reef	Open	VPS reef	2 nd reef	Open	VPS reef	2 nd reef	Open
Jan	99.5	0.0	0.5	99.7	0.1	0.2	95.1	4.3	0.6
Feb	99.9	0.0	0.1	100	0.0	0.0	93.2	6.6	0.2
Mar	99.6	0.0	0.4	99.2	0.0	0.8	92.7	6.9	0.4
Apr	99.3	0.1	0.6	99.6	0.0	0.4	91.8	7.8	0.4
May	99.2	0.0	0.8	99.1	0.0	0.9	91.0	8.3	0.7
Jun	91.2	0.6	8.2	99.0	0.1	0.9	80.7	16.0	3.3
Jul	91.2	0.3	8.5	100	0.0	0.0	77.2	20.7	2.1
Aug	94.5	0.6	4.9	99.5	0.1	0.4	74.1	22.2	3.7
Sep	95.9	0.0	4.1	98.7	0.4	0.9	70.8	25.9	3.3
Oct	96.8	0.0	3.2	99.3	0.0	0.7	65.7	30.9	3.4
Nov	95.4	0.0	4.6	98.4	0.1	1.5	75.4	20.9	3.7
Dec	98.3	0.0	1.7	98.8	0.0	1.2	87.7	10.9	1.4
Mean	96.7	0.1	3.2	99.3	0.1	0.6	83.0	15.1	1.9
SD	3.2	0.2	3.0	0.5	0.1	0.5	10.1	8.8	1.5

F117) used multiple surrounding reef sites. Red snapper F39 was detected on 2 surrounding reef sites (S12 and S13) and the VPS site (R1) for shorter periods of time (<1–58 d) over a 5 mo period (174 d, 3 March–27 August 2014) before leaving the receiver array. Movements were direct, with detections ceasing at 1 site and starting at the new site quickly (minimum <1 min). 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 initially emigrated from the VPS 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 (<1–67 d). Red snapper F117 was tracked on R1 for 34 d post-tagging before temporarily emigrating to 2 nearby (~1.5 km) surrounding reef sites (S12 and S13) for ~12 d in June 2013. This fish then returned to R1 and remained there for 169 d before emigrating (30 November 2013). Fish F117 proceeded to make 21 detectable movements within (maximum <2 km) and outside the surrounding receiver array before returning to R1 on 13 June 2014 (after 195 d) and remaining there until it emigrated outside of the array on 3 September 2014 (Table 2).

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 (Table 2). 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 ca. 2–3.5 km to exit the surrounding receiver array. The exact distances that these fish travelled remains unknown, and any further information was dependent on fisher recaptures. For example, 1 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

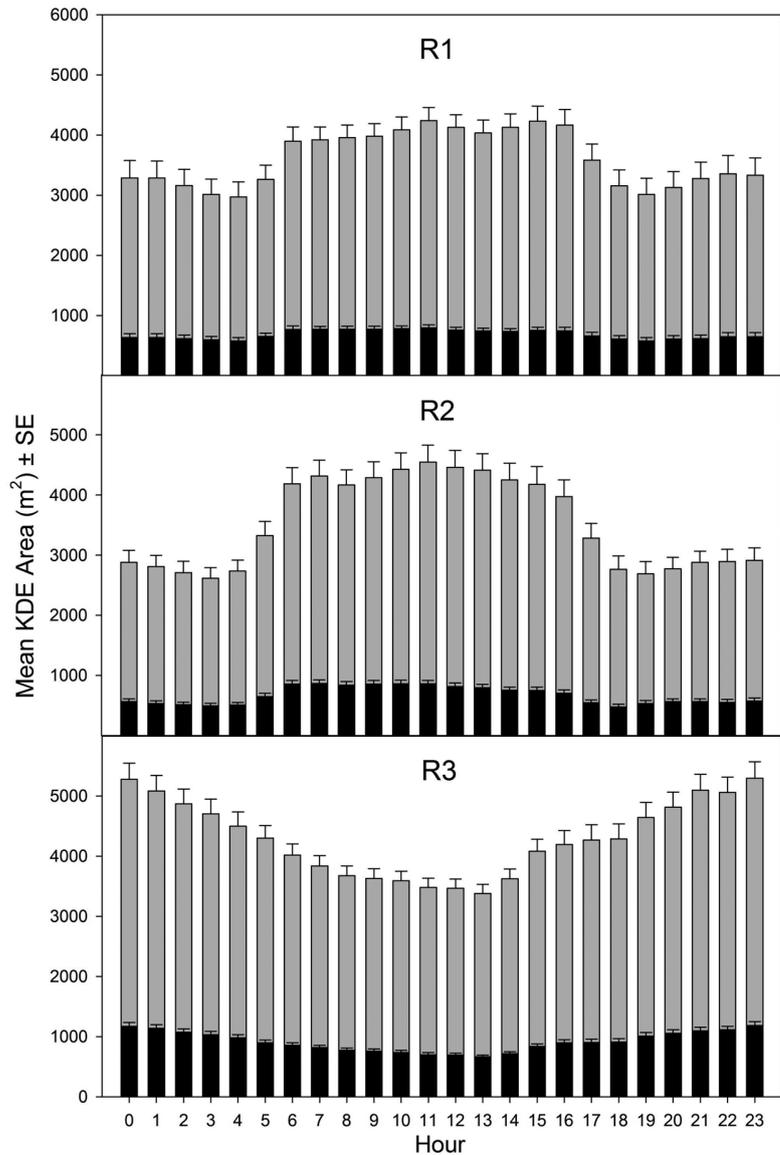


Fig. 7. Mean hourly area use by red snapper *Lutjanus campechanus* on artificial reefs in the northern Gulf of Mexico. Hours begin at midnight (0 h = 00:00–00:59 h) and continue for a 24 h period. Larger movements occurred during daytime hours on Sites R1 and R2, but during nighttime hours at R3. Gray bars: home range (95% KDE); black bars: core area (50% KDE)

fisher. The reported recapture location for this fish was located 4.2 km away from its original VPS site. Only 1 red snapper (F57) that emigrated was not detected on a surrounding reef site. This fish stayed on its VPS release site (R3) for 447 d after release, then emigrated and was only detected on the R3 south receiver for 3 d before its disappearance. Overall, 13% (7 out of 56) of the tagged red snapper made these larger directed emigrations away from the receiver array.

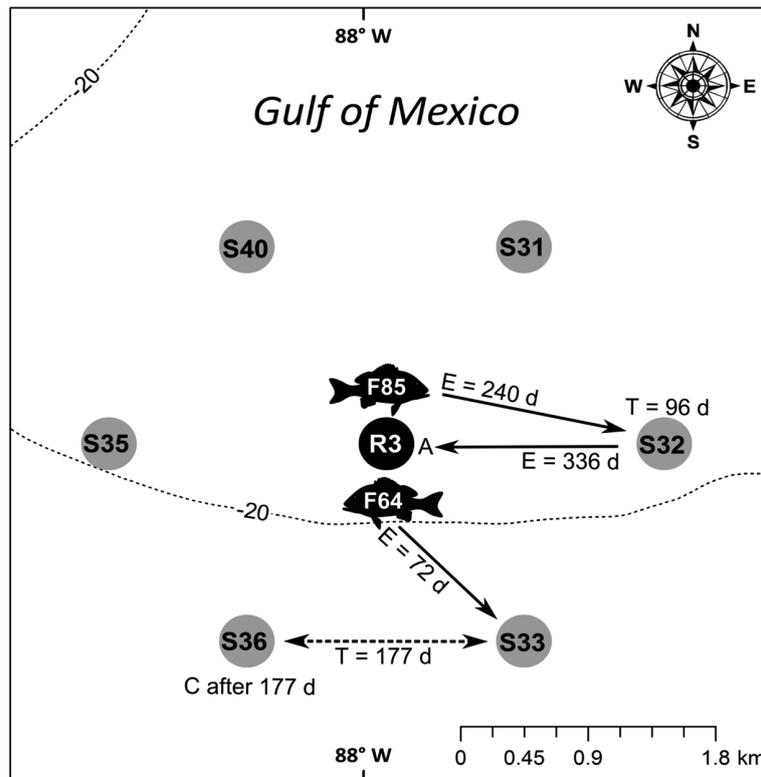


Fig. 8. Larger (~1.5 km) movements made by red snapper *Lutjanus campechanus* from the VPS artificial reef of release to surrounding reef site(s) in the northern Gulf of Mexico. The figure shows the movements of 2 fish (F64 and F85) from a VPS reef site (R3, black circle). Gray circles: surrounding reef 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; C: caught after emigration (total tracking time on VPS and surrounding site = E 72 d + T 177 d = 249 d)

Table 2. Movement patterns of red snapper *Lutjanus campechanus* to sites outside the VPS reef as detected by the 23 surrounding receivers. Fish were considered on an outside site if detections passed the screening criteria for false detections (see 'Materials and methods')

Fish	VPS site	Days on VPS site before E	Days to first travel to alternate site	No. of reef sites visited	Alternate sites used	Total days on surrounding sites	Total days lost between many E	Distance between reefs (km)	Residency after return to VPS site
F25	R2	322	0	2	S3, S14	34	–	1.5	–
F38	R1	643	0	1	S13	23	–	1.5	–
F39	R1	931	0	3	S12, S13	137	–	1.5	38
F42	R3	978	0	1	S32	50	–	1.5	–
F51	R1	511	5	2	S4, S20	82	79	1.5	–
F57	R3	447	–	0	–	–	–	7	–
F64	R3	72	0	2	S33, S36	177	–	1.5	–
F76	R2	145	0	3	S14, R3	0	–	–	–
F83	R3	83	0	1	S35	0	–	1.5	–
F84	R3	388	0	1	S33	0	–	1.5	–
F85	R3	240	0	1	S32	336	–	1.5	125
F87	R3	17	0	1	S33	0	–	1.5	–
F92	R1	152	0	2	S3, S4	0	–	1.5	–
F93	R1	640	–	0	–	–	–	–	–
F95	R2	57	0	0	R1	0	–	1.5	–
F117	R1	269	0	4	S4, S12, S13, S20	74	107	1.5	195
F119	R1	367	0	3	S12, S45, S46	0	–	–	–
Mean		368	0.3	2		61		1.9	

Emigration rates varied by month, with initial emigrations mostly occurring during the winter ($n = 7$; 5 in December, 1 in January, and 1 in February) and spring ($n = 8$; 3 in March and 5 in May). One initial emigration was observed in the fall (September), and 1 emigration occurred during the summer (July). In 2 of the fish that showed homing behaviors a second emigration was made in August and September. Paired emigrations were observed on 2 occasions, when 2 tagged fish emigrated on the same day 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 mo of each other (September–November 2012) and were smaller (497–542 mm TL). The first 2 emigrated on 7 December 2012 (emigrating 8 min apart), and the next 2 fish emigrated 1 yr later on 18 December 2013 (emigrating 3 min apart). In both years fish were then detected on the surrounding reef site S33 for short periods (1–3 d) before making a second emigration. Paired emigrations occurred when the water temperature was 19°C in both years. In addition, 2 tagged red snapper emigrated in the spring on the same day (6 May 2014) but from different VPS sites (F119 from R1 and F42 from R3). We tagged additional fish on both R1 and R3 on 6 May 2014, and, during tagging, Fish 119 was recaptured after being tracked for 1 yr. This fish appeared to be 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. It also 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 (1096 d, $n = 56$) considerably expanded on a previous study that validated the feasibility of VPS acoustic telemetry methods with red snapper (694 d, $n = 17$; Piraino & Szedlmayer 2014). The present study increased red snapper locations to 4.1 million accurate positions over short time intervals (mean detection time <5 min) continuously for up to 1096 d, for unprecedented evaluation of fine-scale movement patterns in this species. In addi-

tion, all tracked fish (mean TL \pm SD, 605 \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 estimate of red snapper median residency was 23 mo and annual site fidelity was 82% yr^{-1} , both of which were higher than most previous telemetry studies in the same region in the northern GOM (Szedlmayer 1997, Szedlmayer & Schroepfer 2005, Peabody & Wilson 2006, Topping & Szedlmayer 2011b, Piraino & Szedlmayer 2014). One other study reported similar high red snapper site fidelity at 88% after 10 mo based on VPS methods (Piraino & Szedlmayer 2014), while another study reported a slightly lower red snapper site fidelity at 72% yr^{-1} over >3 yr based on frequency of tag detections (Topping & Szedlmayer 2011b). Similar to other red snapper telemetry studies (Szedlmayer & Schroepfer 2005, Topping & Szedlmayer 2011b, Piraino & Szedlmayer 2014), the site fidelity in the present study was higher than that in previous mark-recapture studies (Patterson et al. 2001, Patterson & Cowan 2003, Addis et al. 2007, Diamond et al. 2007, Strelcheck et al. 2007). For example, Strelcheck et al. (2007) estimated 51.5% yr^{-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 estimated instantaneous emigration, an estimated decline of recapture rate, and a fixed mortality rate (e.g. Patterson & Cowan 2003, Strelcheck et al. 2007) or estimated site fidelity based on the number of recaptures reported by anglers at release sites versus away from release sites (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 ($E = 0.72 \text{ yr}^{-1}$) 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 by removal of known events (i.e. emigration and mortality) based on accurate positions and movement patterns from the VPS array following a specified 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-Grove & Szedlmayer in press). The greatly increased accuracy provided by telemetry methods has led to increased site fidelity estimates in the present study, as well as in previous studies (Topping & Szedlmayer 2011b, Piraino & Szedlmayer 2014).

Red snapper in the present study were tracked over long periods (up to 1096 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 & Szedlmayer 2012).

Diel movements

In the GOM, fishes typically forage at different times over a 24 h period, 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 independently for each 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 diel patterns support an earlier VPS tracking study that suggested red snapper behaves more like a prey fish species, having significantly larger home ranges during day, less movement at night, and the smallest home ranges during dawn and dusk (Piraino & Szedlmayer 2014). As described previously in other species (Collette & Talbot 1972, Hobson 1972, Helfman 1986, Hixon 1991) and suggested for red snapper (Piraino & Szedlmayer 2014), prey species enter a quiet period during dusk and dawn to avoid predation when larger predators are most efficient. In the present study area in the northern GOM (10–40 m depth) many larger shark species are common, including the 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 fre-

quently (about 1 out of 3 SCUBA dives) encountered larger (>2 m) Carcharhinidae during the quarterly exchange of VR2W receivers.

Red snapper on 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 & Schroepfer 2005, Topping & Szedlmayer 2011a,b).

Thus, in the present study, diel movement patterns agree with both of these contrasting patterns. The movement patterns are likely related to foraging, 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 of 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 due to substrate types. Abele (1974) showed that the abundance of decapod crustacean species 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 & Szedlmayer 2003, Szedlmayer & Lee 2004, McCawley & 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 to allow greater night foraging efficiency than was possible at the deeper reef sites. Several of the previous telemetry studies that detected movements away from the reef at night were at depths similar to that of R3 in the present study (Schroepfer & Szedlmayer 2006, Topping & Szedlmayer 2011a,b). Diel differences among sites could also be related to different reef fish densities, e.g. as reef fish density increases, competition for food may increase forcing resident fish to increase foraging (Gallaway et al. 2009, Jaxion-Harm & Szedlmayer 2015). Red snapper and gray triggerfish, *Balistes capricus*, were consistently at greater densities

on R3 than on 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 warmer months (summer and fall) compared to colder months (winter) and were significantly correlated with water temperature, supporting previous fine-scale red snapper movement patterns (Piraino & Szedlmayer 2014). Seasonal differences in area use and the number of sites visited by red snapper within the VPS arrays are 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 & Dunn 1987).

In the present study, comparisons of time on the VPS reef site, secondary sites, and open habitat showed that most (77%) 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 colder winter months and highest during warmer 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 greatest amount of time over 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 most of their time on the VPS sites (93%), and little time on secondary sites (5%) or over open habitat (2%). Piraino & 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 = 17, 30%), additional movements were successfully detected for 88% of these fish by the surrounding receiver array. Most (53%) remained on a nearby reef site (~1.5 km away from the 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 (minimum: 23 d) or subsequent emigration (minimum: 90 d) supports several concepts: (1) it validates that red snapper emigrated from VPS arrays and were not involved in 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 with artificial reefs; and (3) it indicates reef hopping behavior, during which 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 very short tracking times (<1–30 min), including hatchlings of flatback turtle *Natator depressus* (Thums et al. 2013), southern flounder *Paralichthys lethostigma* (Furey et al. 2013), American lobster *Homarus americanus* (McMahan et al. 2013), burbot *Lota lota* (Cott et al. 2015), and bonefish *Albula vulpes*, permit *Trachinotus falcatus*, and great barracuda *Sphyraena barracuda* (Finn et al. 2014). Other studies that tracked fish for longer periods (27–694 d) also observed migrations, including white croaker *Genyonemus lineatus* (Wolfe & Lowe 2015), gray smoothhound *Mustelus californicus* (Espinoza et al. 2011), lingcod *Ophiodon elongatus* (Andrews et al. 2011), Atlantic cod *Gadus morhua* (Dean et al. 2014) and red snapper (maximum: 694 d; Piraino & Szedlmayer 2014). Emigrations were identified when transmitter-tagged individuals displayed normal behaviors upon exiting the VPS array. In a few studies, emigrations were confirmed when fish returned to their original VPS tagging sites (Dean et al. 2014, Finn et al. 2014, Wolfe & Lowe 2015). For example, Atlantic cod (n = 17 out of 43) returned to the monitored spawning grounds 1 yr 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 15 out of 17 of the VPS-identified emigrations

and large-scale homing behavior (km distances) for 3 red snapper.

Some previous mark-recapture studies that relied on fisher returns to calculate the 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 & 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 estimated the maximum distance moved was 16 km. However, this fisher-reported recapture location was incorrect, as the VPS telemetry position 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 & Schroepfer 2005). Despite these difficulties of false location reports, 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 55–94% of recaptured fish remaining on their initial tagging site (Szedlmayer & Shipp 1994, Watterson et al. 1998, Patterson et al. 2001, 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 & Szedlmayer 2003, Gallaway et al. 2009); however, if prey resources become depleted, fish will move to higher quality habitat (e.g. Chapman & 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 at original release sites, make greater movements, and

show an increased use of other reef sites (Szedlmayer & Schroepfer 2005, Topping & Szedlmayer 2011a, Piraino & Szedlmayer 2014).

Several species of Lutjanidae have shown movements that are also related to spawning (Wicklund 1969, Carter & Perrine 1994, Domeier & Colin 1997). In the GOM, life-history studies on red snapper showed early maturation (earliest: ~2 yr), spawning from May to September, and increased fecundity and spawning in older fish (Szedlmayer & 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 (S. T. Szedlmayer unpubl. data). However, seasonal differences in emigration rates were detected. The majority of red snapper emigrated during the winter (41%) and spring (47%) months. No significant patterns between fish size and emigration were detected; however, emigrations during the spring months were made by larger red snapper (mean \pm SD: 594 \pm 89 mm TL), 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 yr old (Szedlmayer & Shipp 1994, Wilson & Nieland 2001). Older (\geq 6 yr) red snapper have been reported to spawn at a 50% greater frequency compared to younger red snapper (\leq 5 yr; 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 2 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.

Differences in emigration may also be attributed to lower temperatures. For example, seasonal movements of red snapper due to the passage of cold fronts has been reported (Topping & Szedlmayer 2011b). Many other species of coastal marine fish are known to make annual inshore and offshore migrations due to changing water temperatures and regularly overwinter farther offshore in relatively higher water temperatures (Stokes 1977, Pittman & McAlpine 2003). Topping & Szedlmayer (2011b) reported seasonal emigration rates different to those found in the present study, with 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 & Szedlmayer 2011b). No major storm events occurred during the present study.

Paired emigrations

Four fish emigrated from our shallowest VPS site (R3) at the beginning of winter, when the water temperature decreased to 19°C in 2012 and 2013. The day of emigration did not take place the first day that water temperatures fell below 20°C in either year, nor did it take place at the lowest temperature observed during the winter season, which occurred during February (2012 = 13.2°C and 2013 = 14.9°C). Movements were significantly smaller during the winter and spring months but emigration rates were the highest. The paired movements of 2 red snapper during the same month (December) 1 yr 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 than observed. Although the cause of these movements is unknown, their occurrence 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, 1986, Parrish & Edelstein-Keshet 1999, Soria et al. 2007). It is possible that the paired emigrations observed were fish increasing protection from predators by leaving in groups from their 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 at both sites on 6 May 2014 and recaptured 1 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 & Schroepfer 2005, Topping & Szedlmayer 2011a,b, Piraino & Szedlmayer 2014). The tagged red snapper that was recaptured and re-released in 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 4.1 million fish positions used in the present study showed that red snapper were closely associated with artificial reef structures over long periods of time (>1096 d). The present study confirmed previous long-term (>1 yr) telemetry studies that showed red snapper had high residency and site fidelity. Similarly, fish size positively correlated with area used, and monthly movements positively correlated with water temperature, whereby tagged red snapper stayed close to the VPS site (99%) during the coldest winter months. The use of a second reef site was shown for most red snapper (77%), and time spent on the secondary site was greatest in the warmer 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 spawning, shelter, and additional foraging, or due to environmental factors or fisher-capture effects indicate that both 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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