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ABSTRACT

Red snapper (*Lutjanus campechanus*) are at the center of many artificial reef efforts in the Gulf of Mexico. To elucidate red snapper use of artificial structure for fisheries management, their fine-scale movements need to be examined further. Much effort until now has focused on examining movement patterns of red snapper at isolated reef structures, yet fish may behave differently on reefs covering larger areas. To address this, 15 red snapper were internally tagged with V9P transmitter tags and tracked with VR2W receivers for three months at a large artificial reef (PS-1047, 0.8 km^2, bottom depth range 21 m–23 m) that was comprised of a tugboat and over 4800 concrete culverts deployed randomly around the area. Ten receivers were arranged on the reef to calculate center of activity and depth for each fish every 20 min. Kernel densities (KDE) were calculated at 95% (77,905.04 $\pm$ 1843.27 m^2) and 50% (16,797.25 $\pm$ 413.02 m^2) to address home range and core area use, respectively. There were differences in KDE and depth per day, and depth exhibited diel patterns. There were significant decreases in KDE and increases in depth use after a drastic drop in sea surface temperature. Overall fish use of PS-1047 resulted in two key areas (50% KDE), which comprised of two main groups of fish without overlap and highlighted two different structure areas (tugboat vs. culvert). Home range and core area values were more than 4 times larger than reported in other studies on red snapper.

1. Introduction

As the fourth most valuable fishery in the Gulf of Mexico (GOM), red snapper (*Lutjanus campechanus*) require management to lift their overfished status (Brown et al., 1989; Gallaway et al., 2017). For several decades, artificial reefs have been considered an important management tool for increasing available habitat with the intent of increasing sportfish abundance, especially in areas with limited natural habitat (Bombace et al., 1994; Stephan et al., 2013). Red snapper are heavily associated with artificial and natural reefs, and newly deployed material becomes quickly colonized by the species (Arney et al., 2017; Streich et al., 2017a). As a long-lived demersal species, red snapper settle as juveniles on small rubble and oyster beds, moving to larger reefs as they mature, until moving freely on open bottom after 8 + years (Gallaway et al., 2009). During the time of structural dependency, red snapper are found schooling on artificial reefs at all post-larval stages (Arney et al., 2017; Gallaway et al., 2009).

Acoustic telemetry is an important tool in understanding how red snapper use their associated artificial habitats and can provide information regarding the design of effective red snapper habitat. At artificial reefs, some studies suggest that red snapper exhibit high site fidelity (Garcia, 2013; Piraino and Szedlmayer, 2014; Strelcheck et al., 2009; Szedlmayer and Schroepfer, 2005; Topping and Szedlmayer, 2011), while others report low site fidelity (Addis et al., 2016, 2013; McDonough and Cowan, 2009; Patterson et al., 2001; Peabody, 2004), yet the duration of tracking varies amongst studies. Home range studies have found that red snapper vary their behavior with temperature by decreasing home range and going deeper in colder time periods (McDonough and Cowan, 2009; Piraino and Szedlmayer, 2014; Williams-Grove and Szedlmayer, 2017), and by changing behavior with time of day (McDonough and Cowan, 2009; Piraino and Szedlmayer, 2014; Topping and Szedlmayer, 2011; Williams-Grove and Szedlmayer, 2017, 2016), and body size (Piraino and Szedlmayer, 2014; Topping and Szedlmayer, 2011). These studies are important to understand foraging behaviors of red snapper and their dependency and preference for different artificial structures.

Most home range studies have tracked red snapper for 9–24-h periods (Szedlmayer and Schroepfer, 2005; Topping and Szedlmayer, 2011), or 1–2 weeks (McDonough and Cowan, 2009), with only recent studies examining longer movement patterns (Piraino and Szedlmayer,

2014; Williams-Grove and Szedlmayer, 2017, 2016). These projects have only been conducted in the northern GOM, but red snapper vary in morphometric measures (age and length) throughout the GOM (Fischer et al., 2004; Futch and Bruger, 1976; Saari et al., 2014; Streich et al., 2017b; Syc and Szedlmayer, 2012; Wilson and Nieland, 2001). Fishing season for red snapper also varies across the GOM (e.g. Texas waters are open year-round except for 2017), whereas Alabama waters have heavily truncated fishing seasons. These different levels of fishing pressure could impact population age, growth (Coleman et al., 2004; Manooch, 1976), and behavior (Feary et al., 2011; Heino and Godø, 2002). Different states also utilize different man-made reefing materials to construct their reefs. Northern GOM (Alabama and Louisiana) spends much of its deployments on dispersing decommissioned oil platforms, and small-scale reefing units (ex: cars, army tankers, steel cages, and barges), while northwestern GOM (primarily Texas) use decommissioned oil platforms, vessels, and large-scale mid-relief structures sometimes covering $> 1\,km^2$.

Studies that address red snapper home range over 24-h intervals or more have only focused on single or a few closely-associated artificial reefs with large bare-buffer zones, by either studying mid-relief units covering $25\,m^2$ or less area (Piraino and Szedlmayer, 2014; Topping and Szedlmayer, 2011; Williams-Grove and Szedlmayer, 2017, 2016), or a few high-relief petroleum platforms within 100 m from each other (McDonough and Cowan, 2009). However, red snapper behaviors may differ on reefs with larger bottom coverage (Kramer and Chapman, 1999). Thus, the current study addressed movement patterns of red snapper across a large artificial reef, which covered 0.8-km^2 area with material dispersed throughout and in close proximity. Temporal patterns of home range and depth were investigated to further understand red snapper behaviors on the reef. Three hypotheses were examined: (1) red snapper would vary their depth throughout the day and stay deeper in colder temperatures; (2) red snapper home ranges would follow diurnal patterns (larger at night), would be reduced in colder temperatures, and all individuals' home ranges would overlap over the whole reefing area; and (3) red snapper would exhibit relatively high site fidelity to their tagging sites.

2. Methods

2.1. Study area

Red snapper were tagged and tracked at an artificial reef 12 km from Port Mansfield, TX. In 2011, the Texas Parks and Wildlife Department Artificial Reef Program completed deployment of the study site, called Port Mansfield Nearshore Reef (PS-1047, N 26.52736 W −97.15278). The initial reef deployment was completed in 2007 where a 30-m tugboat (Fig. 1) and 800 culverts (~1 m × 3 m) were placed on the southwest portion of the reefing area. Then in 2011, 4,000 additional culverts were added scattered around the center of the reefing area. The reef was also composed of a few small natural patches (~5 m × 10 m) at a 21-m depth (Fig. 1). From the total 647,497-m^2 reefing area, artificial habitat covered roughly 168,000 m^2, preexisting natural habitat covered 3,000 m^2, and the rest was sand and mud bottom (476,497 m^2). Vertical relief varied from 2 m at culverts to 4 m at the tugboat.

2.2. Acoustic telemetry

In August 2012, red snapper were caught at 20 m by scuba divers using underwater hook and line at two different locations over structure (tugboat and northern culvert patch) at the reef (Fig. 1). Each individual was surgically implanted with a V9P transmitter tag (9-mm diameter × 44-mm length, VEMCO LTD, Nova Scotia, Canada) following underwater surgery techniques outlined in Starr et al. (2000). All transmitters operated at 69 kHz to transmit alphanumeric identification and pressure (depth) data on average every three min and had an estimated tag life of 322 d. After capture, individuals were strapped to a table at an 18-m depth underwater, measured for total length (TL mm), and a floy dart tag was injected externally along the dorsal fin. A 15-mm incision was created halfway between the pelvic girdle and anus, the V9P tag was inserted, and the opening was sutured with an absorbable monofilament thread (Ethicon 2-0). Fish were released after full recovery, indicated by active swimming motion until individuals could no longer be held in place by hand. Animal handling protocols were approved by the University of Texas at Brownsville Institutional Animal Care and Use Committee (20011-004-IACUC).

From November 3, 2012 to February 2, 2013, ten VR2W receivers (VEMCO LTD) were set up in a large array (Fig. 1). Receivers were spaced 254.75 ± 19.21 m from each other 3-m above the seafloor with the hydrophone facing upwards, as recommended by the manufacturer. Two reference V9P transmitter tags were deployed in November and December 2012 for several hours to ground-truth receivers. Reference tags were detected up to 400-m away from receivers.

2.3. Data analysis

Sea surface water temperature was compiled from the National Oceanic and Atmospheric Administration's National Data Buoy Center (http://www.ndbc.noaa.gov/obs.shtml) at buoy station 42044 (N 26.191 W -97.051). The buoy did not collect any data on November 3 and 11 in 2012 or after January 7, 2013 in the current study's sampling interval. Thus, three other buoys (station 42019: N 27.907 W -95.352, station 42020: N 26.489 W -96.214, and station 42048: N 27.939 W -96.843) were used to calculate changes in water temperature during those periods since each station had missing data. To account for different regional sea surface temperatures at each buoy, only the change in temperature at each buoy was calculated and averaged across the three buoys. The averaged change in temperature was then applied to the temperature recorded at the buoy station 42,044 to calculate missing temperature data.

Receiver data were downloaded with the VEMCO VUE software, and depth measures of individual fish were averaged across all receivers every 20 min. Daily depth use by fish was analyzed using a two-way mixed model analysis of covariance (ANCOVA), using fish as a random factor, day as a fixed factor, and sea surface temperature as a covariate. Depth use was compared by hour using a two-way mixed model analysis of variance (ANOVA), with fish as a random factor and hour as a fixed factor.

To determine the position of each fish every 20 min for home range and core area measures, short term center of activity (COA) positions were calculated using the arithmetic mean from (Simpfendorfer et al., 2002):

$$\text{latitude} = \left(\sum_{i=1}^{10} \text{latitude}(r_i)^*p_{r_i} \right)/p_{total} \tag{1}$$

$$\text{longitude} = \left(\sum_{i=1}^{10} \text{longitude}(r_i)^*p_{r_i} \right)/p_{total} \tag{2}$$

where p is the number of points in a 20-min time interval, and r is each receiver deployed. The COA methodology has been used successfully in previous studies for home range measurements and has been shown to yield similar results to calculations from acoustic positioning systems (Dance and Rooker, 2015; Moulton et al., 2017). Home range analysis was based on the percent probability that an individual would be located in the area calculated (Seaman and Powell, 1996; Worton, 1989). To calculate home range (95% chance of detecting the fish in the area) and core area (50% chance of detecting the fish), kernel density (KDE) was calculated. KDE calculations were completed in the R program (version 4.3.2) with the adehabitatHR package, using kernel utilization distribution, and visualized in ESRI ArcGIS for Desktop 10.5. The KDE calculations used a bivariate normal kernel:
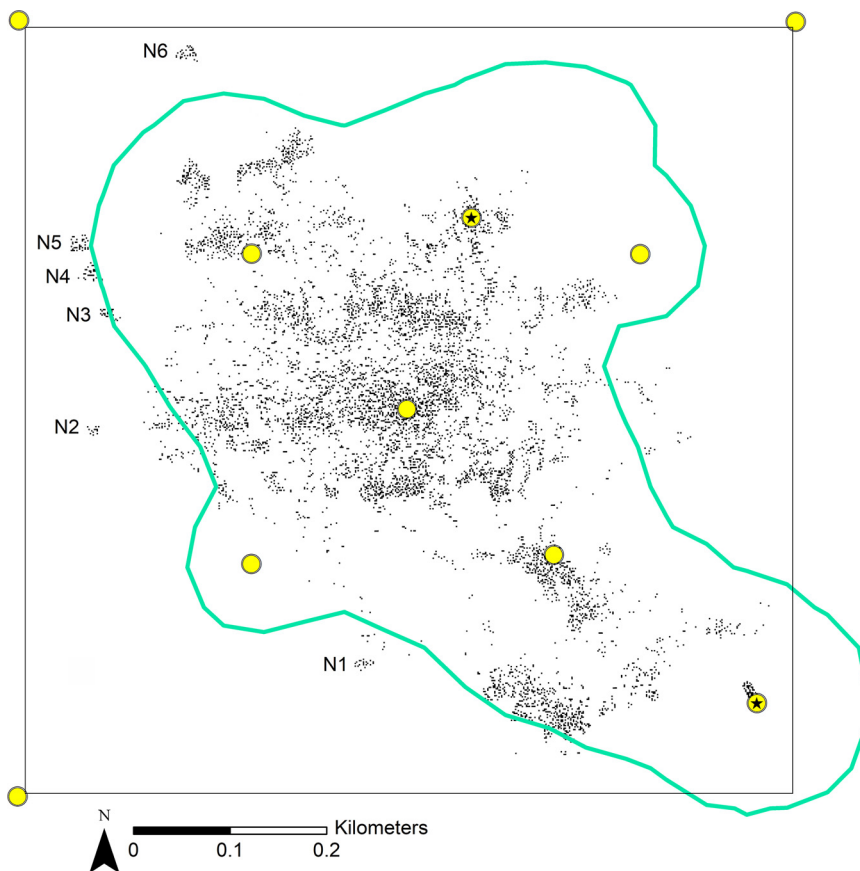
Fig. 1. Sample site, PS-1047, made up of artificial material (black pixeled structures were isolated from a side scan basemap) and natural patches (pixel groups numbered by N#) dispersed throughout sand and mud bottom (background), where red snapper were tagged (star markers; tugboat lies at the southeast tagging location) and tracked with VR2W receivers (yellow circle symbols). The black square identifies reefing area. The blue outline is the 95% kernel density of all fish detections combined. The artificial material includes over 4,800 concrete culverts and one tugboat (at the bottom right tagged location) (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.).

$$K(x) = \frac{1}{2\pi}\exp(-\frac{1}{2}x^t x) \tag{3}$$

$$f(x) = \frac{1}{nh^2}\sum_{i=1}^{n} K\left\{\frac{1}{h}(x\text{-}X_i)\right\} \tag{4}$$

$$h = \sigma \times n^{-1/6} \tag{5}$$

$$\sigma = 0.5 \times (\sigma_a + \sigma_b) \tag{6}$$

where x is the vector containing both coordinates and t is t^{th} sample, h is the smoothing parameter, n is the number of relocations, X_i is the ith relocation of the sample, and σ_a and σ_b are the standard deviations of the coordinates of the relocation.

To compare KDE values per fish, COA positions were only included for 20-min periods when a fish was detected on at least 2 VR2W receivers. Home range and core area per fish were calculated by day, 3-h periods, and day/night (dawn = 0700, dusk = 1800). KDE values were compared by day, hour and day/night with two-way mixed model ANOVA, with fish as a random factor and the temporal measure as a fixed factor. Daily KDE values were compared to sea surface temperature and total length using linear regressions. KDE by 3-h period was compared to total length using linear regressions.

While inspecting sea surface temperature data, three visually noticeable temperature drops were observed with greater than 3 °C drop in 7 days, and 3 respective time blocks (TB) were identified to address red snapper behaviors in those blocks: TB1 = November 2–14, 2012 (24–26 °C), TB2 = November 15, 2012–January 2, 2013 (20–24 °C), and TB3 = January 3–February 2, 2013 (14–20 °C). KDE values were calculated per time block per fish and were then compared using two-way mixed model ANOVAs, using fish as a random factor and time blocks as a fixed factor. A dataset of all red snapper that were present throughout the study (Table 1) was used to determine which areas of the reef were most heavily used (Fish 3, Fish 11 and 13 were omitted due to limited detection in each time block). Two areas of reef were

used by different fish groups, and a combined kernel density was calculated per fish group for each time block.

To test whether red snapper exhibited site fidelity to their original tagged locations, distance (d) of red snapper positions relative to their original tagged locations were calculated with the Pracma package in R using the haversine formula (Sinnott, 1984):

$$a = \sin^2(\Delta latitude/2) + \cos(latitude_1) * \cos(latitude_2) * \sin^2(\Delta longitude/2) \tag{7}$$

$$c = 2\arctan2(\sqrt{a}, \sqrt{(1-a)}) \tag{8}$$

$$d = Rc \tag{9}$$

where R is the earth's radius (mean radius = 6,371 km). Distances to tagged locations were compared with a two-way mixed model ANCOVA, with fish as a random factor, tagged location as a fixed factor, and total length as a covariate.

All analyses were tested for normality with Q-Q plots, boxplots, and homoscedasticity with Levene's test. To meet normality, the following variables were square-root transformed: daily KDE, day and night KDE, and time block KDE per fish. Tukey HSD tests pairwise comparisons were completed for pairwise comparisons. Two-way ANOVAs were reported as analyzed because the test was robust even if Levene's homogeneity was not met (Sokal and Rohlf, 2012). Data analysis was completed in IBM SPSS Statistics (v24). All data in text was reported as mean with standard error and significance tested at α = 0.05.

3. Results

Fifteen red snapper were tagged at two different locations in the month of August, and their presence-at-reef ranged from a few days to three months during the length of the study (Table 1). There were 6 natural patches at the study location. However, only four of the 15 fish

Table 1

Presence-at-reef of tagged red snapper at PS-1047 and kernel density per fish. Tugboat = N 26.52278 W −97.15000. Culvert = N 26.52736 W −97.15278. TL = total length, KDE = mean daily kernel density and standard error.

FISH ID	TL (mm)	Tagging Area	Tagging Date	Presence-at-reef during Study	# Days Present	95% KDE (m²)	50% KDE (m²)
1	368	Culvert	08/22/2012	11-3-2012–2-2-2013	92	72,134 ± 5,579	15,974 ± 1,199
2	379	Tugboat	08/21/2012	11-3-2012–2-2-2013	92	33,701 ± 3,055	7,055 ± 669
3	400	Tugboat	08/21/2012	11-14-2012–2-2-2013	81	53,610 ± 5,477	11,789 ± 1,119
4	370	Culvert	08/30/2012	11-3-2012–2-2-2013	92	123,368 ± 7,311	25,310 ± 1,726
5	420	Tugboat	08/20/2012	11-3-2012–2-2-2013	92	86,995 ± 7,561	17,895 ± 1,621
6	450	Tugboat	08/21/2012	11-3-2012 to 12-3-2012	27	60,583 ± 19,389	13,248 ± 4,314
7	440	Culvert	08/30/2012	11-3-2012–2-2-2013	92	158,970 ± 10,246	32,514 ± 2,322
8	428	Culvert	08/22/2012	11-3-2012–2-2-2013	92	73,252 ± 5,036	14,969 ± 1,039
9	395	Tugboat	08/21/2012	11-3-2012–2-2-2013	92	149,841 ± 10,839	32,107 ± 2,436
10	470	Tugboat	08/21/2012	11-3-2012–2-2-2013	92	66,825 ± 3,907	14,871 ± 974
11	450	Culvert	08/22/2012	11-3-2012 to 11-7-2012	5	72,282 ± 12,167	15,880 ± 3,774
12	398	Culvert	08/22/2012	11-3-2012–2-2-2013	92	107,487 ± 6,268	22,470 ± 1,453
13	401	Culvert	08/22/2012	11-3-2012 to 11-10-2012	8	133,017 ± 33,352	25,675 ± 6,886
14	470	Culvert	08/30/2012	11-11–2012 to 12-30-2012	50	99,455 ± 7,011	19,965 ± 1,242
15	450	Culvert	08/30/2012	11-3-2012–2-2-2013	92	135,043 ± 11,376	28,794 ± 2,683

were ever recorded at natural patches for a total of 6 individual 20-min recordings, and all six were detected at the same natural patch (N1 south patch in Fig. 1). For the presence-at-reef of each individual (Table 1), fish were detected 91.38 ± 1.97% of the time. When fish were detected, there were on average 7.063 ± 0.018 detections (maximum = 38) per fish per 20 min and 3.071 ± 0.007 number of receivers (maximum = 10) that detected the same fish per 20 min. When all fish were combined, a 95% kernel density (KDE) suggested that the majority of artificial habitat was used by fish on a consistent basis (Fig. 1).

3.1. Depth

Red snapper depth was on average 18.73 ± 0.01 m and ranged from 4.27 to 22.84 m over the reef (structure was anywhere from 19 m to 23 m). Depth varied significantly among sampling days (Fig. 2, ANCOVA: $F_{(91,31186)}$ = 14.930, p < 0.001), and depth increased significantly as surface water temperature decreased ($F_{(1,31186)}$ = 10.226, p = 0.001). Depth varied by sampling hour throughout the study (Fig. 3, ANOVA: $F_{(23,72852)}$ = 7.160, p < 0.001). There was a peak in
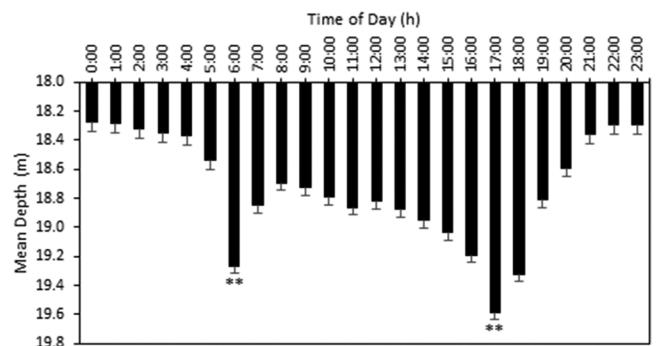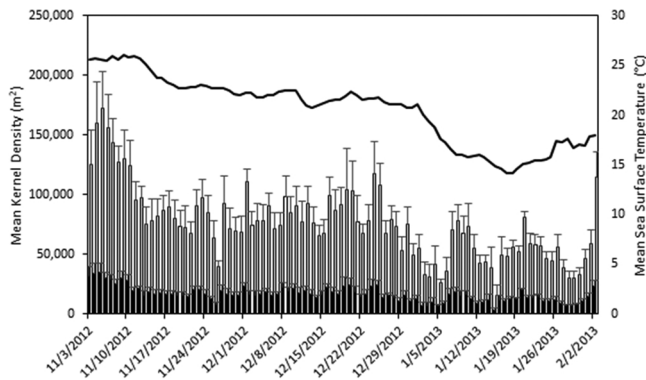
Fig. 3. Mean (± standard error) depth of 15 red snapper by sampling hour on PS-1047. Asterisks highlight hours that are significantly different from all other hours.

maximum depth around 0600-0700 and 1700–1800 throughout the study, which coincided with the onset of sunrise and sunset, and fish were deeper during the day (19.00 ± 0.05 m) than at night
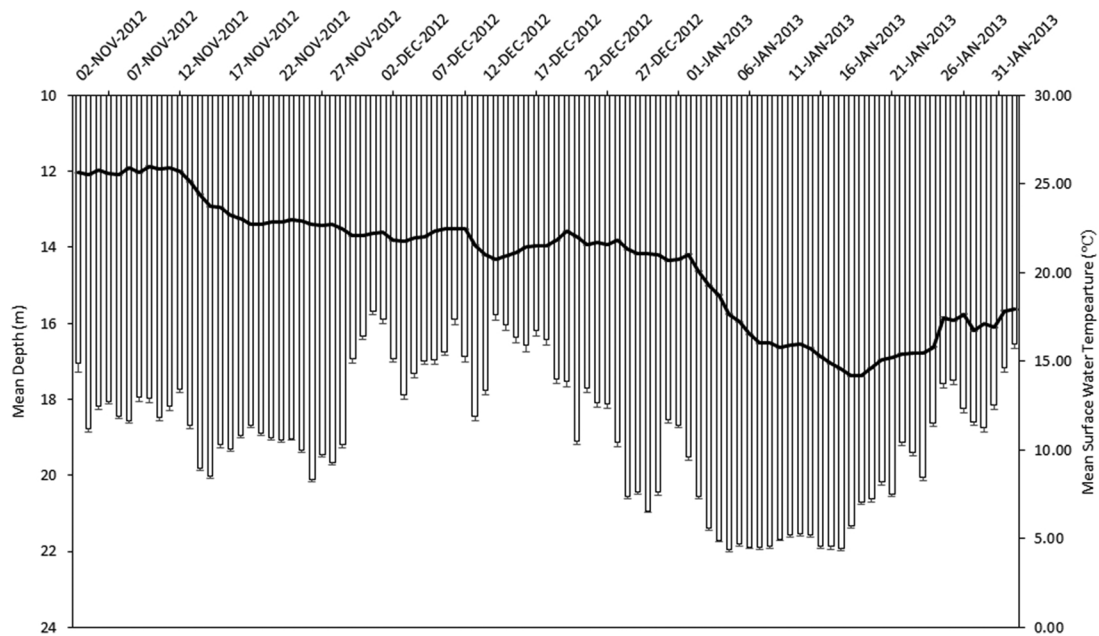
Fig. 2. Mean (± standard error) depth (white bars) of 15 red snapper from November 2012 to February 2013 at PS-1047, with changes in surface water temperature (black line) at nearby weather buoys (station 42044: N 26.191, W −97.051, station 42019: N 27.907 W −95.352, station 42020: N 26.489 W −96.214, and station 42048: N 27.939 W −96.843) from the National Oceanic and Atmospheric Administration's National Data Buoy Center.
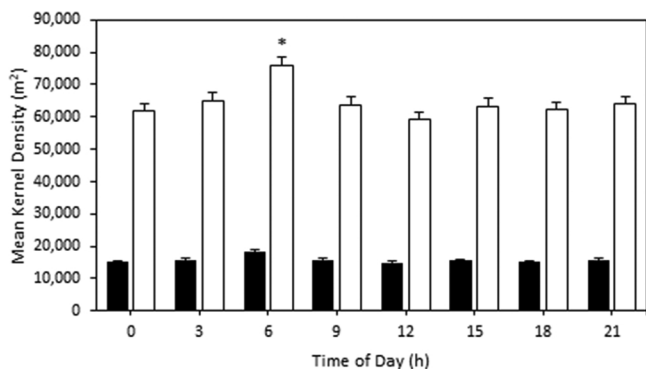
Fig. 4. Mean (± standard error) home range (95%, white bars) and core area (50%, full bars) of 15 red snapper on PS-1047 by sampling date with mean water temperature (black line) overlay.

(18.41 ± 0.06 m, $p < 0.05$, Fig. 3).

3.2. Kernel density patterns

Daily kernel density (KDE) values were on average $77,905.04 \pm 1,843.27$ m^2 for 95% (range 199.81 m^2–$418,528.18$ m^2) and $16,797.25 \pm 413.02$ m^2 for 50% (range 410.00 m^2–$104,346$ m^2). Daily home range KDE values (95%) varied significantly between sampling days (Fig. 4, ANOVA: $F_{(91,909)} = 5.437$, $p < 0.001$). There was a positive relationship between daily home range KDE values and water temperature ($F_{(1,1013)} = 149.544$, $r^2 = 0.128$, $p < 0.001$). Daily core area KDE values (50%) varied significantly between sampling days (Fig. 4, $F_{(91,926)} = 4.516$, $p < 0.001$). As sea surface temperatures decreased, there was a decrease in daily core area KDE values ($F_{(1,1030)} = 108.795$, $r^2 = 0.095$, $p < 0.001$). Larger fish had slightly larger daily home range KDE values ($F_{(1,1013)} = 8.799$, $r^2 = 0.008$, $p = 0.003$) and core area KDE values ($F_{(1,1030)} = 9.379$, $r^2 = 0.008$, $p = 0.002$).

There were significant differences throughout the study between 3-h time periods and KDE home ranges (Fig. 5, $F_{(7,5423)} = 2.981$, $p = 0.004$). Yet, the only time period that was significantly higher than other blocks was period 0600–0900 ($p \le 0.001$) and all other 3-h periods were not significantly different ($p > 0.05$). There was no significant difference between 3-h time periods and KDE core areas (Fig. 5, $F_{(7,6252)} = 1.546$, $p = 0.149$). Per 3-h periods, there was no relationship between fish total length and home range ($F_{(1,5536)} = 1.648$, $r^2 < 0.001$, $p = 0.199$) or core area ($F_{(1,6368)} = 2.854$, $r^2 < 0.001$, $p = 0.091$). Home range KDE values were not significantly different between day ($72,557.95 \pm 1,973.04$ m^2) and night ($72,087.33 \pm 1,873.03$ m^2; $F_{(1,1872)} = 0.009$, $p = 0.923$). Core area

Fig. 5. Mean (± standard error) home range (95%, white bars) and core area (50%, black bars) of 15 red snapper on PS-1047 per 3-h time periods over 24-h cycle throughout the study. Asterisks highlight significant differences.

KDE values also did not vary significantly between day ($16,230.39 \pm 453.84$ m^2) and night ($16,105.08 \pm 414.795$ m^2; $F_{(1,1939)} = 0.012$, $p = 0.914$).

3.3. Time blocks

Due to the changing water temperatures throughout the sampling period, 3 temperature time blocks (TB) were identified to address red snapper behaviors in those blocks (Fish 3, 6, 11 and 13, 14 were removed from analysis due their minimal detection in each time block). There were significant differences between time blocks for home range KDE values (ANOVA: $F_{(2,18)} = 18.542$, $p < 0.001$) and core area KDE values ($F_{(2,18)} = 27.800$, $p < 0.001$). However, TB2 and TB3 were not significantly different from one another for home range (Tukey: $p = 0.586$) or core area ($p = 0.976$). Thus, additional analysis only included two blocks of time: NTB1 = November 2–14, 2012, and NTB2 = November 15, 2012–February 2, 2013 (Fish 3, 11, 13 were removed from analysis due to limited detection in each time block). There were significant differences between NTB1 ($141,020.19 \pm 20,197.83$ m^2) and NTB2 ($88,633.01 \pm 10,501.22$ m^2) for home range KDE values ($F_{(1,11)} = 12.500$, $p = 0.005$) and between NTB1 ($25,005.06 \pm 3,709.35$ m^2) and NTB2 ($15,330.80 \pm 2,201.03$ m^2) for core area KDE values ($F_{(1,11)} = 27.426$, $p < 0.001$). From observing individual kernel densities in both time blocks, there were two groups of fish that were observed (Table 2): (1) around the central culvert area (Culvert group) and (2) around the tugboat and adjacent culvert area (Tugboat group, Fig. 6). Two fish originally tagged at the tugboat area were only ever observed at the culvert area, and one individual tagged at the culvert was only ever observed at the tugboat area (Table 2).

When kernel densities were calculated per fish group for each time block (NTB1 and NTB2), less combined area was used during the colder NTB2. Overall, the culvert fish group used more combined area than the tugboat group (Table 2, Fig. 6). Kernel areas of 50% surrounded the Tugboat area and central culvert area and each were in proximity to a tagged location. When comparing kernel areas of individual fish to the kernel areas derived from all combined fish, different groups of fish were identified. For 50% kernel areas, the central culvert area comprised of the same 8 fish in NTB1 and NTB2, and the tugboat area was comprised of 4 fish in NTB1 and 5 fish in NTB2 (Table 2). There was no overlap between the combined core areas (50%), and each fish stayed in their respective area throughout both time blocks.

3.4. Site fidelity to tagged location

Maximum distances between red snapper positions and tagged locations ranged from 0.06 m to 1037.58 m, and were significantly higher for fish tagged at the culvert location (165.46 ± 1.88 m) than at the tugboat (82.68 ± 1.48 m, $F_{(1,56189)} = 11223.139$, $p < 0.001$). Total length significantly explained some of the variation with larger fish

Table 2
Overlapping kernel density (KDE) core ranges (50%) of red snapper tracked at PS-1047 reef in two time blocks at two key areas. Time Block 1 = November 2–14, 2012, and Time Block 2 = November 15, 2012–February 2, 2013. Numbers represent Fish ID and letters represent where the fish was tagged (C = culvert, T = tugboat). Tugboat = N 26.52278 W −97.15000. Culvert = N 26.52736 W −97.15278.

Area	Time Block 1	Time Block 2
Culvert	4(C), 5(T), 7(C), 8(C), 9(T),	4(C), 5(T), 7(C), 8(C), 9(T),
95% KDE	12(C), 14(C), 15(C)	12(C), 14(C), 15(C)
50% KDE	264,108.60 m^2	137,501.20 m^2
	52,318.08 m^2	23,886.26 m^2
Tugboat	1(C), 2(T), 6(T), 10(T)	1(C), 2(T), 6(T), 10(T)
95% KDE	69,927.17 m^2	57,867.80 m^2
50% KDE	9,734.52 m^2	5,802.11 m^2

(A)

(B)
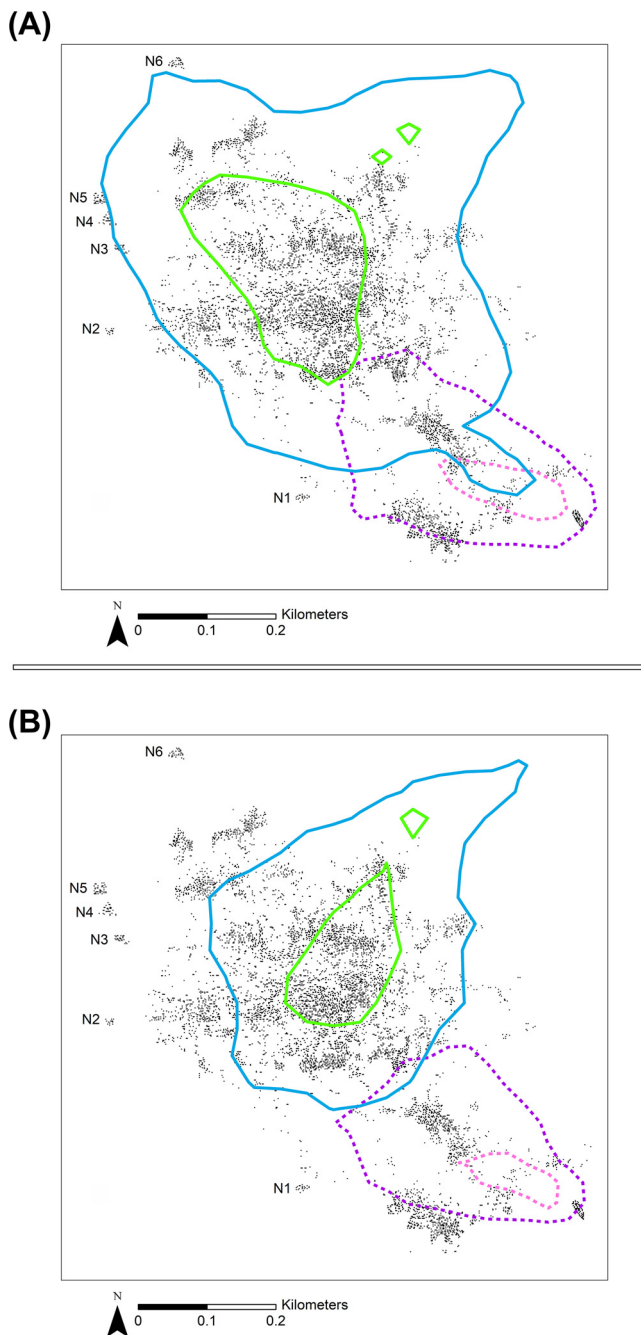
Fig. 6. Kernel densities (KDE) of red snapper (n = 12) at PS-1047 separating two groups of fish (culvert = CG and tugboat = TG) that were present throughout the study in two time blocks (Table 1): (A) Time Block 1 = November 2–14, 2012, and (B) Time Block 2 = November 15, 2012–February 2, 2013. Black pixeled structures were isolated from a side scan sonar image of the site to highlight artificial structure and existing natural patches (numbered by N#) dispersed throughout sand and mud bottom (background). The black square identifies reefing area. 50% KDE of CG = light green solid outline; 95% KDE of CG = dark blue solid outline; 50% KDE of TG = light pink dashed outline, 95% KDE of TG = dark purple dashed outline (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.).

travelling less distance from tagged locations ($F_{(1,56189)}$ = 9182.521, p < 0.001). Two fish out of six tagged at the tugboat and one fish out of nine tagged at the culvert site exhibited larger movement away from the tagged location (Fig. 7); these findings agreed with the fish

identified to have moved away from the tagged location in the kernel densities of overall habitat use prior to the study period (Table 2).

4. Discussion

Red snapper in the current study of a 0.8-km^2 reef exhibited at least four times larger home ranges (95% kernel: 77,905.04 ± 1,843.27 m^2) and core areas (50% kernel: 16,797.25 ± 413.02 m^2) than reported in other studies, in which reef area ranged from 9 m^2 to less than 1,400 m^2 (Piraino and Szedlmayer, 2014; Szedlmayer and Schroepfer, 2005; Topping and Szedlmayer, 2011; Williams-Grove and Szedlmayer, 2016). More studies should publish red snapper home range values to statistically compare home range size with a covariate of artificial reef size. Nevertheless, red snapper in other home range studies were on average larger than in the current study, and exhibited highest home range movement during the spawning season (Piraino and Szedlmayer, 2014; Szedlmayer and Schroepfer, 2005; Topping and Szedlmayer, 2011; Williams-Grove and Szedlmayer, 2016). Such studies suggest that red snapper from the current study might exhibit even higher movement if observed during the spawning season. Having more available habitat may have allowed individuals to be more selective in prey items or may reduce fishing pressure (Kramer and Chapman, 1999). It is also possible that larger area use was due to lower prey availability associated with additional structure and predation (Bortone et al., 1998; Jordan et al., 2005; Lindberg et al., 1990; Strelcheck et al., 2005). Froehlich and Kline (2015) quantified red snapper abundance and size through the same reef as the current study, and found no difference in red snapper abundance throughout the reef but found larger individuals at less structurally dense areas. Size differences may be due to red snapper conspecific aggression in which larger fish occupying reefs push away smaller individuals (Ouzts and Szedlmayer, 2003; Szedlmayer and Lee, 2004). Thus, to increase the efficiency of artificial structure, these findings suggest dispersing material farther apart, which in turn provides more artificial reefs with the same amount of material, increases prey diversity, reduces fishing pressure, and potentially reduces conspecific aggression. As red snapper are one of the leading predators and most abundant fish on artificial reefs (Froehlich and Kline, 2015; Ouzts and Szedlmayer, 2003), providing more reefs may allow more diversity to include other large reef fish species. Compared to other fish species, red snapper in the current study had smaller home ranges than red grouper (*Epinephelus morio*), black grouper (*Mycteroperca bonaci*), and mutton snapper (*Lutjanus analis*) (Farmer and Ault, 2014). On the other hand, red snapper had larger home ranges than Nassau grouper (*Epinephelus striatus*) (Bolden, 2001), coral trout (Zeller, 1997) and gray triggerfish (*Balistes capriscus*) (Herbig and Szedlmayer, 2016), and comparable home ranges to Bermuda chub (*Kyphosus sectatrix*) (Eristhee and Oxenford, 2001).

In some studies, red snapper exhibited more movement during the day (Piraino and Szedlmayer, 2014; Williams-Grove and Szedlmayer, 2017), others had more movement at night (McDonough and Cowan, 2009; Topping and Szedlmayer, 2011), while some had mixed findings based on individuals and study sites (Szedlmayer and Schroepfer, 2005; Williams-Grove and Szedlmayer, 2016). However, in the current study, very few diel patterns were observed for home range or core area values, with more area use only occurring during dawn. The only other diel patterns were observed with red snapper depth, where fish were deepest at dawn and dusk by at least 0.3 m, and fish were deeper during the day than at night by at least 0.5 m. Several studies have presented foraging behaviors as an explanation for diel patterns and suggested more feeding at night away from structure (Gallaway et al., 2009; McDonough and Cowan, 2009; Ouzts and Szedlmayer, 2003; Williams-Grove and Szedlmayer, 2017). Yet peak depth at dusk and dawn and shallowest movement at night suggested crepuscular foraging behaviors coinciding with water column crepuscular prey and benthic prey (Danilowicz and Sale, 1999; Darbyson et al., 2003; Piraino and Szedlmayer, 2014).
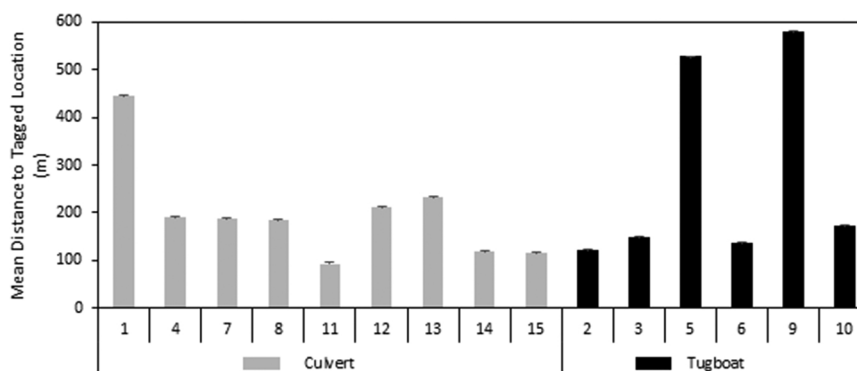
Fig. 7. Site fidelity to tagged locations using mean (± standard error) distances from 15 red snapper positions to their original tagged locations throughout the study at PS-1047. Gray bars indicate fish tagged at the culvert location. Black bars indicate fish tagged at the tugboat location.

Sea surface temperature was an important indicator of fish movement throughout the study. Deeper movement and less activity were observed after cold fronts, similar to other studies (Piraino and Szedlmayer, 2014; Williams-Grove and Szedlmayer, 2017, 2016). Emigration was another response to cold fronts in a study tracking red snapper movement at a similar depth (~20 m) when temperatures reached below 20 °C; the same fish then returned once the 20 °C threshold was surpassed in the spring (Topping and Szedlmayer, 2011). These sensitivities to temperature fluctuations with reduced, deeper activity may be important for energy conservation and keeping body temperatures higher (Gallaway et al., 2009; Schwartzkopf and Cowan, 2017), because deeper waters were less affected by cold fronts. Thus, colder waters resulted in reduced red snapper activity, as seen in another closely associated species, gray triggerfish (Herbig and Szedlmayer, 2016).

Red snapper activity was also affected by the size of individuals, even though fish size in the current study only ranged from 368 to 470 mm, which placed fish at 2–4 years of age (Froehlich et al., 2018). The current study found that larger fish had larger home ranges, which has also been reported in other studies (Piraino and Szedlmayer, 2014; Williams-Grove and Szedlmayer, 2016). Such findings may be attributed to different factors, including the need for more prey, or less energy requirements for swimming (Kramer and Chapman, 1999). However, no relationship was found between depth and length. Thus, sampling a larger size range is warranted to address depth use further.

Two areas were heavily used by red snapper, were identified by the 50% kernel densities, and two distinct groups of fish were observed accordingly. The two areas highlighted two different types of artificial structure: (1) large concentration of culverts versus (2) a single tugboat with interspersed culverts. It is important to note that the two areas were deployed at different times: (1) 2011 and (2) 2007. Individuals tagged at either area were primarily resident in the area initially tagged, with only a few individuals having moved to the other area before the commencement of the telemetry data collection. All individuals were tagged in August, but the latter individuals may have moved away from the original tagged locations before tracking began (November) because they may have preferred a different location during warmer months over colder months due to prey availability or aggression by conspecifics (Almany, 2004; Ouzts and Szedlmayer, 2003). However, all individuals exhibited high site fidelity during the extent of the tracking period, with higher fidelity for those observed at the tugboat. Structural dispersion was higher in the main culvert area, which may explain larger movements away from tagged location by those associated individuals and larger home ranges at the culverts versus the tugboat. Yet, movements by the tugboat fish group may have been underestimated since data receiver coverage was limited. Using the COA method to estimate location may have also reduced home range calculation during times of bad signal detection and range decreases, because reduced detection at peripheral receivers would be

more frequent than at central receivers. Although, the COA methodology has been found comparable to results from acoustic positioning systems (Dance and Rooker, 2015; Moulton et al., 2017), fish may have left the receiver range but still been in the periphery of structure. Thus, home range calculations were only an estimate of minimal possible home range, and red snapper most likely used even more area outside detectable range.

Finding two groups of fish was not surprising since schooling behaviors have been well established for the species (Coleman et al., 2000; Gallaway et al., 2009). There may also have been more than two schooling cohorts in the study site. Red snapper were seldom detected at the dispersed natural reef patches in and around the study site. Froehlich and Kline (2015) observed red snapper at the same study site and found no difference in abundances between natural and artificial reef patches. These findings provide evidence that artificial reefs may not steal individuals from neighboring natural reefs, as was largely hypothesized in the attraction versus production debate (Bohnsack, 1989; Bohnsack and Sutherland, 1985). Instead, different populations of red snapper may exist at the neighboring natural patches. It is also possible that the receiver array design did not allow fish to be detected over natural patches, as these patches were on the periphery of the array. To discern this, red snapper should be tagged at adjacent artificial and natural reefs to assist fisheries management in selecting the placement and construction of future artificial reefs.

5. Conclusion

The current study identified extensive movement of red snapper on a large artificial reef. Contrary to other studies, red snapper in this study used over four times more area than previously recorded. Diel patterns were observed in depth use, but only dawn hours showed differences in home range sizes. Reduced movement patterns of fish and deeper activity coincided with cold fronts. Longer telemetry tracking periods may be warranted to address peak activity during spawning months. It is likely red snapper in the current study may exhibit even higher recorded home ranges during warmer months, especially during spawning and pre-spawning periods. Additionally, two key areas with two associated groups of fish were identified, both groups exhibiting site fidelity. Such findings suggest preference for different types of structures, age of reef, and/or structural dispersion. The current study recommends that fisheries management alter future deployments using two tactics: (1) vary the structural type at a reef to accommodate different habitat preferences; and (2) disperse material over sandy areas to create many isolated reefs from the same amount of material.

Acknowledgements

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