Depth preferences and three-dimensional movements of red snapper, *Lutjanus campechanus*, on an artificial reef in the northern Gulf of Mexico

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Abstract

Several studies have examined the horizontal or two-dimensional (2-D) movements of red snapper, *Lutjanus campechanus*, but none have described the long-term depth preferences of this economically important fish species. Red snapper were tagged with depth transmitters and tracked (n = 7) on an artificial reef site 28 km south of Dauphin Island, Alabama in the northern Gulf of Mexico and movements were tracked for 2 years (VR2W Positioning System, Vemco Ltd, Nova Scotia). More than 3.5 million accurate positions (~ 1 m) were obtained and used to assess red snapper depth patterns over monthly and hourly time periods. In addition, three-dimensional (3-D) patterns of red snapper volume use (m^3) were estimated based on depth and location (latitude, longitude) from > 700,000 3-D positions. Red snapper depth preferences and volume use varied over time periods. Red snapper tended to stay at deeper depths during the colder months (< 3 m from seafloor), and move up in the water column more frequently in the late spring and summer months ($F_{23, 127} = 45.5$, $P < 0.0001$). Similarly, volume use patterns varied significantly by month (core, $F_{23, 127} = 13.14$, $P < 0.0001$; home range, $F_{23, 127} = 27.6$, $P < 0.0001$) with the smallest movements in February and largest in August (2013) or October (2014) depending on year. Diel home range volume showed that red snapper made fewer movements during night (1900 – 0400 h) compared to day (0600 – 1700 h; $F_{23, 3585} = 13.2$, $P < 0.0001$). The present habitat use patterns were surprising, because for the most part red snapper was previously considered a benthic oriented reef species. However, in the present study depth and volume shape patterns showed use of the entire water column during the spring and summer. These higher water column use patterns were likely related to spawning patterns and prey availability over both diel and monthly time periods, but further studies are needed to help confirm such correlations.

Running head: RED SNAPPER 3-D MOVEMENTS AND DEPTH USE

Keywords: ultrasonic, 3-D, VPS telemetry, kernel density estimates, volume use

1. Introduction

The study of depth patterns has mainly been focused on highly mobile fish species of high economic value (e.g. family Scombridae, Istiophoridae, Xiphiidae, Carcharhinidae, Lamnidae). In these species, long-term depth data has been used to describe movement patterns during large-scale migrations over various habitats (Block et al., 1992; Brill and Lutcavage, 2001; Boustany et al., 2002; Block et al., 2005). Depth data has also been used to describe short-term movements often related to specific behaviors such as spawning, foraging, or use of nursery habitats (Josse et al., 1998; Goldman and Anderson, 1999; Dewar et al., 2004; Seitz et al., 2005; Semmens et al., 2006; Starr et al., 2007; Witteveen et al., 2008; Whitney et al., 2010). For example, acoustic telemetry depth tags have been used to describe vertical movement patterns of several exploited species (Erickson and Hightower, 2007; Stevens et al., 2008; Currey et al., 2014), deep water species (Starr et al., 2002; Hulbert et al., 2006; Andrews et al., 2009), and reef-associated species (Luo et al., 2009; O'Toole et al., 2011; Bryars et al., 2012).

Most previous studies have analyzed depth and two-dimensional (2-D) locations (latitude, longitude) patterns in two separate analyses, then combined the results to make inferences about overall fish movements (Simpfendorfer et al., 2012). Few studies have simultaneously examined fish movements in a single three-dimensional (3-D; depth, latitude, and longitude) analysis even though their environment is 3-D. To date, 3-D movements have been examined in captive goldfish, *Carassius auratus* and zebrafish, *Danio rerio* (Zhu and Weng, 2007; Maaswinkel et al., 2013), coastal habitat use in Norway by European eel, *Anguilla anguilla* (Simpfendorfer et al., 2012), movement and spawning season off California of barred sand bass, *Paralabrax nebulifer* (McKinzie et al., 2014), and in long-term movement patterns on the Great Barrier Reef by grey reef shark, *Carcharhinus amblyrhynchos* (Heupel and Simpfendorfer, 2014; Heupel and Simpfendorfer, 2015).

Red snapper have been extensively studied due to their broad distribution in both shallow and deeper waters (~ 10 – 350 m), close association to reef structures (artificial and natural; Gallaway et al., 2009; Dance et al., 2011) and economic importance to both commercial and sport fisheries (SEDAR, 2013). Several tagging studies have used both conventional and transmitter tags to study the horizontal movements of red snapper and have shown high residency (up to 23 months) and site fidelity (up to 88% yr^{-1}) to artificial reef structure (Szedlmayer, 1997; Szedlmayer and Schroepfer, 2005; Strelcheck et al., 2007; Topping and Szedlmayer, 2011b; Piraino and Szedlmayer, 2014; Williams-Grove and Szedlmayer, 2016a). In contrast, other studies have reported greater movements (up to 352 km) and moderate to low annual site fidelity (e.g., 20 to 50%; Watterson et al., 1998; Patterson et al., 2001; Addis et al., 2007; Diamond et al., 2007; Strelcheck et al., 2007). More recently telemetry studies have examined fine-scale (m) 2-D movements of red snapper around artificial reefs and showed smaller movements during dusk and dawn diel periods and winter months (Piraino and Szedlmayer, 2014; Williams-Grove and Szedlmayer, 2016a).

In contrast, there are few studies on the vertical movement patterns of red snapper. For the most part previous studies have inferred that red snapper are a demersal fish species and describe benthic settlement for juvenile stages, a high association with low relief reef structure throughout their life span, and regularly consume benthic-oriented or reef-associated prey species (Goodyear, 1995; Gallaway et al., 2009). However, anecdotal reports from fishers and an earlier study have suggested upper water column use by this species (Collins, 1887). The objectives of the present study were to evaluate these suggestions of upper water column use through long-term (two-year) examination of red snapper vertical movements and 3-D use patterns over monthly and diel time periods.

2. Methods

2.1 Study Site

The present study site was a steel cage artificial reef (2.5 x 2.4 x 1.3 m), at 28 m depth, located 28 km south of Dauphin Island, Alabama, USA in the northern Gulf of Mexico (Figure 1). A Vemco VPS array was deployed at the reef site that included a central VR2W receiver located 20 m north of the reef and four surrounding receivers located 300 m to the north, south, east, and west of the central receiver (reef site). This receiver array design permitted maximum (100%) detection of transmitter tagged red snapper (Piraino and Szedlmayer, 2014). Receivers were positioned ~ 4.5 m above the seafloor and synchronization transmitters were attached 1 m above each receiver (Vemco V16-6x; 69 kHz; transmission delay: 540 – 720 sec). A stationary control transmitter was positioned at a known location within the VPS array to validate the accuracy of Vemco calculated fish positions (Vemco Ltd, Nova Scotia). Additional steel cage artificial reefs were positioned 1.4 – 1.6 km away from the VPS reef. These surrounding reef sites (n = 25) had a single VR2W receiver to verify emigrations from the VPS array (Figure 2). All reef sites were deployed from 2006 to 2010 at unpublished locations (Syc and Szedlmayer, 2012). The VPS receivers (n = 5) were exchanged every three months and surrounding receivers were exchanged every six months by SCUBA divers. Data were subsequently downloaded in the laboratory.

2.2 Fish Tagging and Release Procedures

Red snapper were tagged and released on 17 October 2012 (n = 4), 2 November 2012 (n = 6) and 17 October 2013 (n = 1) and VPS positions determined up to 31 October 2014 (Table 1). The number of red snapper tagged in the present study was limited to about 10 before signal collisions caused decreased detections. With 10 fish we can obtained frequent (< 10 min intervals) and accurate (m) fish positions (Piraino and Szedlmayer, 2014). If more transmitter tagged fish were added transmitter collisions would increase and the frequency of valid detections would decrease (Topping and Szedlmayer, 2011b). All tagged red snapper were larger than the recreational minimum length limits (> 406 mm TL; SEDAR, 2013). In the first attempt of tagging (25 Sep 2012) five red snapper were captured and implanted with transmitters, however hypoxic conditions at depth caused mortality of these fish, while they were still enclosed within the release cage. After this initial failure, DO measures were taken prior to tagging attempts and not carried out if bottom DO < 2.5 ppm. Dissolved oxygen (DO) and temperature were measured at depth prior to fish release (YSI model 6920, YSI Inc., Yellow Springs, Ohio).

Fish tagging methods followed Topping and Szedlmayer (2011a; 2011b; 2013). We caught red snapper by hook-and-line (8/0 circle hook baited with Gulf menhaden, *Brevoortia patronus*). Fish were immediately anesthetized (~ 2 min) with MS-222 (150 mg tricaine methanesulfonate/L seawater) in a seawater tank (70 L) onboard the research vessel. Anesthetized red snapper were weighed (kg) and measured (mm SL, FL, TL). Individually coded depth transmitters (Vemco V16P-6x-R64k, transmission delays = 20 – 69 sec) were inserted into the peritoneal cavity of the red snapper through a small vertical incision (20 mm). The incision site was closed with absorbable, sterile, plain gut surgical sutures (Ethicon 2-0, metric 3). Red snapper were also tagged with internal anchor tags (Floy® FM-95W) with unique identification numbers for external identification by SCUBA divers and fishers. Post-surgery tagged red snapper were held in a recovery tank (185 L) until regular opercula and fin movements were observed before release (< 5 min).

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

In November 2012 (n = 6) and October 2013 (n = 1) red snapper were released using a remotely opening cage (46 x 61 x 61cm; Williams et al., 2015). Recovered fish were placed into the cage at the surface and fish condition was observed for 10 – 20 seconds at ~ 1 m depth. Red snapper in good condition (active upright swimming) were lowered to the seafloor (28 m) where the cage door automatically opened and the recovered fish left on their own initiative (Williams et al., 2015). Cages were retrieved after ≥ 15 min and if a tagged fish had not left the cage on its own initiative it was considered in poor condition and not released.

2.3 Temperature Measures

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

2.4 Residency Analysis

Red snapper positions were calculated by Vemco based on the millisecond time differential of signal arrival at three or more receivers. Fish positions were used to determine the status of tagged fish as active, emigrated, or deceased within the VPS array area. Active fish made continuous movements around the reef, emigrated fish made progressive movements away from the reef center before exiting the VPS array, and deceased fish became stationary (natural morality) or were suddenly absent near the reef (fishing mortality; Williams-Grove and Szedlmayer, 2016b). Residence time was defined as the time period when 50% of the active tagged red snapper were still present.

2.5 Depth Preferences

Depth data were downloaded from the Vemco receivers and statistical analyses were completed with Statistical Analysis Software (SAS Institute Inc., Cary, NC, USA). All depth analyses used Central Standard Time (CST). Depth preferences were evaluated over monthly and diel time periods. Prior to statistical analyses, equality of variances was examined with Levene's test, if variances were unequal the Satterthwaite correction was applied in the SAS Proc Mixed procedure (Satterthwaite, 1946). The effect of time period (month or hour) on depth use was tested with a mixed-model repeated measures analysis of variance (rmANOVA) with fish as a random factor, time period as a repeated measure, and covariance structure as "variance component" (Littell et al., 1998; Cody and Smith, 2006; Zar, 2010). This covariance structure was selected based on comparisons of several different structures and AIC measure of best model fit (Burnham and Anderson, 2002). Depth use was compared to temperature with rmANOVA with temperature as a continuous predictor variable and individual fish as repeated measures. If significant differences were detected with the rmANOVA, a Tukey-Kramer test was applied to show specific differences in depth use over time intervals. We reported depth positions as least square mean ± standard error (SE). Sea floor depth was assumed to be uniform (28 m) throughout the receiver array.

2.6 3-D Kernel Density Estimations

All horizontal positions (latitude and longitude) were converted to Universal Transverse Mercator projection (m) for comparison to depths (m). Three-dimensional (3-D) KDEs were calculated in the R statistical environment with the "ks" package (Duong, 2007; Simpfendorfer et al., 2012; RCoreTeam, 2014). Red snapper VPS locations were used to estimate core volumes or 50% kernel density estimates (KDE) and home range volumes or 95% KDE (Piraino and Szedlmayer 2014). For example, red snapper will be located 50% of the time within the core volume. The effects of month and diel time periods on volume use were tested with rmANOVA as above. Volume was compared to temperature with rmANOVA with temperature as a continuous predictor variable and individual fish as repeated measures. If significant differences were detected with the rmANOVA, a Tukey-Kramer test was applied to show specific differences in volume use over time intervals.

3. Results

3.1 Tagging and Residency

Depth and 3-D fine-scale movements of red snapper were recorded for two years (November 2012 to October 2014) on an artificial reef site in the northern Gulf of Mexico. Fish size ranged from 489 to 702 mm TL (595 ± 69 mm TL; mean ± SD). Subsequently, 11 red snapper were released with depth transmitters. After release, four fish left immediately (within a two day tagging recovery period) for unknown reasons and were not included in any statistical analyses. All other tagged fish (n = 7) were tracked continuously from their release date (379 – 744 d). All seven fish that remained after the two day recovery period stayed on the reef site for the duration of the study. Thus, residency time exceeded the duration of the study, i.e., no fish emigrated, and annual site fidelity was 100% (Table 1). In addition, no fishing or natural mortalities were observed for these tagged red snapper that stayed on the VPS site (survival = 100%) during the present study period (17 Oct 2012 to 31 October 2014).

Additional movements outside the VPS area were detected for the three (out of 4) fish that left the VPS site during the two day tagging recovery period. Fish F71 moved 1.5 km away to a surrounding artificial reef site with a single receiver on the day of tagging (2 November 2012), and remained at this second site for 599 d until 24 June 2014, then was lost. Fish F73 moved south of the VPS area on the day of tagging (2 November 2012) and was intermittingly detected by only the south receiver for the duration of the study (no detections on other receivers). Fish F73 continued to produce depth tag data (> 40,000 detections) on the south receiver that showed changing depths, verifying its survival outside the VPS site. Fish F75 moved away from the VPS site one day after tagging (3 November 2012), was detected on 9 November 2013 at a surrounding reef site 1.5 km away, and remained at the second reef site for 204 d, then was caught and returned by a fisher on 1 June 2013. We were able to reuse the depth transmitter to tag fish F135 in October 2013.

3.2 Depth Preferences

Over 3.5 million depth positions were collected from the seven tracked red snapper (~ 500,000 positions per fish) over the two-year study period. Mean ± SD depth was 21.8 m ± 6.0 m but fish also used the entire water column from the seafloor (28 m) to the water surface (0 m). Mean depth use by red snapper was significantly different for all months ($F_{23, 127} = 45.5$, $P < 0.0001$). Monthly mean depths (mean ± SE) were greater in the winter months (December – February; with a maximum in February 2013 = 27.2 ± 0.77 m and 2014 = 25.5 ± 0.77 m), and shallower in spring and summer (March – August; with a minimum in May 2013 = 17.3 ± 0.77 m and in July 2014 = 14.1 ± 0.77 m). Red snapper mean monthly depth use was significantly related with bottom water temperature ($F_{1, 149} = 40.7$, $P < 0.0001$, $r^2 = 0.38$; Figure 3). Red snapper were significantly deeper at night (2100 – 0200 h) than day periods (0900 – 1300 h, but maximum differences were only 1.7 m ($F_{23, 3738} = 6.2$, $P < 0.0001$).

3.3 3-D Kernel Density Estimations

The present study recorded > 700,000 red snapper positions (latitude, longitude, and depth) to evaluate the fine-scale 3-D movements. A control transmitter showed a mean horizontal (latitude and longitude) accuracy of 2.4 m (SD, 1.5 m) and vertical (depth) position accuracy < 1 m.

Red snapper 3-D movement patterns varied significantly by month-year (core, $F_{23, 127} = 13.14$, $P < 0.0001$; home range, $F_{23, 127} = 27.6$, $P < 0.0001$). For both years, February showed the smallest monthly core volume (2013 = 253 ± 66 m^3; 2014 = 251 ± 282 m^3) and home range volume (2013 = 4664 ± 522 m^3; 2014 = 16890 ± 1620 m^3; Figure 4). The largest core and home range volumes were observed in August 2013 (core = 35679 ± 11311 m^3; home range = 271468 ± 56523 m^3) and October 2014 (core = 43866 ± 8799 m^3; home range = 354332 ± 48822 m^3;

Figure 4). For example, Figure 5 shows a comparison for one year (Jan to Dec 2013) of red snapper 3-D core and home range volumes. Temperature was a significant predictor of month-year core volume ($F_{1, 148}$ = 81.6, P < 0.0001, r^2 = 0.39) and home range volume ($F_{1, 148}$ = 181.4, P < 0.0001, r^2 = 0.57).

Significant diel changes were detected in red snapper volume use (core volume $F_{23, 3585}$ = 6.7, P < 0.0001; home range volume $F_{23, 3585}$ = 13.2, P < 0.0001; Figure 6). Red snapper made smaller movements during the night (1700 – 0500 h) and larger movements during the day (0600 – 1600 h). The smallest core and home range volumes occurred near dawn (0300 – 0400 h) and dusk (1900 h), while the largest core and home range volumes occurred in the late morning (1000 h) and early afternoon (1300 – 1500 h; Figure 6).

4. Discussion

4.1 Seasonal Depth Preferences

The present study is the first to examine detailed annual depth patterns in red snapper and showed significant vertical differences across seasons. Red snapper moved higher up in the water column in summer months, used intermediate depths during spring and fall, and moved closest to the bottom during the winter months (Figure 3). There are several possible factors that could contribute to the observed vertical movement patterns. For example, in the northern Gulf of Mexico, red snapper spawning peaks from May to July (Jackson et al., 2007). In the present study the shallowest monthly depth use corresponded with the peak spawning season period (May 2013 and June 2014). Spawning behaviors in some Lutjanidae has been observed (lane snapper, *Lutjanus synagris*, dog snapper, *L. jocu*, and cubera snapper, *L. cyanopterus*). In these other species, rapid vertical ascents (2 – 40 m) were immediately followed by the release of gametes higher in the water column (in some cases < 10 m from the surface; Wicklund, 1969; Carter and Perrine, 1994; Heyman et al., 2005). At present red snapper spawning behaviors have not been reported in detail, but anecdotal data from the late 1800's observed an abundance of red snapper at the surface during spawning season (Warren, 1898) and in recent years SCUBA divers have observed red snapper making rapid vertical ascents and spawning similar to other Lutjanidae (unpub. per. obs. Szedlmayer and Williams-Grove).

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

Another potential factor that could be increasing vertical movements is foraging activity. Red snapper are known to be active, opportunistic predators consuming a variety of prey species including benthic shrimp and crustaceans, reef-associated fishes, pelagic fishes, squids, and zooplankton (Ouzts and Szedlmayer, 2003; Szedlmayer and Lee, 2004; McCawley et al., 2006; Wells et al., 2008). Thus, it is possible that vertical movements may be related to prey availability higher in the water column.

Lastly, as reported by fishers and observed on sonar during tagging in the present study, red snapper would rise up in the water column upon vessel arrival at the VPS reef site. In fact, this attraction to vessel activity was first reported over 130 years ago (e.g., Stearns, 1885; Collins, 1887). However, the quantity and consistency of vertical movements in the present study suggests that the regular use of the water column is a normal part of red snapper biology, and the significance of vessel attraction to vertical movements is still unknown.

4.2 Seasonal 3-D Movement Patterns

Red snapper showed greater monthly volume use in August 2013 and October 2014 when water temperatures were warmer (fall months) and smaller volumes (core and home range) in February (2013 and 2014) when water temperatures were lower. Few studies have examined the 3-D movements of fish species and in those studies seasonal 3-D movement patterns varied. Similar to the present study, European eels from Norwegian coastal waters showed reduced 3-D movements in winter and greater movements in summer (Simpfendorfer et al., 2012). In contrast, no clear patterns were detected in redthroat emperor, *Lethrinus miniatus*, on Australian coral reefs (Currey et al., 2014). The movement patterns in the present study were consistent with previous fine-scale 2-D patterns where red snapper decreased movements during cooler months and increased movements during warmer months (Piraino and Szedlmayer, 2014; Williams-Grove and Szedlmayer, 2016a). It is likely that these seasonal increases in core volume and home range are positively related to foraging activity. Thus, increased metabolic rates in the warmer months would increase foraging activity and decreased temperatures in the cooler months would reduce foraging activity (Helfman, 1986; Hidalgo et al., 1987; Johnston and Dunn, 1987).

Red snapper used larger volumes during the late spring and summer months. This increase in volume corresponded with regular movements to shallower depths and the spawning season peak (May and June; Collins et al., 2001), but also could be related to other events such as changing abiotic factors (e.g., temperature, dissolved oxygen) or biotic factors (e.g., pelagic prey availability). To date, other 3-D KDE studies in European eel and barred sand bass have shown a positive relation between volume use and spawning activities (Heupel and Simpfendorfer, 2014; McKinzie et al., 2014).

4.3 Diel Depth Preferences

Red snapper showed a small difference (1.7 m) in depth use between night and day hours. Red snapper were marginally closer (1.7 m) to the bottom at night (1900 – 0400 h) and higher in the water column during the day hours (0600 – 1600 h). McDonough (2009) examined hourly depth use for red snapper around oil platforms in the northern Gulf of Mexico, but did not detect diel patterns. However, in that study sampling period was limited to a few weeks, but more importantly artificial lighting is common on oil platforms during the night hours, and is known to alter the behaviors of marine bird and fish species (Wiese et al., 2001; Longcore and Rich, 2004; Keenan et al., 2007). In the northern Gulf of Mexico, a recent 2-D study showed that diel movements of red snapper also differed by reef site (Williams-Grove and Szedlmayer, 2016a) thus, the lack of substantial diel depth preferences on a single reef site in the present study may not be representative of all reef sites.

4.4 Diel 3-D Movement Patterns

Earlier 2-D telemetry studies (manual and remote tracking) reported that red snapper moved farther away from reefs during night hours. These studies suggested that these movements were driven by foraging behaviors allowing red snapper to access additional prey sources during night hours (Peabody, 2004; Szedlmayer and Schroepfer, 2005; McDonough and Cowan, 2007; Topping and Szedlmayer, 2011a, b). In contrast, the first VPS tracking study showed that red snapper had significantly smaller area use during night hours and made larger movements during day hours (Piraino and Szedlmayer, 2014). However, a more recent VPS area study showed that red snapper diel movement patterns differed by reef site and may be related to site depth, substrate, water clarity, and available prey species (Williams-Grove and Szedlmayer, 2016a). Hourly 3-D movement patterns (m^3) in the present study were similar to these previous greater 2-D areas in the day (Piraino and Szedlmayer, 2014). The use of greater volume (m^3) during the day suggests that red snapper largely rely on their vision for activities such as foraging or escaping predation. Laboratory studies have suggested that red snapper are a visual species. Parsons et al. (2012) assessed the ability of juvenile red snapper to exit a test chamber in the laboratory, and a bycatch reduction device attached to a shrimp trawl in the field. In both cases, red snapper more frequently made the appropriate escape movements in the presence of illumination.

Similar to red snapper, the use of smaller volume during the night has also been observed in other common reef-associated fish species. For example, at night western blue groper, *Achoerodus gouldii*, tagged with depth transmitters moved to deeper waters and remained relatively stationary suggesting that this species may seek refuge in caves and crevices (Bryars et al., 2012). Similarly, short-term tracks of white trevally, *Pseudocaranx dentex*, tagged with depth transmitters remained close to the substrate at night and during dawn and dusk periods (Afonso et al., 2009).

In the present study, the smallest movements (m^3) were also observed just before dawn (0300 – 0400 h) and at dusk (1900 h). Similar crepuscular patterns were reported for red snapper in an earlier telemetry study (Piraino and Szedlmayer, 2014). As previously suggested the movements of red snapper during the crepuscular periods resemble prey-like behaviors. Several studies have shown that prey species reduce movements, while apex predators increase foraging during crepuscular periods (Hobson, 1972, 1975; Helfman, 1986). For example, reef-associated apex predators tagged with depth transmitters, such as Caribbean reef shark, *Carcharhinus perezi*, and whitetip reef shark, *Triaenodon obesus*, showed increased movements and shallower depth use at night (Chapman et al., 2007; Whitney et al., 2007; Fitzpatrick et al., 2011). In the northern Gulf of Mexico there are several larger shark species that are potential opportunistic predators on red snapper and common in our study area (10 – 40 m depth), for example, blacktip shark, *Carcharhinus limbatus*, bull shark, sandbar shark, spinner shark, *C. brevipinna*, scalloped hammerhead, *Sphyrna lewini*, and tiger shark, *Galeocerdo cuvier* (Drymon et al., 2010).

4.4 Volume Shape Comparisons

Simpfendorfer et al. (2012) and Zhu and Weng (2007) were the first to evaluate 3-D fish movements in detail. These studies suggested that an advantage to assessing 3-D movements was the ability to separate fish that vertically differed that might otherwise be considered in the same habitat based on 2-D comparisons. This is an advantage in species that vertically separate (i.e., to reduce competition) however, in the present study we observed 3-D volumes that were similar to previous 2-D estimates (Piraino and Szedlmayer, 2014; Williams-Grove and

Szedlmayer, 2016a). These similarities were likely due to many similarities between the studies, including the same reef type (small, isolated artificial reef), high residency of tagged fish, similar size classes, and the same geographical locations of study sites.

In the present study there were differences over time in the shape of volume use. Volume shape had the highest symmetry in months when the water temperature was similar throughout the water column (late summer and winter months). During these months, red snapper made vertical and horizontal movements away from the reef site in similar proportions. During the mid to late fall, surface water temperatures cooled, but home range remained high. Red snapper home range patterns became more compressed making greater lateral movements and fewer vertical movements. In contrast, during the spring months when water temperatures remained cooler red snapper made fewer horizontal movements while vertical movements increased. The consistent patterns of vertical movements made by red snapper over reefs during the late spring and early summer months has not been previously reported. These patterns suggest that in addition to the size of volume, changes the shape of 3-D patterns is important to better understand fish movements especially in species with high residency.

5. Conclusions

This study provided the first detailed depth patterns and 3-D movements for red snapper showing that this previously considered demersal reef species regularly used the entire water column during the late spring and summer months. Over two years we evaluated over 3.5 million depth positions and 700,000 3-D fish positions. The 3-D volume use was significantly related to temperature and increased 3-D movements in the fall, and was likely linked to elevated metabolism and foraging during those months. Depth patterns showed the use of significantly shallower waters during the summer months and deeper waters during the winter months. Future research is needed to better define the effects biotic (e.g. spawning or foraging), and abiotic (e.g. dissolved oxygen or water temperature) factors in water column use differences observed in red snapper. In addition, the further use of depth tags on different size classes of red snapper could provide improved understanding of changing habitat preferences for this long lived species.

6. Acknowledgements

We thank M. Albins, R. Brewton, L. Grove, J. Herbig, D. Horn, J. Jaxion-Harm, S. Landers, P. Mudrak, C. Roberts, and N. Wilson for field assistance. We thank M. Albins and B. Staton for assistance with R-code. This project was funded by the National Oceanic and Atmospheric Administration, National Fisheries Service (MARFIN program award number NOAA-NA11NMF4330126) and the Marine Resources Division of the Alabama Department of Conservation and Natural Resources (Sportfish Restoration Fund AL-F-F14AF00228). This study is a contribution of the Alabama Agricultural Experiment Station and School of Fisheries, Aquaculture, and Aquatic Sciences, Auburn University.

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Figure Captions

Figure 1: Steel cage artificial reef site used in the present study. Dimensions of reef are 2.5 m length x 2.4 m width x 1.3 m height).

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

Figure 3: Temperature and mean monthly depth used by red snapper, *Lutjanus campechanus*, in the northern Gulf of Mexico from November 2012 to October 2014. Primary axis: Gray bars = depth and SD. Line = water temperature at depth.

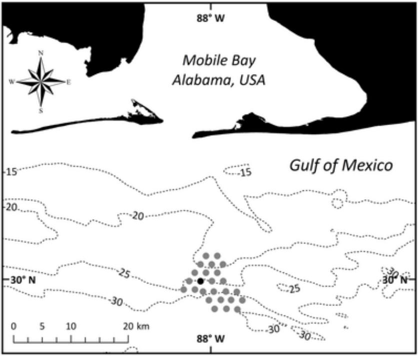
Figure 4: Monthly patterns of 3-D core volume (50% KDE, m^3) and home range volume (95% KDE, m^3) and water temperature for tagged red snapper, *Lutjanus campechanus*, around artificial reefs in the northern Gulf of Mexico. Black bars = core volume (50% KDE), gray bars = home range volume (95% KDE), and error bars = SE.

Figure 5: Comparison of 3-D volume (m^3) use for all tagged red snapper around an artificial reef from January through December 2013. Core volume (50% KDE) = dark gray; home range volume (95% KDE) = light gray; horizontal position (latitude and longitude) = range of 400 m (0 m at reef to 200 m away); and vertical position (depth) = 0 – 30 m.

Figure 6: Diel volume use (m^3) by red snapper, *Lutjanus campechanus*, on an artificial reef in the northern Gulf of Mexico. Hours begin at midnight (0 hour = 00:00 – 00:59 h) and continue for a 24-h period. Black bars = core volume (50% KDE); gray bars = home range volume (95% KDE); and error bars = SE.

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

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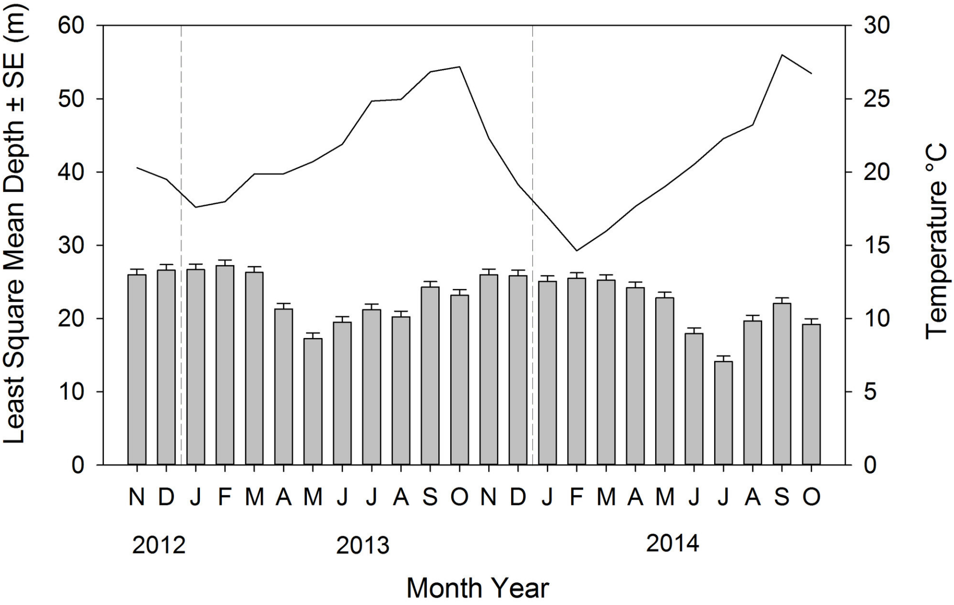
Least Square Mean Depth ± SE (m)
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Temperature °C
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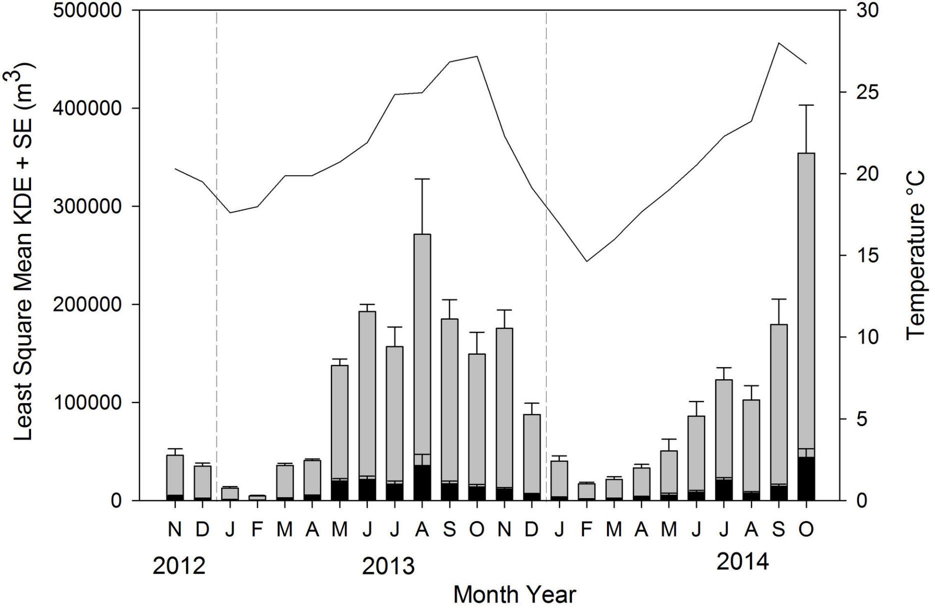

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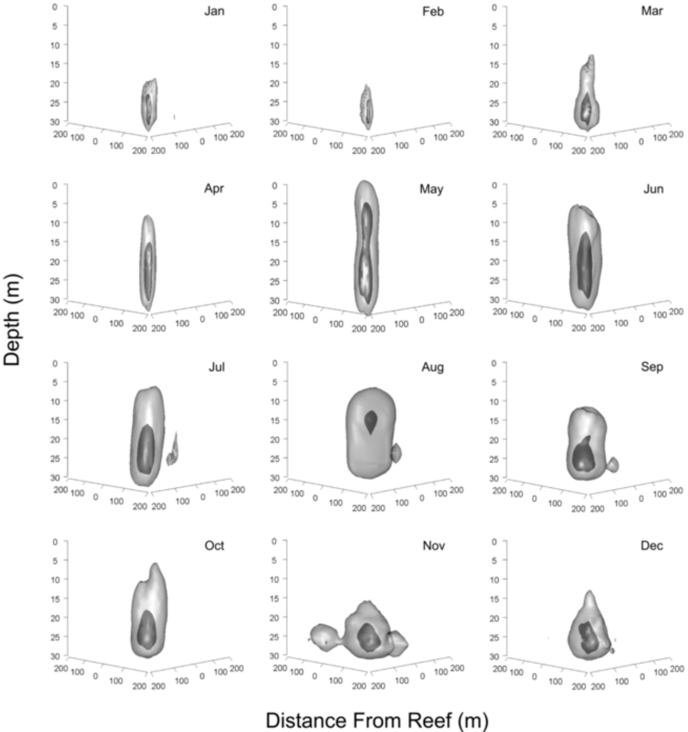
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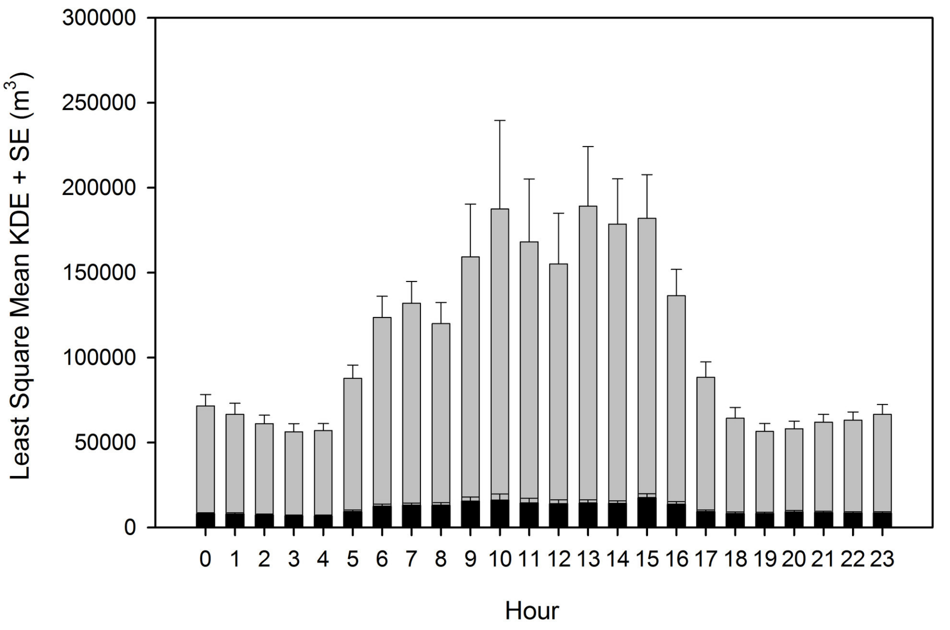
Depth (m)
Distance From Reef (m)



Least Square Mean KDE + SE (m^3)
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Hour