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NOTE

# Influence of Hurricane Activity on Acoustic Array Efficiency: A Case Study of Red Snapper within an Artificial Reef Complex

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***Abstract***

**Meteorological disturbances, such as hurricanes, can cause wide distributional changes to fish populations, but studies documenting fish movement in response to these disturbances are rare and serendipitous. We opportunistically examined how a hurricane influenced behavior of Red Snapper *Lutjanus campechanus* at an artificial reef complex in the western Gulf of Mexico. Red Snapper had a variety of responses, with some fish emigrating and some remaining on site during Hurricane Harvey—a category 4 storm. Hurricane-induced destruction or alteration of habitat may alter space use behavior of fish. However, caution should be used when interpreting behavior without the inclusion of array performance, which may change due to environmental conditions. Importantly, when acoustic array efficiency was not accounted for in space use analyses, mean kernel utilization distribution ($m^3$) was marginally different among the periods before, during, and after Hurricane Harvey. However, when mean daily array efficiency was included as a covariate, space use among the three periods was not significantly different. Hurricanes can affect the movement and residency of marine species and can be an important driver in the displacement of populations and degradation of habitats, but array efficiency should be incorporated to prevent misinterpreting the behaviors of tagged fish.**

Meteorological disturbances, such as hurricanes, can be destructive both on land and in the ocean, causing significant and prolonged alterations in habitat. These physical changes can include relocated structures, increased turbidity for extended periods of time (Bell and Hall 1994), changes in temperature due to vertical mixing, increased turbulence, and increased current velocity gradients (Ginis 2002; Huang et al. 2009). The importance of singular meteorological disturbances for driving changes in movement behaviors of marine fishes has been emphasized in the scientific literature. Disturbance-driven habitat alterations have been reported to potentially alter spawning behavior, recruitment patterns (Locascio and Mann 2005), and trophic structure (Fabricius et al. 2008), as well as leading to mortality due to degraded habitat and water conditions (Paerl et al. 2001; Gardner et al. 2005). They can also cause significant shifts in species composition and abundance for fish communities (Ebeling et al. 1985; Bouchon et al. 1994; Byrnes et al. 2011; Wiernicki et al. 2020).

While advances in acoustic telemetry technology have allowed for continuous observations of various fish species' movement and distribution patterns in their natural environment (Heupel et al. 2003), the limitations of acoustic telemetry are less understood and vary with environmental variables (Huveneers et al. 2016). Wind speed, biological noise, and currents have all been demonstrated to strongly influence detection frequency (Heupel et al. 2006; Simpfendorfer et al. 2008; Novak et al. 2020). Exploration of fish movement and responses to extreme meteorological disturbances, such as hurricanes, is often opportunistic and poses additional challenges and limitations. It requires previously deployed tracking equipment (e.g., receivers and transmitter-tagged fish) to be near or within the hurricane's unpredictable path and to remain there without being relocated or destroyed (Greening et al. 2006). However, the removal of receivers is usually

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suggested to reduce the chance of receiver loss and the loss of previously collected data.

The small but growing number of studies that have acoustically monitored fish movement during hurricanes have reported varied responses. Storm-driven emigration has been reported for Blacktip Sharks *Carcharhinus limbatus* (Heupel et al. 2003), Gray Triggerfish *Balistes capriscus* (Bacheler et al. 2019), Striped Bass *Morone saxatilis* (Bailey and Secor 2016), Summer Flounder *Paralichthys dentatus* (Sackett et al. 2007), and Black Sea Bass *Centropristis striata* (Secor et al. 2019). However, other studies have reported decreased movement and tighter association with structured habitat for reef fish communities during disturbances (Williams 1984; Syms and Jones 2000). Blacktip Reef Sharks *Carcharhinus melanopterus* were also reported to be resident during meteorological disturbances (Udyawer et al. 2013). Some species have been observed to have a mixed response to disturbances, including Red Snapper *Lutjanus campechanus*, which were reported to both remain on site during the storm (Topping and Szedlmayer 2011; Bacheler et al. 2021) and emigrate during or prior to the storm (Peabody 2004; Szedlmayer and Schroepfer 2005; Topping and Szedlmayer 2011).

The Red Snapper is a long-lived, demersal fish that supports economically important commercial and recreational fisheries in the Gulf of Mexico (Nieland and Wilson 2003). Red Snapper are commonly associated with structure (Wells and Cowan 2007; Gallaway et al. 2009) and often account for a significant proportion of the total fish abundance at both natural and artificial habitats (Stanley and Wilson 2000; Gledhill 2001). Subsequently, this species is often targeted by commercial and recreational fisheries at these habitats (Garner and Patterson 2015). Thus, space use and site fidelity to these structures have been a focus of prior research, which has suggested that structure may provide benefits such as increased prey accessibility and protection from predators (Szedlmayer and Lee 2004; Gallaway et al. 2009; Streich et al. 2017). Determining changes in space use and movement around these structures during extreme disturbances may help to predict future impacts of these events on economically important fisheries (Udyawer et al. 2013). Thus, the objectives of this study were to use acoustic telemetry to (1) explore fine-scale movements of Red Snapper during a hurricane at a nearshore artificial reef complex and (2) determine how space use and residency of Red Snapper were influenced by hurricane activity while considering the consequent effects on acoustic array efficiency.

## METHODS

*Study site.*— The Corpus Christi Nearshore Reef (CCNR) is an artificial reef complex in the western Gulf of Mexico off the coast of Texas. The reef complex is approximately 23 m deep and is comprised of multiple reef materials, including 470 prefabricated reef pyramids, 203 concrete culverts, and the 47.2-m cargo ship M/V *Kinta S* (hereafter, *"Kinta"*; Figure 1). In 2016, a VEMCO Positioning System (VPS; VEMCO, Ltd., Novia Scotia) comprising 20 submersible receivers (12 VR2W and 8 VR2AR receivers) was deployed on the site to determine the fine-scale movements and behaviors of Red Snapper (for detailed deployment methods, see Banks et al. 2021). The VPS is an acoustic positioning system that is able to triangulate more accurate positions (~1-m accuracy; Piraino and Szedlmayer 2014) that can include depth estimations. Each receiver was placed approximately 150 m apart with a sentinel tag (VEMCO V16-069 k-2 L; transmission delays = 500–700 s) to synchronize internal clocks and to verify that continuous data collection occurred throughout the study period. Near the center of each reef material (i.e., pyramids, culverts, and the ship), a reference tag (VEMCO V9-069k-2H; transmission delays = 500–700 s) was deployed to determine the distance at which the receivers detected acoustic tags as part of the in situ range test. The VR2AR receivers were equipped with sensors to continuously monitor water temperature and the tilt of the receiver.

Handling and tagging of Red Snapper were conducted in accordance with guidelines approved by the Institutional Animal Care and Use Committee at Texas A&M University–Corpus Christi (Animal Use Protocol 10–14). VEMCO V9P acoustic transmitters (V9P-2H069k-1; transmission delays = 155–215 s; battery life = 366 d) equipped with pressure sensors were surgically implanted in the peritoneal cavity of Red Snapper (as described by Banks et al. 2021). An external dart tag (Hallprint Pty., Ltd.) with contact information and “REWARD” printed on the tag was inserted into the dorsal musculature below the dorsal fin in case of angler recapture. After tagging, Red Snapper were descended to depth to minimize depredation at the surface by using SeaQualizers on the same reef material from which they were captured.

*Data analysis.*— The data collected using the VPS array require proprietary position software; therefore, data downloaded from the receivers were sent to VEMCO for processing, and triangulated positions were returned for analysis. Using VPS-estimated positions, kernel utilization distribution (KUD) analysis was performed to determine space use patterns (core volumes and home ranges) during the hurricane (Simpfendorfer et al. 2012) because they are robust to autocorrelation and outlying positions (Worton 1989; Seaman and Powell 1996; De Solla et al. 1999). The probability of the tagged fish being absent half the time was defined as the 50% KUD (core volume), while the probability of the tagged fish being absent 5% of the time was defined as the 95% KUD (home range; Piraino and Szedlmayer 2014).

Statistical analyses were completed in R version 3.5.0 using the *ks* package to calculate three-dimensional

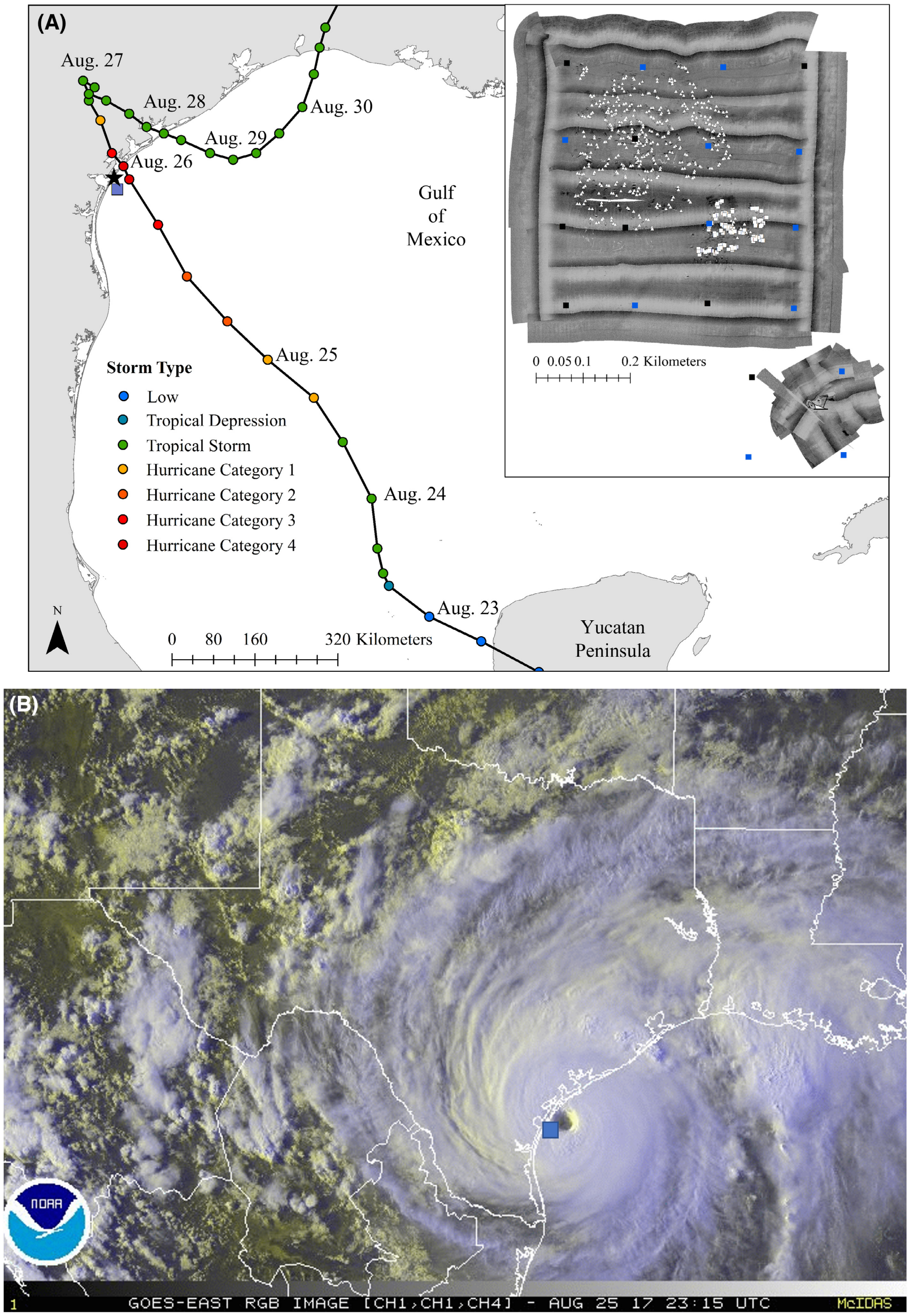

FIGURE 1. **(A)** Hurricane Harvey (black line denotes the path of Harvey, and circle colors indicate storm type; https://www.nhc.noaa.gov/data/tcr/). Harvey's eye passed 32 km northeast of the Corpus Christi Nearshore Reef (CCNR; purple square) with the VEMCO Positioning System array and made landfall near Port Aransas, Texas (black star). Black squares represent receiver locations within the array that could not be recovered, and blue squares represent receivers that were recovered and included in the analysis. **(B)** Satellite imagery depicts Harvey making landfall north of the CCNR near Port Aransas (obtained from https://www.ospo.noaa.gov/Organization/History/imagery/Harvey/index.html).

KUDs, which accounted for vertical and horizontal movements (Duong 2007; Simpfendorfer et al. 2012; R Core Team 2014). Positions were then classified into those recorded during three periods: before Hurricane Harvey (hereafter, "Harvey"; August 1–22, 2017), during Harvey (August 23–30, 2017), and after Harvey (August 31–October 29, 2017). We considered August 23–30 to represent the period during Harvey because it was a strong storm within the western Gulf of Mexico on those dates. Environmental data, including wind speed, water temperature, and barometric pressure, were obtained from the National Data Buoy Center (https://www.ndbc.noaa.gov/). Using triangulated positions from the VPS, space use was compared to environmental data using Pearson's correlation tests. Depth and presence–absence patterns were obtained using all detections and were compared to wind speed, water temperature, and barometric pressure using Pearson's correlation tests. Data for Harvey were obtained from the National Hurricane Center's Tropical Cyclone Reports, which contain post-analysis tracks with positions and intensity classifications every 6 h (https://www.nhc.noaa.gov/data/tcr/). Variation in array efficiency was assessed by calculating the proportion of successful detections at each station from neighboring sentinel tags and interpolating across the VPS array in ArcMap version 10.5 (ESRI, Redlands, California) to identify potential low-detection zones (TinHan et al. 2018). Array efficiency was visually evaluated for the periods before, during, and after Harvey passed by the reef complex. Receivers and associated sentinel tags that shifted during the study were geographically adjusted in the array efficiency estimations on the date of movement as triangulated by the VPS array. The relationships between daily mean array efficiency estimations and wind speed, water temperature, and barometric pressure were evaluated using Pearson's correlation tests.

Generalized linear models were used to test the influence of array efficiency on mean space use and depth of Red Snapper in relation to Harvey's position (i.e., the period before, during, or after Harvey). Prior to testing, space use data (i.e., KUDs) were log transformed to minimize heteroscedasticity. Individual differences in space use of fish present in the VPS array prior to Harvey (i.e., the “before” period) were tested with a one-way ANOVA to confirm that observed changes in behavior during or after Harvey were in fact representative of tagged Red Snapper and not a predator that consumed a tagged fish. If significant differences were detected, pairwise differences were evaluated using Tukey–Kramer multiple comparison tests. All tests were conducted at the significance level $\alpha$ of 0.05.

## RESULTS

These data were opportunistically collected from an acoustic array that was deployed before Harvey entered the Gulf of Mexico. On August 22, 2017, fragments of Tropical Storm Harvey crossed the Yucatan Peninsula and began strengthening (Figure 1). On August 24, Harvey had intensified to a category 4 hurricane before making landfall in Port Aransas, Texas, on August 25 at 2200 hours (CST). Harvey made landfall with sustained winds estimated at 59.1 m/s and a minimum central pressure of 937 millibars, where it then stalled before moving back offshore on August 27 (Blake and Zelinsky 2018). The eye of Harvey passed approximately 32 km northeast of the CCNR and the VPS array on August 25 around 1900 hours, with environmental conditions that were strong enough to shift the bow of the 47.2-m *Kinta* about 26 m south. Around 1200 hours (noon) on August 25, Buoy 42,020 (26.968, −96.693), the closest weather station to the CCNR that measured marine environmental variables (e.g., wave height, sea surface temperature, and wave period), broke loose from its mooring and went adrift. Therefore, environmental variables (e.g., wind speed, air temperature, and barometric pressure) were obtained from Station ANPT2 (27.837, −97.039), which was located inside the Port Aransas Jetties about 24 km northwest of the CCNR. No significant differences in wind speed, water temperature, and barometric pressure data were detected between Station ANPT2 and Buoy 42,020 before the buoy went adrift (Welch *t*-tests: $P > 0.05$). However, Station ANPT2 was not equipped to measure marine environmental variables, so wind speed was used as a proxy for wave height (Pearson's product–moment correlation coefficient $r = 0.9478$, $P < 0.0001$; Young et al. 2011). Because Harvey reached Station ANPT2 3 h after passing the CCNR, time was adjusted backwards by 3 h to reflect the time during which the hurricane passed near the array for analyses. Using this adjusted time, the maximum wind speed and gust were recorded at 49.6 and 59.3 m/s, respectively, as Harvey passed near the array.

Of the 20 receivers comprising the VPS array, 12 were retrieved in spring 2018. Three of the eight irretrievable receivers ceased reporting during the hurricane on the morning of August 25 between 0130 and 0825 hours, or ≥12 h before the eye passed the CCNR. These receivers were in the southwest portion of the array (Figure 2). Two irretrievable receivers from the northern outside corners of the array were relocated during the hurricane and were still detected in spring 2018 by recovered receivers. Of these two receivers, one was not physically located by scuba divers, while the other was found inverted too deeply into the mud substrate to be recovered. Of the 12 recovered receivers, two moved within the array on the day of the hurricane, one of which had also previously moved 4 d before Harvey (August 21). Another receiver, which had been deployed in the center of the array near the culverts, went adrift at the end of November 2017 (91 d after Harvey). It washed ashore on Padre Island National Seashore, Texas, and was returned by an angler who noted that the float and metal pole used to attach the receiver to the concrete anchor were still attached to the receiver; the pole may have sheared near the >68-kg concrete base, which likely remained in place at the CCNR. Of the 11 receivers that were recovered by divers, most were found tilted at an angle of about 45°, which was confirmed by the four VR2AR receivers, which were equipped with internal tilt sensors.

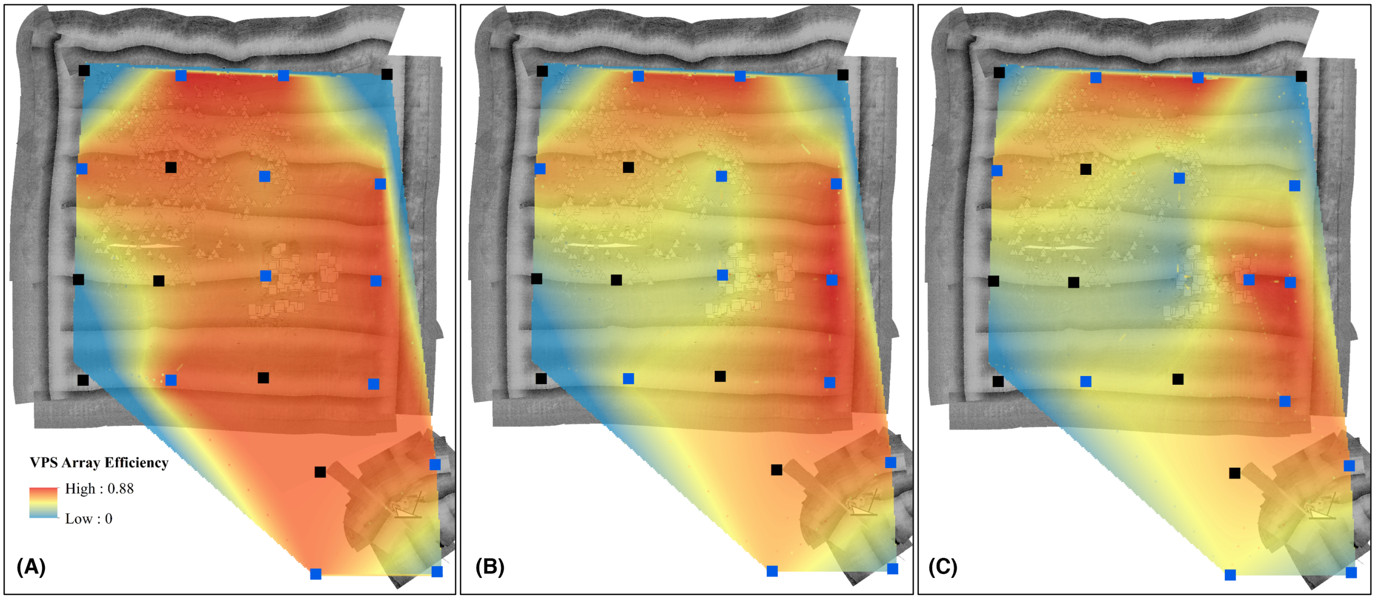

FIGURE 2. VEMCO Positioning System (VPS) array efficiency was calculated **(A)** before Hurricane Harvey (August 1–22, 2017), **(B)** during Harvey (August 23–30, 2017), and **(C)** after Harvey (August 31–October 29, 2017), with the sentinel tags associated with nearest neighboring receivers that were recovered (blue squares). Receivers and associated sentinel tags that shifted during the study were geographically adjusted in the array efficiency estimations on the date of movement as triangulated by the VPS array. Black squares represent receivers that were not recovered and were omitted from the array efficiency analysis.

TABLE 1. Mean, minimum, and maximum array efficiency by receiver before, during, and after Hurricane Harvey. Asterisks denote receivers that moved during the hurricane.

| | Before Harvey | | | During Harvey | | | After Harvey | | |
|---|---|---|---|---|---|---|---|---|---|
| Receiver | Mean | Min | Max | Mean | Min | Max | Mean | Min | Max |
| St03 | 0.7367 | 0.6319 | 0.8194 | 0.4861 | 0.0347 | 0.8403 | 0.6547 | 0.3125 | 0.9097 |
| St04 | 0.8116 | 0.7755 | 0.8403 | 0.6837 | 0.4630 | 0.8218 | 0.7689 | 0.6042 | 0.9028 |
| St06 | 0.7877 | 0.7477 | 0.8403 | 0.7131 | 0.4514 | 0.8958 | 0.8951 | 0.8160 | 0.9410 |
| St07 | 0.7705 | 0.6979 | 0.8009 | 0.8186 | 0.6493 | 0.9236 | 0.8655 | 0.7500 | 0.9236 |
| St08* | 0.7653 | 0.7153 | 0.8090 | 0.8037 | 0.6366 | 0.9259 | 0.8407 | 0.6944 | 0.9213 |
| St10 | 0.7405 | 0.6759 | 0.8009 | 0.6063 | 0.2118 | 0.8403 | 0.6962 | 0.4479 | 0.8542 |
| St11 | 0.7339 | 0.6146 | 0.8438 | 0.5577 | 0.3021 | 0.8229 | 0.4792 | 0.3958 | 0.5764 |
| St12 | 0.3717 | 0.2813 | 0.4792 | 0.2313 | 0.1250 | 0.4236 | 0.1650 | 0.1076 | 0.2569 |
| St14 | 0.6826 | 0.6042 | 0.7656 | 0.3017 | 0.0139 | 0.7431 | 0.1944 | 0.0208 | 0.3657 |
| St17 | 0.6677 | 0.6097 | 0.7403 | 0.3583 | 0.1319 | 0.7378 | 0.3613 | 0.1441 | 0.6215 |
| St19* | 0.7515 | 0.6620 | 0.8009 | 0.7135 | 0.5625 | 0.8125 | 0.7474 | 0.5810 | 0.8727 |
| St20 | 0.7601 | 0.6250 | 0.8403 | 0.4688 | 0.0625 | 0.7917 | 0.4887 | 0.0833 | 0.8403 |
| Mean | 0.7150 | | | 0.5619 | | | 0.5964 | | |

Over the 10 months during which transmitter-tagged fish were present in the VPS array, the mean number of receivers used to triangulate positions decreased from 3.89 receivers (range = 3–6 receivers) before the storm (January 20–August 22, 2017) to 3.05 receivers (range = 3–5 receivers) after the storm (August 31–October 29, 2017). Using sentinel tag detections, the overall array had a mean detection efficiency ± SD of 0.7150 ± 0.1181 before Harvey (August 1–22, 2017), which decreased to 0.5964 ± 0.2612 after Harvey (August 31–October 29, 2017) due to loss or movement of receivers (Table 1; Figure 2). Array efficiency was negatively correlated with wind speed ($r =$

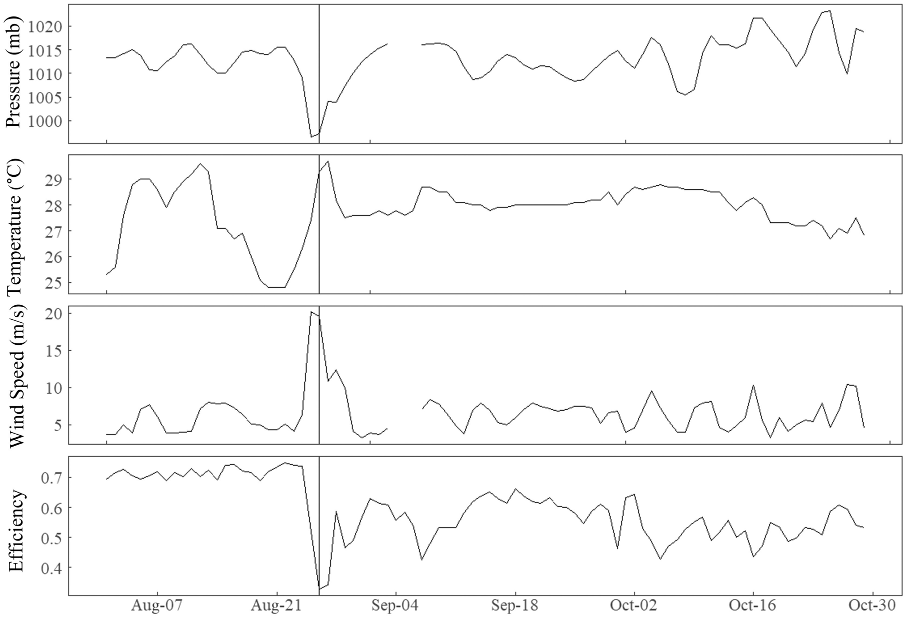

FIGURE 3. Mean daily array efficiency was negatively correlated with water temperature (recorded by receivers deployed on site) and wind speed. Barometric pressure was not correlated with array efficiency. The vertical black line denotes the date on which Hurricane Harvey passed near the Corpus Christi Nearshore Reef.

TABLE 2. Movement of Red Snapper on the VEMCO Positioning System (VPS) array at the Corpus Christi Nearshore Reef. Release structure was the structure type where the fish was caught and released after tagging on January 20, 2017. Days at liberty were calculated from August 1, 2017 (first day of the study period), until the date of the last triangulated position or harvested recapture. Recapture fate and structure were reported by the angler that recaptured the fish, and the structure was confirmed via coordinates submitted by anglers. Fate of each fish is denoted by letters (H = harvest; R = released; E = emigration; M = mortality). Asterisks denote recaptured fish that died after being released. ST Rig = standing oil and gas platform.

| Fish number | Release structure | Tagging TL (mm) | Days on VPS site | Last date in VPS array | Recapture fate | Recapture structure | Fate at end of study |
|---|---|---|---|---|---|---|---|
| 2 | Culvert | 273 | 20 | Aug 20, 2017 | H | Unknown | M |
| 7 | *Kinta* | 293 | 11 | Aug 11, 2017 | R | *Kinta* | M* |
| 9 | *Kinta* | 329 | 25 | Aug 25, 2017 | H | ST Rig | E |
| 12 | *Kinta* | 300 | 25 | Aug 25, 2017 | – | – | E |
| 10 | *Kinta* | 318 | 90 | Oct 29, 2017 | – | – | E |

−0.3753, $P < 0.0001$) and water temperature (as recorded by receivers; $r = -0.4032$, $P < 0.0001$) but was not correlated with barometric pressure ($r = 0.0424$, $P = 0.6968$; Figure 3).

Of the 21 Red Snapper that were tagged as part of the original study (Banks et al. 2021), five (TL = 273–329 mm) were present at the study site on August 1 (Table 2). One Red Snapper (fish 7) was recaptured and released on August 11 but suffered mortality after release. Another (fish 2) was recaptured and harvested on August 20. One individual (fish 10) remained on site until October 29, 2017 (65 d after Harvey), and then emigrated off site to an unknown location. Two Red Snapper (fish 9 and 12) remained on site until around 1000 hours on August 25, when they both emigrated from the array within 10 min of one another. One emigrated from the pyramids, and the other emigrated from the *Kinta* (Figure 4). Neither of these fish was detected in the array after Harvey; however, the fish that emigrated from the *Kinta* was recaptured 65 d after Harvey at a standing oil and gas platform about 5 km southwest of the CCNR and was the only fish in the study to be reported as recaptured at a site other than the CCNR (the initial tagging site). The presence of fish determined by detections at the CCNR was positively correlated with air temperature ($r = 0.14085$, $P < 0.0001$) but negatively correlated with water temperature ($r = -0.3213$,

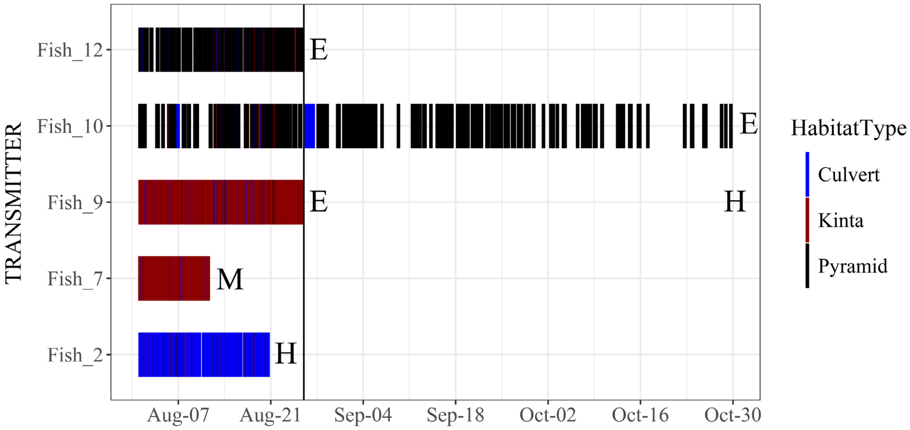

FIGURE 4. Tracking periods for transmitter-tagged Red Snapper that were present immediately before, during, or after Hurricane Harvey passed near the VEMCO Positioning System (VPS) array and the Corpus Christi Nearshore Reef (CCNR). The colored bars represent the structure on which the tagged Red Snapper was positioned during the active tracking period. Fish 9 emigrated from the study site but was later recaptured on a nearby standing oil and gas platform. The vertical black line represents the date on which Harvey passed near the CCNR (August 25, 2017). Letters denote the fate of fish on the VPS site (H = harvested; E = emigrated; M = mortality). No fish were still being detected when the receivers were recovered.

$P < 0.0001$) and wind speed ($r = -0.0554$, $P < 0.001$). Barometric pressure ($r = 0.0051$, $P = 0.7458$) did not significantly influence the absence of fish.

Mean daily depth of fish was negatively correlated with wind speed ($r = -0.2150$, $P < 0.0001$) and water temperature at receiver depth ($r = -0.3258$, $P < 0.0001$), which was recorded by the VPS array receivers (Figure 5), but daily depth was positively correlated with sea surface temperature ($r = 0.1330$, $P < 0.01$). Mean depth ± SD after Harvey (14.5 ± 3.19 m) was significantly different ($F_{2,574} = 121.31$, $P < 0.0001$) from the mean depth during Harvey (16.9 ± 2.40 m) or before Harvey (17.3 ± 1.83 m), with shallower depths after the hurricane. Depth was significantly different by day ($F_{9,130} = 30.26$, $P < 0.0001$), with the shallowest depths observed on the day of Harvey (14.42 ± 3.20 m), when temperatures were increasing. However, fish returned to depth (~20 m) 13 h before Harvey passed the array.

Fish positions from 25 d before Harvey made landfall (August 1, 2017) through October 29, 2017 (the last day of detection), were used in space use analysis unless otherwise noted. Space use patterns were not significantly different ($F_{4,86} = 1.930$, $P = 0.113$; Figure 6) among individual fish ($n = 5$) that were present on the study site in August, supporting that all fish were of the same species (i.e., tagged Red Snapper) and that the estimated space use patterns were not those of a mobile predator. Comparisons of individual space use patterns were limited to August to account for seasonal differences in space use by Red Snapper (Banks et al. 2021).

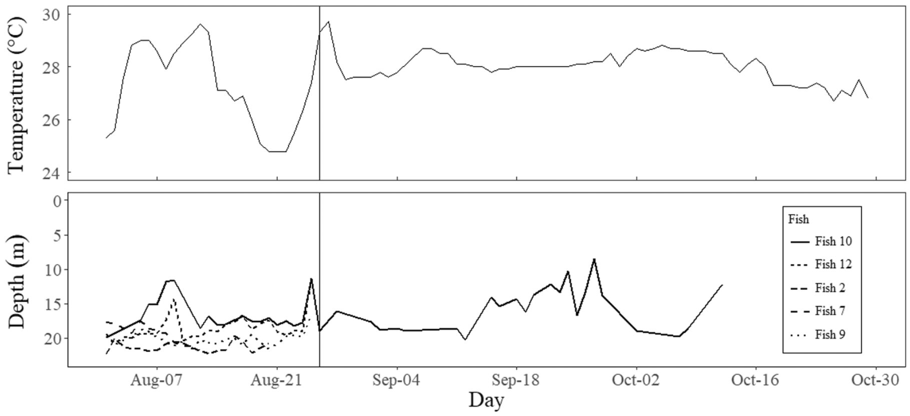

FIGURE 5. Daily depth patterns (bottom panel) for individual Red Snapper were negatively correlated with water temperature recorded by receivers deployed on site (top panel). The vertical black line denotes the date on which Hurricane Harvey passed near the Corpus Christi Nearshore Reef.

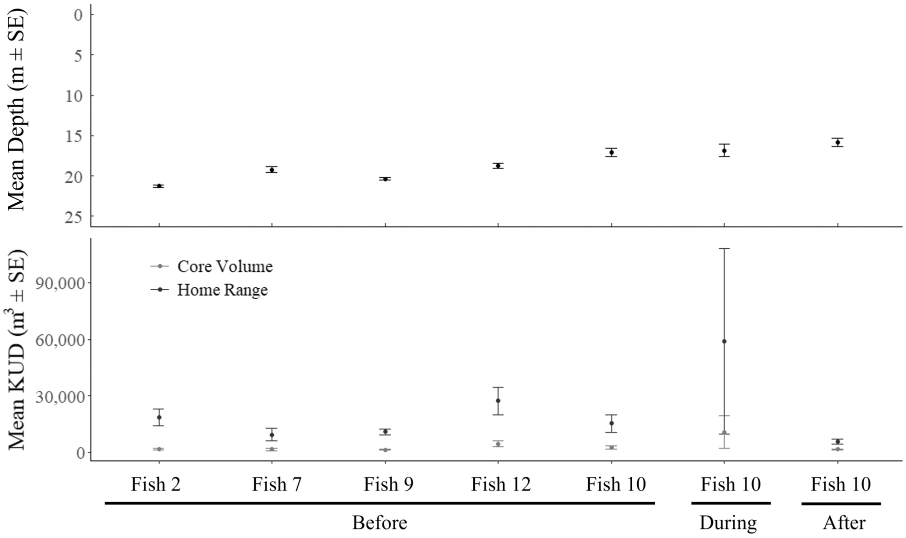

FIGURE 6. Mean depth and space use of individual Red Snapper before, during, and after Hurricane Harvey. Fish 10 was the only individual to remain on site through the hurricane.

The lack of difference in space use patterns among individual fish allowed for behavior analyses to be performed separately on the single Red Snapper (fish 10) that remained on site during and after the hurricane. Without accounting for variation in array efficiency, space use was marginally different before Harvey (February 1–August 22, 2017), during Harvey (August 23–30, 2017), and after Harvey (August 31–October 29, 2017; core volume: $F_{2,47} = 2.54$, $P = 0.087$; home range: $F_{2,47} = 2.45$, $P = 0.097$). Daily space use for this fish was negatively correlated with wind speed (core volume: $r = -0.2524991$, $P < 0.05$; home range: $r = -0.2436998$, $P < 0.05$) and water temperature, which was recorded by the VPS array receivers (core volume: $r = -0.2972$, $P < 0.05$; home range: $r = -0.3665$, $P < 0.01$; Figure 7). When variation in the array was accounted for, the covariate of hurricane position (i.e., before, during, or after Harvey) was not significantly related to space use (core volume: $F_{2,46} = 0.168$, $P = 0.848$; home range: $F_{2,46} = 0.296$, $P = 0.745$).

## DISCUSSION

Although the sample size was limited for this study, we were able to examine Red Snapper movements and space use during a category 4 hurricane using a VPS array that was deployed months before the storm, providing baseline data for space use comparisons of the periods before, during, and after Harvey. This unique opportunity to collect Red Snapper space use data during a hurricane relied on equipment being previously deployed in the path of the hurricane, remaining intact on site, and being retrievable afterwards.

Red Snapper movement was influenced by rapidly changing environmental conditions. While individual responses to the hurricane varied, the timing of the responses was synchronized. About ≥12 h before Harvey passed by the CCNR, Red Snapper were shallower in the water column compared to previous time periods, which coincided with rapidly increasing water temperatures. As water temperatures reached their maximum and Harvey neared the site, fish emigrated from the site or returned deeper in the water column closer to structure. Increased wave action would have resulted in increased wave orbital velocity (although this was not measured in our study), which could be noticeable in advance of the storm arriving and the resulting drop in barometric pressure (Bacheler et al. 2019). However, presence–absence patterns, space use, and depth were not influenced by barometric pressure in this study but were influenced by water temperature, air temperature, and wind speed, suggesting that the fish were potentially responding to other environmental cues, such as wave orbital velocity. Bacheler et al. (2019) reported that the emigration of demersal reef fish (e.g., Gray Triggerfish) immediately before two hurricanes was correlated more with wave orbital action than with barometric pressure or water temperature and that the change in barometric pressure may have had less influence at depth than the dynamic pressure range of the increased water movement caused by large surface waves. Opposite of Gray Triggerfish, Red Snapper that were tagged off North Carolina spent more time near the bottom and were somewhat less likely to move during storms when the movement of water was high (Bacheler et al. 2021). Bacheler et al. (2021) suggested that the difference in residency during storms may

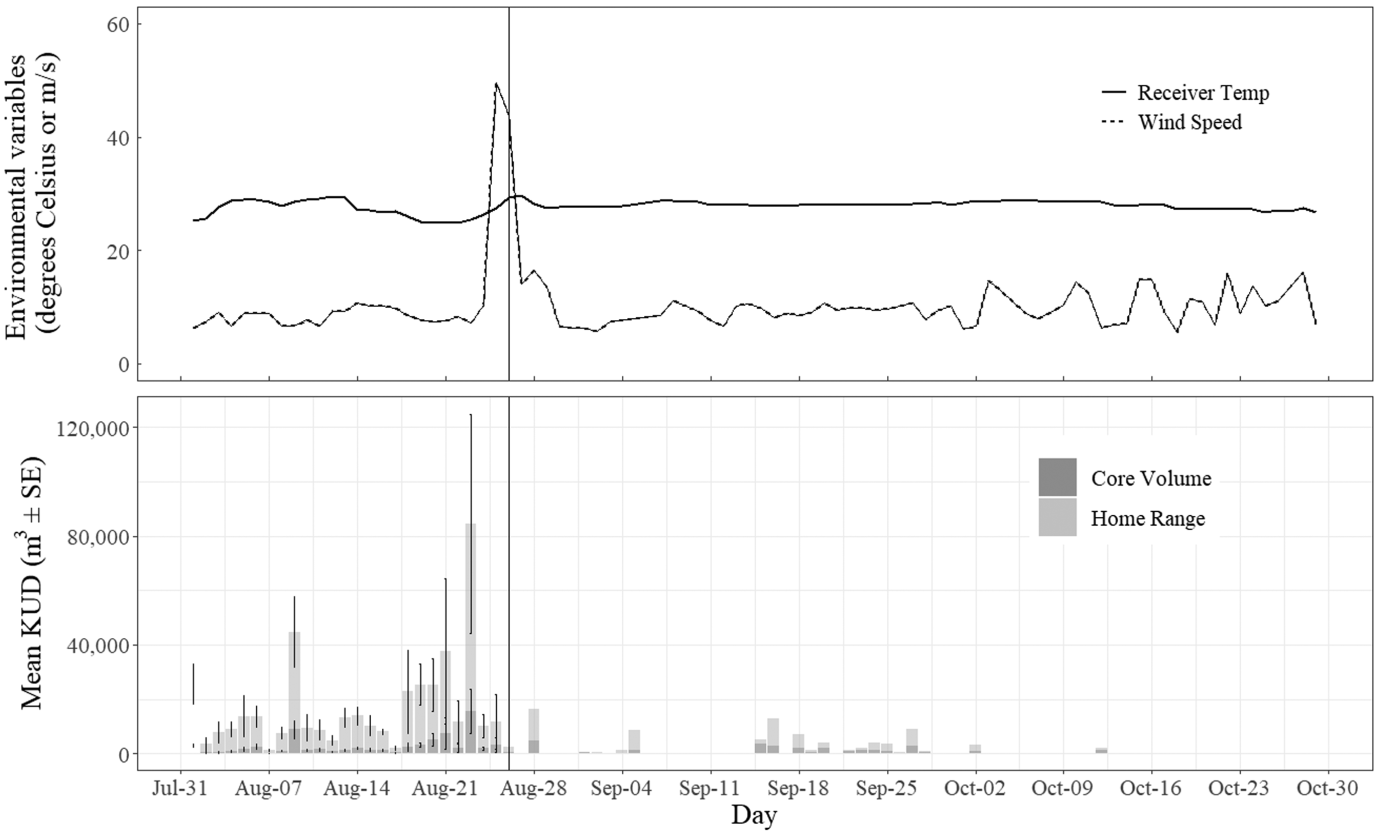

FIGURE 7. Daily space use of Red Snapper (kernel utilization distribution [KUD]; bottom panel) was negatively correlated with maximum daily wind speed (m/s; dotted line, top panel) obtained from a weather station approximately 24 km northwest of the Corpus Christi Nearshore Reef (CCNR) and mean daily water temperature (°C; solid line, top panel) recorded by receivers deployed on site. The vertical black line denotes the date on which Hurricane Harvey passed near the CCNR.

be due to differences in body morphology and the larger mean body size of Red Snapper compared to smaller Gray Triggerfish. However, the Red Snapper tagged in the Bacheler et al. (2021) study were about two times larger than the fish tagged in this study, which could potentially explain the mixed residency results in this study.

Intense wave and storm activity from hurricanes has the potential to drastically change habitat. The *Kinta*, which was the largest structure on the CCNR, shifted 26 m during Harvey, suggesting that while the size of the structure may decrease the chance of habitat destruction (Szedlmayer and Schroepfer 2005), habitats can still be significantly altered. The present results as well as the results of Topping and Szedlmayer (2011) indicated various responses in fidelity (i.e., emigration and residence) of Red Snapper to major disturbances on larger reefing structures. However, similar to Bacheler et al. (2021), Szedlmayer and chroepfer (2005) reported continuous residence during all disturbances (i.e., cold fronts, four tropical storms [Helene, Barry, Hanna, and Bill], and two hurricanes [Isidore and Lili]) that passed near their study site in Alabama between 2000 and 2004, which was in contrast to the findings of large movements reported by Watterson et al. (1998) and Patterson et al. (2001). Differences in artificial reef structure size may explain the differences in findings among these studies. Larger and more permanent structures (e.g., army tanks and ships) were hypothesized to be more stable than the smaller structures (e.g., plastic drums, newspaper vending machines, and washing machines) previously studied, which may be destroyed during major disturbances (Szedlmayer and Schroepfer 2005). The CCNR is a large artificial reef complex that comprises multiple structures of various sizes covering more area than the army tanks studied by Szedlmayer and Schroepfer (2005) and Topping and Szedlmayer (2011), suggesting that while permanence and size may have played a role in residency during these disturbances, environmental factors may play a larger role.

Baseline data collected at this site prior to Harvey (Banks et al. 2021) allowed for a comparison of space use and depth patterns among the periods before, during, and after Harvey. Space use by fish 10 did not differ before, during, or after Harvey, but depth was shallower after the hurricane, suggesting that the storm had some influence on Red Snapper behavior. Before Harvey, Red Snapper that were acoustically monitored on this site were found to generally frequent greater depths, likely due to the compressed nepheloid layer and thermocline (Banks et al. 2021). Storm-induced mixing can cause destratification and temperature homogenization throughout the water column (Secor et al. 2019), which likely disrupted the compressed nepheloid layer and thermocline that are common in August at the CCNR (Ajemian et al. 2015). If the nepheloid layer was shallower, this may have allowed Red Snapper, which are frequently observed moving into and out of this layer (Ajemian et al. 2015), to frequent shallower depths, maintaining potential protection from predators. Furthermore, the temperature homogenization may have minimized or eliminated the thermocline, below which fish commonly remained during the warmer months (Banks et al. 2021), thus possibly contributing to the shallower depth use observed during this study in the time leading up to the hurricane.

Storms have impacts not only on fish distribution, but also on performance of the array by causing equipment loss and, thus, decreased array efficiency. The receiver array provided adequate coverage of the reefing site to offer some insight into Red Snapper movement during a hurricane. However, the array efficiency was negatively influenced by Harvey through the relocation and reangling of receivers, decreasing coverage in various areas around the array. The array efficiency represented the minimum efficiency of the study site, as fish were frequently positioned by multiple receivers in the VPS array and not just the neighboring receivers that were used to estimate mean daily efficiency.

Inclusion of the variation in array efficiency is important for interpreting results to determine whether movements represent fish behavior or are artifacts of the acoustic array (Huveneers et al. 2016). For example, without accounting for variation in array efficiency, space use by fish 10 was originally thought to differ during the hurricane compared to the period before or after the hurricane. However, after daily array efficiency throughout the study was accounted for, space use was not significantly different among the periods before, during, and after the hurricane. Wide variability in receiver performance has been found among and within various studies due to the environmental conditions influencing the ability of receivers to detect transmitters (Domeier 2005; Heupel et al. 2006; Hobday and Pincock 2011; Kessel et al. 2014; Novak et al. 2020). Without a full understanding of an array's variability, the space use and behavior of tagged fish can be misinterpreted (Payne et al. 2010).

The body of research examining storm effects on Red Snapper has produced conflicting results (see Williams-Grove and Szedlmayer 2020 for further review), including the results of this study. Although the present work provides valuable insight, there were some limitations. First, sample size was low in this study, which is characteristic of telemetry studies—especially those using VPS arrays, in which the probability of signal collisions greatly increases with more transmitters, thereby decreasing the amount of data collected. Second, the opportunistic nature of sampling an unpredictable meteorological disturbance does not allow for secure, large-scale deployment of gear in the path of the storm. Third, the Red Snapper that were tagged in this study were of sublegal size (>381 mm TL), so caution should be taken when extrapolating the results to larger fish. However, as more studies on the effects of storms on fish are completed, the compilation of data could lend insight into population-level trends.

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