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Grouper Tales: Use of Acoustic Telemetry to Evaluate Grouper Movements at Western Dry Rocks in the Florida Keys

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Abstract
The Western Dry Rocks (WDR) area off Key West, Florida, is an open fishing area that contains a multispecies fish spawning aggregation site, but grouper spawning there has yet to be confirmed. The movements of 18 adult and subadult grouper at WDR were tracked using acoustic telemetry to determine how this area is used by grouper species and whether it contains a grouper spawning aggregation site. Tagged fish consisted of 10 Black Grouper *Mycteroperca bonaci*, 5 Nassau Grouper *Epinephelus striatus*, 2 Gag *M. microlepis*, and 1 Yellowfin Grouper *M. venenosa*. Overall, tagged grouper were more likely to be present in the WDR array during winter spawning months, with species-specific seasonal differences. Our results indicated that grouper presence increased during spawning months, although some adults and subadults were present year-round. Grouper made more movements per day during non-spawning months compared to spawning months, although the north side of WDR was the most heavily used area, regardless of the time of year. Additionally, spatial graphs of grouper movement suggested that different grouper species utilized different areas of WDR. Increased presence of grouper during spawning months suggests that the WDR area may contain a grouper spawning aggregation site, which would mean that fish species aggregate to spawn at this location year-round. The success of the Florida Keys fisheries critically depends on the protection of multispecies spawning aggregations like that potentially contained at WDR.

Traditional fisheries management focuses on maximizing the catch of a target species while often ignoring ecosystem components, such as habitat usage and trophic interactions (Pikitch et al. 2004). Failing to integrate fish movement and habitat usage into the management of marine fisheries and their ecosystems weakens the process of sustainable fisheries (Armstrong and Falk-Peterson 2008; Lowerre-Barbieri et al. 2019). Obtaining valuable information on movements of individual fish can bridge knowledge–action gaps and should be integrated into local fisheries management. For example, Brownscombe et al. (2019) used acoustic telemetry to track Permit *Trachinotus falcatus* and found that individuals were present at a spawning aggregation site earlier than previously known. After this telemetry information was presented to the Florida Fish and Wildlife Conservation Commission (FWC), the decision was made to expand the Permit harvest closure from April to July instead of May–July.

In modern fisheries research, acoustic telemetry is widely used because it can provide spatial and temporal information in both fine and broad scales and has substantially increased our knowledge of animal movements, habitat usage, and management effectiveness across the globe (Hussey et al. 2015). For example, acoustic telemetry has been used to assess the adequacy of a marine protected area (MPA) in Pohnpei (Weeks et al. 2017), support the expansion of MPAs in the Seychelles (Lea et al. 2016), and demonstrate the recovery of a Mutton Snapper

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Lutjanus analis spawning aggregation after the establishment of an MPA in the Dry Tortugas, Florida (Feeley et al. 2018). As in the above examples, tracking animals through acoustic telemetry not only provides information on individual movements but also gives valuable insight on habitat usage and indicates areas where spatial protection would be most beneficial.

Spatial protection is one of the tools available for achieving sustainable fisheries management and has been shown to increase both the size and density of fish populations (Nemeth 2005; Sadovy de Mitcheson 2016; Erisman et al. 2017; Feeley et al. 2018). Spatial protection may be particularly beneficial to protogynous hermaphrodites (e.g., many grouper species) when fishing efforts usually target the largest and most fecund individuals, potentially resulting in sperm limitation, decreased fertilization rates, and decreased population sizes (Alonzo and Mangel 2004). Spatial management can also be used to protect fish spawning aggregations (FSAs) when fish aggregate by the hundreds to thousands to spawn and are particularly vulnerable to overfishing. For managers, protecting spawning aggregations is critical because it maximizes the reproductive output and recruitment of a species (Levin and Grimes 2002) and increases the likelihood of sustaining regional fish populations and improving local fisheries (Nemeth et al. 2007).

The Western Dry Rocks (WDR) area located southeast of Key West, Florida, is one of the more heavily fished sections of the Florida Keys reef tract (FWC, unpublished aerial survey data; Supplementary Figure S.1 available separately online). This location was identified as a potential FSA site for multiple species of snapper (Lindeman et al. 2000) and is well known as an FSA site for Permit (Brownscombe et al. 2020). We suspect that WDR could have potential as a spawning aggregation site similar to Riley's Hump, a documented multispecies FSA utilized by both snapper and grouper species at different times of the year, which is located 70 km away from Key West in the Dry Tortugas region and has been protected as a no-take marine reserve since 2001 (Locascio and Burton 2015; Sanchez et al. 2017; Feeley et al. 2018). If the WDR area is an FSA for multiple species year-round, spatial protection could increase larval production and encourage growth of FSAs during both summer and winter months, similar to Riley's Hump.

Local fishermen have identified locations in the WDR area where grouper aggregate, but direct observations of grouper spawning at this location have yet to be formally documented. High winds in the Florida Keys are common during winter months (when grouper are reported to spawn in the region; Table 1) and can increase water turbidity while limiting the number of days on which a small craft can safely operate, thereby impeding the visual confirmation of (1) aggregation formation and (2) the actual release of gametes. The high fishing activity in the WDR area also complicates the logistics and safety protocols of scientific diving. For example, in May 2011 the FWC conducted an aerial survey that documented 41 boats participating in recreational or commercial fishing within 0.05 km^2 in the WDR area (FWC, unpublished data; Figure S.1). Therefore, acoustic telemetry was deemed a valuable avenue for collecting data on grouper movement patterns in the area while avoiding the difficulties associated with direct observation.

The purpose of this study was to (1) describe the movements and habitat usage of adults and subadults of four grouper species (Black Grouper *Mycteroperca bonaci*, Gag *Mycteroperca microlepis*, Yellowfin Grouper *Mycteroperca venenosa*, and Nassau Grouper *Epinephelus striatus*) and (2) use acoustic telemetry to determine whether WDR is a potential FSA site for these species. In addition, our results provide a first assessment of grouper behavior in WDR by determining home range sizes of individual grouper as well as spatial and temporal factors influencing grouper species presence within WDR. Knowledge of the spatial behavior of species of interest, such as groupers, is necessary to understand the potential benefits of spatial protection in this area.

STUDY AREA

Our study took place offshore of WDR, a high-relief bank reef located approximately 18 km southeast of Key West, Florida (Figure 1A). The study site focused on a hardbottom bank reef (~1.6 km long and 0.6 km wide) that lies seaward of the main reef structure and is typified by areas of scoured calcium carbonate pavement interspersed with areas of low hard and soft coral cover. The hardbottom portion of the study area is part of an outlier reef that runs parallel to the main reef tract, from approximately 81°51′W to 82°02′W, referred to locally as “Boca Grande Bar.” The bar is separated from the main reef structure by an approximately 500-m-wide sand-/mud-bottom channel with a depth of about 33–38 m. Water depths on Boca Grande Bar range from approximately 13 m on top of the bar to 39 m on the offshore side of the bar. Hereafter, we refer to the general study area as “WDR” and the area of Boca Grande Bar that our acoustic receiver array enclosed as “the bar.” Benthic habitat data displayed in figures are from the Unified Florida Coral Reef Tract Map (FWRI 2017).

We deployed a receiver array of 16 Vemco VR2W acoustic receivers (69 kHz; Vemco, Ltd., Amirix Systems, Halifax, Nova Scotia) that surrounded the bar formation and four more receivers placed near areas that were suspected to be corridors for fish movement. Due to the

TABLE 1. Reproductive information summary for grouper tagged in this study (L_{50} = size at which 50% of females were found to be spawning capable).

Species	Spawning period	Peak spawning months	Size at maturity	Current Florida minimum size regulations
Black Grouper	Dec–Apr: Riley's Hump, Florida (Sanchez et al. 2017); Jan–Mar: Cuba (Claro and Lindeman 2003)	Apr: Riley's Hump, Florida (Sanchez et al. 2017); Feb–Mar: Cuba (Claro and Lindeman 2003)	L_{50} for females: 856 mm TL (SEDAR 2010)	610 mm TL
Yellowfin Grouper	Jan–Mar: Cuba (Claro and Lindeman 2003); Jan–May: Puerto Rico (Schärer et al. 2012)	Jan–Feb: Cuba (Claro and Lindeman 2003); Apr–May: Puerto Rico (Schärer et al. 2012); Mar–Apr: Bahamas (Cushion et al. 2008)	L_{50} for females: 510 mm FL (García-Cagide et al. 2001)	508 mm TL
Gag	Feb–Apr: northeastern Gulf of Mexico (Collins et al. 1998)	Mar: eastern Gulf of Mexico (Koenig et al. 1996)	L_{50} for females: 551 mm TL (SEDAR 2014)	610 mm TL
Nassau Grouper	Dec–Feb: Cuba (Claro and Lindeman 2003)	Dec–Jan: Cuba (Claro and Lindeman 2003); Jan–Feb: Little Cayman (Whaylen et al. 2007)	L_{50} for females and males: 440–504 mm TL (Sadovy and Eklund 1999)	Harvest prohibited

high use of this area and previous experiences with equipment tampering and unsafe interactions between divers and boaters, it was decided to deploy the array in a rectangle around the feature of interest to avoid user conflicts and ensure longevity of equipment throughout the study. Receivers were housed in polyvinyl chloride cups mounted in concrete blocks as described by Herbig et al. (2019). An additional 12 receivers that were part of an existing array located to the east of WDR and directly south of Key West were also utilized in the present study to determine whether there was connectivity from this location to WDR (Figure 1A). In addition to these 32 receivers owned by the FWC's Fish and Wildlife Research Institute (FWRI), we participated in two telemetry sharing networks: the FACT network (https://secoora.org/fact/) and the integrated Tracking of Aquatic Animals in the Gulf of Mexico (iTAG) network (Lowerre-Barbieri et al. 2017; https://itagscience.com/). Additionally, FWRI has a partnership with the Bonefish and Tarpon Trust (https://www.bonefishtarpontrust.org), a nonprofit conservation group that also utilizes acoustic receivers. Through these networks and partnerships, an additional 40 receivers were maintained near the study area, with hundreds of additional receivers monitored throughout southern Florida.

METHODS

Acoustic Tagging

Eighteen grouper were tagged at four locations in WDR from March 2015 through August 2016. Tagged fish consisted of 10 Black Grouper, 5 Nassau Grouper, 2 Gag, and 1 Yellowfin Grouper. Tagging was attempted at four locations throughout the WDR array; however, the previously mentioned high boat use in this area resulted in tagging at location 1 more often than at the other locations (Figure 1B; Table 2). All fish were captured using baited chevron traps. Tagging was performed in situ (12–34 m) to reduce fish stress, similar to methods described by Feeley et al. (2018) and Tuohy et al. (2015). Fish were retrieved from the traps by using a plastic-coated net and were held ventral side up with the eyes covered, inducing a catatonic state considered to be an ethical alternative to sedatives (Lowerre-Barbieri et al. 2014). The TL of each fish was recorded as the fish was held ventral side up and before the start of the surgery.

Thirteen of the 18 fish were implanted with Vemco V16 acoustic tags (69 kHz; high powered; 60–180-s or 50–130-s random delay; 1,229–1,825-d tag life), and 5 smaller fish were implanted with Vemco V13 tags (69 kHz; high

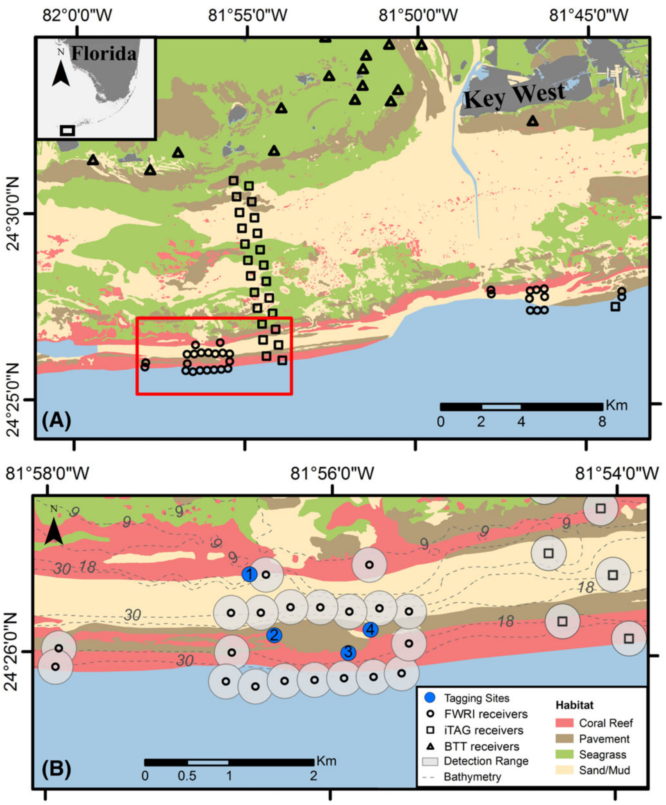

FIGURE 1. **(A)** Broader study area in the Florida Keys, showing benthic habitat and locations of receivers that are managed by the Fish and Wildlife Research Institute (FWRI), the integrated Tracking of Aquatic Animals in the Gulf of Mexico (iTAG), and Bonefish and Tarpon Trust (BTT). The red box in panel A indicates the study area, encompassing **(B)** Western Dry Rocks, including grouper tagging locations, 50% detection probability range of receivers, and bathymetric contour lines (m). The light blue color indicates areas where benthic habitat data are missing.

powered; 60–180-s random delay; 653-d tag life). Tags were implanted in each fish's abdominal cavity via an incision made along the midline posterior to the pelvic girdle (Feeley et al. 2018). The incision was closed using sterile synthetic absorbable sutures (Vicryl Plus; Ethicon, Inc., Somerville, New Jersey) with an antibacterial coating and a size-0 cutting needle. Fish were then positioned dorsal side up, tagged with an external dart tag (Hallprint, Hindmarsh Valley, Australia) in the musculature between the dorsal fin spines, and released. Surgery times ranged from 1 to 10 min, while total handling times ranged from 5 to 15 min.

Range Test

Because numerous biological, environmental, and anthropogenic factors can affect the transmission of an acoustic signal (particularly in rugose coral reef habitat), we evaluated the effect of distance, habitat, and time of day on the detection range of the receivers deployed around the WDR bar to avoid misinterpreting patterns in detections (McCallister et al. 2018). Four Vemco VR2Tx receivers were placed along a north/south line spanning the WDR bar, and two VR2W receivers in the box array were replaced with VR2Tx receivers (Figure S.2). The VR2Tx receivers contain a built-in transmitter, which allows these receivers to also transmit a tag ID. The range test receivers were deployed from May to November 2018 and were set to transmit on high power (154 dB) with a random transmission delay between 60 and 120 s.

To examine the effects of habitat (sand or reef), distance between transmitter and receiver, and hour (time of day) on the detection rate, a generalized linear mixed model (GLMM) with a binomial distribution was used with both date and transmitter ID as random effects (Farmer et al. 2013; McCallister et al. 2018). Detection rate was calculated as the number of detections heard in an hour divided by the maximum number of detections possible in an hour. Distance was scaled to a mean of 0 and an SD of 1 to improve model fit, and the analysis was run in R (R Core Team 2018) by using the glmmTMB package (Brooks et al. 2017). Model selection was based on the lowest value of Akaike's information criterion corrected for small sample size (AIC_c), which ranks models based on explained deviance and the number of parameters included in each model (Burnham et al. 2011; Herbig et al. 2019). A pseudo-R^2 value was calculated for the best approximating model (lowest AIC_c value) by using the MuMIn package (Bartoń 2018). The mean 50% detection probability range (averaged between the two habitat types) was used as the location error distance in the home range calculations.

Validation and Filtering of Detection Data

To minimize potential biases associated with the handling of fish (e.g., tagging), the initial 24 h of detections were removed before analysis (Farmer and Ault 2011). We then applied a series of filters (detailed in the following sentences) to remove repeated or false detections. We ensured that two fish were not detected at the same location at the exact same time, as the receivers cannot receive more than one transmission at a time. We also removed any single detections within an hour, as they are not considered reliable. To avoid overinflation of detections and decrease the potential for misinterpretation of the data, detections were removed if the time interval from the last detection was less than the minimum time it should have taken the tag to transmit another signal (Farmer et al. 2013; Becker et al. 2016), a situation that can be caused by an echo effect or by a fish being located between receivers.

TABLE 2. Summary information for tagged grouper, sorted by tagging date (DD = number of days on which the fish was detected; TP = total tracking period or number of days tracked; residency index [R_i] = DD/TP). Asterisks indicate that the fish was at or above the length at 50% maturity at the time of tagging. References for length at 50% maturity are listed in Table 1. Depth tagged for fish at tagging site 1 varied because it was located at a slope from a coral ledge down to sand. Shaded rows indicate fish with more than 30 d detected, which were used in analyses.

Fish ID	Species	Tag type	TL (cm)	Tagging date	Tagging site	Depth tagged (m)	Expiration date	Total detections	Receiver locations visited	DD	TP	R_i
01	Black Grouper	V16	104*	Mar 18, 2015	2	16	Jul 29, 2018	170,980	8	473	1,176	0.40
02	Black Grouper	V16	54	Mar 19, 2015	2	16	Jul 30, 2018	91,566	20	337	337	1.00
03	Nassau Grouper	V16	72*	Mar 25, 2015	3	17	Aug 5, 2018	132	7	25	71	0.35
04	Nassau Grouper	V13	40	Apr 22, 2015	1	15	Feb 3, 2017	11,984	14	381	641	0.59
05	Nassau Grouper	V16	62*	Apr 22, 2015	1	15	Apr 20, 2020	1,981	18	115	265	0.43
06	Gag	V16	71*	Apr 22, 2015	4	16	Sep 2, 2018	10,721	2	104	231	0.45
07	Black Grouper	V16	72	Apr 22, 2015	4	16	Sep 21, 2018	42,367	16	635	787	0.81
08	Gag	V16	65*	Apr 23, 2015	1	15	Sep 22, 2018	3,460	5	50	69	0.72
09	Yellowfin Grouper	V16	57*	Jun 23, 2015	1	15	Nov 3, 2018	18,467	13	317	322	0.98
10	Nassau Grouper	V16	57*	Aug 3, 2015	1	15	Jan 2, 2019	47,497	14	362	394	0.92
11	Black Grouper	V13	43	Aug 4, 2015	4	16	May 18, 2017	0	0	0	0	
12	Black Grouper	V13	44	Aug 4, 2015	1	15	May 18, 2017	0	0	0	0	
13	Nassau Grouper	V16	51*	Aug 5, 2015	1	15	Jan 4, 2019	454	23	9	538	0.02
14	Black Grouper	V16	80	Aug 13, 2015	1	34	Dec 24, 2018	14,190	9	50	50	1.00
15	Black Grouper	V16	77	Aug 14, 2015	1	34	Aug 12, 2020	11,597	11	66	67	0.99
16	Black Grouper	V13	42	Aug 10, 2016	1	12	May 25, 2018	37,861	5	530	581	0.91
17	Black Grouper	V13	51	Aug 10, 2016	1	12	May 25, 2018	566	2	63	152	0.41
18	Black Grouper	V16	66	Aug 10, 2016	1	12	Aug 9, 2021	307	1	19	397	0.05

After filtering detections, a total tracking period (TP) was calculated for each fish as the total number of days for which the fish was at liberty from 24 h after tagging until the tag was detected for the last time. The number of detection days (DDs) was calculated as the total number of days on which a fish had valid detections. Because we were interested in seasonal trends, fish with less than 30 d of detections were not included in further analyses.

Evaluating Western Dry Rocks as a Potential Grouper Spawning Site

Seasonal and diel activity patterns for tagged grouper were characterized by grouping the detection data into 1-h time bins by day. Each detection was given a value of 1, and the total number of detections in an hour was recorded for that time bin. If a fish was not detected within a 1-h period, a value of 0 was given to that time bin. All detections were assigned a diel period, a lunar phase, a month, a season, and a spawning period. Diel periods were dawn (30 min before to 30 min after sunrise), day (30 min after sunrise to 30 min before sunset), dusk (30 min before to 30 min after sunset), and night (30 min after sunset to 30 min before sunrise). Sunrise and sunset times were calculated daily at each receiver location by using the "StreamMetabolism" package (Sefick 2016). Lunar period was assigned based on data from the National Aeronautics and Space Administration (https://eclipse.gsfc.nasa.gov/SKYCAL/SKYCAL.html). Season was defined as winter (December–February), spring (March–May), summer (June–August), and fall (September–November). Months were assigned as "spawning" or "nonspawning" based on spawning periods reported in the literature (determined by gonadosomatic indices, direct observations of gamete releases, histology of hydrated eggs, or indirect observations via fishermen; Table 1). Due to variability in regional peak spawning months and our desire to capture staging behavior before spawning, the months of December–April were considered to be spawning months for all species. All analyses in this study were completed in R (R Core Team 2018).

Temporal patterns in grouper presence.— To examine the effects of time of year, diel period, and lunar phase on the presence of tagged grouper within the array, we used a GLMM with a binomial distribution via the glmmTMB package (Brooks et al. 2017). Diel period, lunar phase, and time of year were fixed effects, with all two-way interactions included; date and transmitter ID were included as random effects. For the Yellowfin Grouper, only the date was used as a random effect. Time of year was the month, the season, or the spawning period for each species. Month was the finest scale of the time frame and was included as a possible factor because fish may begin to arrive at an aggregation site to "stage" before the actual spawning period. Season was included as a factor because most grouper are believed to spawn in winter (Table 1). However, winter may not encompass the full time frame of spawning for all grouper species tagged here, so spawning period was included as a possible factor. Because month, season, and spawning period are correlated, three different models were run using the different time frame factors (month, season, or spawning period) in addition to the factors previously mentioned and all interaction terms. The model with the lowest AIC_c was chosen and used as the full model to begin the model parameterization selection process. In an effort to identify the most parsimonious description of grouper presence within an array, the model parameterization selection process included the iterative removal of explanatory variables, with each representing a unique hypothesis, until the best approximating model was then chosen based on the lowest AIC_c value. If there was substantial support for more than one model (AIC_c difference [ΔAIC_c] < 2), then model predictions were averaged (Burnham and Anderson 2002). The overall fit of the best approximating model was determined by creating receiver operating curves and calculating the area under the curve using the ROCR package (Sing et al. 2005). Essentially, this test estimates how well the model correctly classifies outcomes with values that range from 0 to 1, with 0.5 having no more predictive ability than a random model and 1.0 having high predictive power (Fielding and Bell 1997). A pseudo-R^2 was also calculated for the best approximating model by using the MuMIn package (Bartoń 2018).

Grouper Habitat Use at Western Dry Rocks

Grouper movements.— Movements between receiver locations by tagged grouper were compared and examined for hot spots of activity. We used network analysis to create spatial movement graphs, where nodes represented actual locations of receivers and edges represented the movement of fish between these locations (Finn et al. 2014; Becker et al. 2016; Boucek et al. 2017). Node size was proportionate to node degree (the number of edges connecting to the node), and edge width was proportionate to the total number of times fish moved between receivers. The igraph package (Csárdi and Nepusz 2006) was used to calculate node degree and edge weights in each network. Spatial movement graphs were created to compare how grouper used WDR habitat between spawning and nonspawning seasons and how usage varied among species and individuals.

Site fidelity and home range.— To determine site fidelity, a residency index (R_i) was calculated for each tagged fish as follows: $R_i = DD/TP$, with values ranging between 0 (no residency) and 1 (full-time resident; Abecasis et al. 2009). We evaluated grouper home range estimates using Brownian bridge movement models and compared them to published home range estimates. The Brownian bridge method considers not only the locations of detections but also the time interval and the estimated path traveled between successive detection locations (Calenge 2006; Horne et al. 2007) and incorporates location error, which is appropriate for acoustic telemetry studies when receivers detect a tagged animal within a defined detection range rather than at a specific location (Pagès et al. 2013; Aspillaga et al. 2016). The Brownian bridge method assumes that locations are not independent and models uncertainty in the movement path between observed locations (Horne et al. 2007). The parameter estimating the variance of the fish's position between two detections is based on maximum likelihood (Calenge 2006; Horne et al. 2007). Brownian bridge home range estimates were calculated using the "adehabitatHR" package (Calenge 2006) for 50% and 95% utilization distributions, and outputs from this package were exported to ArcGIS version 10.3 (ESRI 2014) for the creation of contours that represented the core use (50%) and home range (95%) borders. The mean 50% detection probability from the range test was used as the distance of location error in the home range calculations. To examine grouper size in relation to home range, a linear regression was used to compare core use and home range estimates to fish TL.

RESULTS

Acoustic Tagging

The TL of the 18 tagged grouper ranged between a 40-cm Nassau Grouper and a 104-cm Black Grouper (mean ± SE = 62 ± 4 cm; Table 2). Ten of the grouper were subadults (below the length at which 50% of the population reaches sexual maturity), and eight were sexually mature adults. Of the 18 tagged grouper, 2 were never detected. The total number of validated detections for all 16 grouper detected was 464,130, with a range from 132 to 170,984 detections/fish (mean ± SE = 29,008 ± 11,290 detections/fish). Time at liberty ranged between 50 and 1,176 d (380 ± 77 d), and the actual number of days detected was 9–635 d (221 ± 52 d; Table 2; Figure 2). Three of the 16 grouper were detected for less than 30 d and were not used in any subsequent analyses. The two undetected individuals were both Black Grouper (<50 cm) tagged on the same day, while the three fish with less than 30 d of detection were two Nassau Grouper and one Black Grouper of varying sizes tagged at different times (Table 2).

Range Test

Habitat and the interaction between habitat and scaled distance had the strongest effect on detection probability (pseudo-R^2 = 0.81). The mean 50% detection probability was 208 m and ranged from 163 to 167 m for coral reef habitat and from 246 to 251 m for unconsolidated sediment (Figure S.3). The greater range at 50% detection probability in unconsolidated sediment (sand and/or mud) was most likely due to differences in biological noise between the habitat types (Figure S.4). Since the effect of hour was very small in the model (odds ratio was ~20 times smaller than the interactive effect of habitat and distance), detection rates were not weighted by hour. Model ranking and model parameters from the top-ranked model can be found in the Supplementary Material available separately online (Supplementary Tables S.1, S.2).

Evaluating Western Dry Rocks as a Potential Grouper Spawning Site

Temporal patterns in grouper presence.— Time of year (e.g., month, season, or spawning) had a relatively large effect on all four species, with tagged subadult and adult grouper being more likely to be detected in the array during their respective spawning time frames. The effect of diel period varied based on species and time of year except for Nassau Grouper, which showed little variation in presence due to diel period. Lunar phase had the smallest effect on the presence of all grouper species (Tables 3–6). Model ranking for each species can be found in Tables 3–6, whereas model parameters from the top-ranked GLMMs can be found in Tables S.3–S.6.

In general, the probability of Black Grouper presence was highest during spawning months (December–May) across all diel periods and lunar phases (Figure 3A). From June through November, Black Grouper were less likely to be present and there was a greater effect of diel period, as fish were less likely to be present from dusk until dawn. Nassau Grouper were more likely to be present from

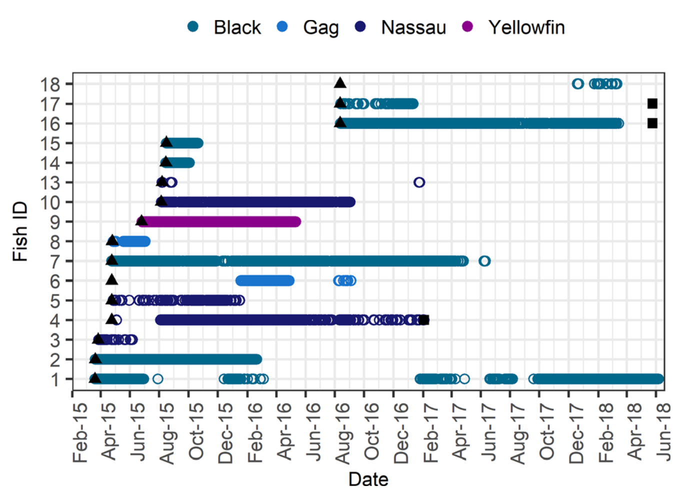

FIGURE 2. Abacus plot of tagged grouper ordered by date of tagging and colored by species (Black Grouper, Gag, Nassau Grouper, and Yellowfin Grouper). Triangles indicate the date of tagging, and squares indicate the end of tag life.

February through April and in August except during the new moon (Figure 3B). There was not as much variability in the probability of presence among diel periods compared to Black Grouper and Yellowfin Grouper, although there was an increase in variation during the last quarter and new moon phases. Gag were more likely to be present during spawning months regardless of diel period or lunar phase (Figure 3C). Gag were less likely to be present during dawn and day—a pattern that was much more pronounced during the last quarter moon phase. There was support for two models for the Yellowfin Grouper ($\Delta AIC_c < 2$; Burnham and Anderson 2002), so the model predictions were averaged. Averaged model predictions showed that the Yellowfin Grouper was more likely to be present during the dawn and day, except in the spring, in all lunar phases (Figure 3D). The probability of Yellowfin Grouper presence increased during the spring, regardless of lunar phase or diel period, but dusk and night had the largest variation in presence based on season.

Grouper Habitat Use at Western Dry Rocks

Grouper movements.— Spawning-capable grouper (Table 2) moved greater distances per day during nonspawning months (mean = 124.9 m/d) compared to spawning months (mean = 95.4 m/d; Welch's two-sample t-test: $t = 5.16$, df = 358.8, $P < 0.001$). Grouper also visited more receiver locations during nonspawning months, although the north side of the bar had the most activity regardless of the time of year (Figure 4). A Nassau Grouper (fish 05) was the only spawning-capable grouper to leave the WDR array during the spawning season, but it was only detected on a single day in January 2016 on two iTAG receivers (~2.5 km away) during the new moon. The only spawning-capable fish to make movements across the bar and be detected on the deeper, south side of the bar was a single Black Grouper (fish 01) for a few days in March 2015 during the new moon and first quarter moon. However, these movements may not be related to spawning, as the detections occurred only 1 week after fish 01 was tagged and such behavior was not seen during subsequent spawning seasons.

Separating movements of both adult and subadult grouper by species revealed overlapping habitats but different movement patterns. The Black Grouper was the only species to regularly move across the bar, but the most frequent movements were detected at receiver locations on the north-central side of the bar (Figure 5). Except for the movements from fish 01 (described in the previous paragraph), Black Grouper movements across the bar and detections on the south side of the bar were of individuals that were likely immature (i.e., TL at tagging was less than the reported length at 50% maturity). These smaller fish also made movements from the main

TABLE 3. Set of ranked models for the generalized linear mixed model analysis for Black Grouper presence (Diel = diel period; Phase = lunar phase). Models were ranked based on the number of parameters (k), the corrected Akaike's information criterion (AIC_c), the change in AIC_c from the top-ranked model (ΔAIC_c), and model weight. A pseudo-R^2 was also calculated for the best approximating model (the model with the lowest AIC_c).

Model	k	AIC_c	ΔAIC_c	Weight	Pseudo-R^2
Diel + Month + Phase + (Diel × Month) + (Diel × Phase)	62	67,155.75	0.00	0.99	0.77
Diel + Month + Phase + (Diel × Month)	53	67,164.27	8.52	0.01	
Diel + Month + (Diel × Month)	50	67,170.73	14.98	0.00	
Diel + Month + Phase + (Diel × Month) + (Phase × Month) + (Diel × Phase)	95	67,179.25	23.50	0.00	
Diel + Month + Phase + (Diel × Month) + (Phase × Month)	86	67,188.22	32.47	0.00	
Diel + Month + Phase + (Diel × Phase)	29	67,359.50	203.74	0.00	
Diel + Month + Phase	20	67,372.57	216.82	0.00	
Diel + Month + Phase + (Diel × Phase) + (Phase × Month)	62	67,377.83	222.08	0.00	
Diel + Month	17	67,379.12	223.37	0.00	
Diel + Month + Phase + (Phase × Month)	53	67,391.48	235.73	0.00	
Phase + Month	17	67,685.07	529.32	0.00	
Phase + Diel + (Diel × Phase)	18	67,689.73	533.97	0.00	
Month	14	67,691.17	535.42	0.00	
Phase + Month + (Phase × Month)	50	67,702.45	546.70	0.00	
Phase + Diel	9	67,702.81	547.06	0.00	
Diel	6	67,711.82	556.06	0.00	
Phase	6	68,014.17	858.42	0.00	
Null	3	68,022.60	866.84	0.00	

TABLE 4. Set of ranked models for the generalized linear mixed model analysis for Nassau Grouper (Diel = diel period; Phase = lunar phase). Models were ranked based on the number of parameters (k), the corrected Akaike's information criterion (AIC_c), the change in AIC_c from the top-ranked model (ΔAIC_c), and model weight. A pseudo-R^2 was also calculated for the best approximating model (the model with the lowest AIC_c).

Model	k	AIC_c	ΔAIC_c	Weight	Pseudo-R^2
Diel + Month + Phase + (Diel × Month) + (Phase × Month) + (Diel × Phase)	95	25,084.08	0.00	1.00	0.61
Diel + Month + Phase + (Diel × Month) + (Diel × Phase)	62	25,110.06	25.98	0.00	
Diel + Month + Phase + (Diel × Month) + (Phase × Month)	86	25,129.30	45.22	0.00	
Diel + Month + Phase + (Diel × Month)	53	25,154.91	70.83	0.00	
Diel + Month + (Diel × Month)	50	25,159.79	75.71	0.00	
Diel + Month + Phase + (Diel × Phase) + (Phase × Month)	62	25,404.71	320.63	0.00	
Diel + Month + Phase + (Diel × Phase)	29	25,440.74	356.66	0.00	
Diel + Month + Phase + (Phase × Month)	53	25,462.53	378.45	0.00	
Diel + Month + Phase	20	25,496.50	412.42	0.00	
Diel + Month	17	25,499.48	415.40	0.00	
Phase + Diel + (Diel × Phase)	18	25,676.63	592.55	0.00	
Phase + Diel	9	25,732.39	648.31	0.00	
Diel	6	25,733.41	649.33	0.00	
Phase + Month + (Phase × Month)	50	26,169.52	1,085.44	0.00	
Phase + Month	17	26,205.26	1,121.18	0.00	
Month	14	26,207.97	1,123.89	0.00	
Phase	6	26,438.29	1,354.21	0.00	
Null	3	26,439.05	1,354.97	0.00	

WDR array both eastward to the iTAG receivers and westward.

Nassau Grouper made multiple movements from the WDR array eastward to the iTAG receivers, but they also traveled westward and were detected on all receivers in the WDR array (Figure 5). However, they were rarely detected as moving across the bar; instead, they moved along the outer edges of the array. The receiver locations with the largest proportion of Nassau Grouper movements were located on a coral ledge northwest of the bar.

Due to the low sample sizes of Gag and Yellowfin Grouper, grouped species movements are not shown in Figure 5, but individual movements of the Yellowfin Grouper and one of the two Gag are displayed, overlaying their home range estimates (Figure 6E, F). Gag were detected on the fewest receivers, were not detected as moving across the bar, and were only detected at receivers on the north or east side of the WDR array (Figure 6E). The Yellowfin Grouper made most of its movements in the northwest section of the WDR array (Figure 6F), but it also traveled eastward to the iTAG receivers, where it was detected for 3 d in May and then was never detected again.

Site fidelity and home range.— In general, site fidelity (calculated as the residency index R_i) at WDR was high for all tagged grouper ($R_i = 62.8 \pm 8.4\%$ [mean ± SE]; Table 2). Site fidelity was highest for the Yellowfin Grouper ($R_i = 98\%$), followed by Black Grouper (69.60 ± 11.90%) and then Gag (58.50 ± 23.70%), and was lowest for Nassau Grouper (46.20 ± 15%). There was no significant relationship between fish TL and site fidelity, regardless of species ($F_{1,\ 6} = 0.298$, $P = 0.851$, $R^2 = -0.422$).

Home ranges and core use areas were small for all species (Table 7; Figure 6). Nassau Grouper had the largest average 95% home range ($1.58 \pm 0.59\ km^2$ [mean ± SE]), followed by Black Grouper ($0.96 \pm 0.18\ km^2$), Yellowfin Grouper ($0.78\ km^2$), and Gag ($0.68 \pm 0.07\ km^2$). Core use areas followed a similar pattern, with Nassau Grouper having the largest average core use area ($0.20 \pm 0.03\ km^2$ [mean ± SE]), followed by Black Grouper ($0.17 \pm 0.01\ km^2$), Gag ($0.16 \pm 0.03\ km^2$), and Yellowfin Grouper ($0.15\ km^2$). There was no significant relationship between fish TL and 95% home range area ($F_{1,\ 6} = 1.867$, $P = 0.233$, $R^2 = 0.302$) or between TL and 50% core use area ($F_{1,\ 6} = 0.245$, $P = 0.945$, $R^2 = -0.606$), regardless of species.

DISCUSSION

Grouper movements detected in this study using acoustic telemetry support the hypothesis that the WDR area is important habitat for subadult and adult grouper and potentially contains a grouper spawning aggregation site. Detection data of tagged grouper indicated high site fidelity to WDR and showed seasonal movement patterns that varied across individuals and, to some extent, across species.

TABLE 5. Set of ranked models for the generalized linear mixed model analysis for Gag (Diel = diel period; Phase = lunar phase; Spawn = spawning period). Models were ranked based on the number of parameters (k), the corrected Akaike's information criterion (AIC_c), the change in AIC_c from the top-ranked model (ΔAIC_c), and model weight. A pseudo-R^2 was also calculated for the best approximating model (the model with the lowest AIC_c).

Model	k	AIC_c	ΔAIC_c	Weight	Pseudo-R^2
Diel + Spawn + Phase + (Diel × Spawn) + (Phase × Spawn) + (Diel × Phase)	25	3,854.59	0.00	1.00	0.92
Diel + Spawn + Phase + (Diel × Spawn) + (Diel × Phase)	22	3,867.28	12.69	0.00	
Diel + Spawn + Phase + (Diel × Spawn) + (Phase × Spawn)	16	3,882.77	28.18	0.00	
Diel + Spawn + Phase + (Diel × Spawn)	13	3,894.11	39.52	0.00	
Diel + Spawn + (Diel × Spawn)	10	3,898.38	43.78	0.00	
Diel + Spawn + Phase + (Diel × Phase) + (Phase × Spawn)	22	4,000.54	145.95	0.00	
Diel + Spawn + Phase + (Diel × Phase)	19	4,009.35	154.75	0.00	
Diel + Spawn + Phase + (Phase × Spawn)	13	4,017.28	162.69	0.00	
Diel + Spawn + Phase	10	4,025.89	171.29	0.00	
Diel + Spawn	7	4,029.33	174.73	0.00	
Phase + Spawn + (Phase × Spawn)	10	4,126.09	271.50	0.00	
Phase + Spawn	7	4,131.93	277.34	0.00	
Spawn	4	4,133.37	278.78	0.00	
Phase + Diel + (Diel × Phase)	18	4,168.10	313.50	0.00	
Phase + Diel	9	4,184.05	329.46	0.00	
Diel	6	4,200.16	345.57	0.00	
Phase	6	4,290.38	435.79	0.00	
Null	3	4,304.42	449.82	0.00	

In general, tagged grouper of all species were more likely to be present at WDR during spawning months compared to nonspawning months, although some individuals (both adults and subadults) were present year-round.

During peak spawning months, for all species except Gag, the probability of presence in the WDR array increased during dusk and night. This further supports WDR as a potential grouper spawning aggregation site, as most grouper spawn during dusk (Colin 1992; Schärer et al. 2012). In contrast, during nonspawning months, tagged adult and subadult grouper made more movements away from WDR and in general were more likely to be absent from the entire array. While the grouper were not as likely to be present at WDR during nonspawning months, the individuals (both adults and subadults) that were present year-round indicate that WDR may be important not only as a potential spawning aggregation site but also as habitat to support feeding or growth to maturity.

Mature grouper that were likely spawning capable spent most of their time on the north side of WDR during spawning months. More detections on the south side of the bar were expected because there is a drop-off to a deeper reef system and grouper species have been shown to aggregate at depths greater than 20 m during spawning periods (Eklund et al. 2000; Claro and Lindeman 2003; Starr et al. 2007). The sand channel on the north side of WDR reaches a depth of 35 m but does not have a steep drop-off between the sand channel and the bar. If fish were moving into deeper water to spawn, we expected that they would be detected on the south-side receivers and then would be absent from the array at times during spawning months, but this pattern was not detected. In fact, only fish 01 (the largest and most active Black Grouper) was detected on the south-side receivers during spawning months, but this behavior was only seen during one of the four spawning seasons in which fish 01 was present in WDR (and only during the week after its tagging) and therefore was most likely not linked to spawning. Removal of the movements made by fish 01 across the bar did not change the overall spatial use pattern wherein the north side of the array had the most detections during the spawning season.

The increase in grouper presence during spawning months and detections on the north side of the bar may indicate that the fish are spending time on top of the bar or in the sand just off the coral ledge on the north side of the sand channel. There is a steep ledge on the north side of the northern sand channel, but the 50% detection range does not extend to that ledge. Increased scouting in the area and re-evaluation of the array design would be beneficial before additional telemetry studies in the area commence. Further work investigating a potential grouper spawning aggregation site in this area is needed, preferably with a larger sample size of sexually mature fish, an expanded array design, and a supplement to the telemetry

TABLE 6. Set of ranked models for the generalized linear mixed model analysis for Yellowfin Grouper (Diel = diel period; Phase = lunar phase). Models were ranked based on the number of parameters (k), the corrected Akaike's information criterion (AIC_c), the change in AIC_c from the top-ranked model (ΔAIC_c), and model weight. A pseudo-R^2 was also calculated for the best approximating model (lowest AIC_c).

Model	k	AIC_c	ΔAIC_c	Weight	Pseudo-R^2
Diel + Season + Phase + (Diel × Season) + (Diel × Phase)	29	8,243.06	0.00	0.48	0.47
Diel + Season + Phase + (Diel × Season) + (Phase × Season) + (Diel × Phase)	38	8,243.24	0.19	0.44	
Diel + Season + (Diel × Season)	17	8,247.04	3.98	0.07	
Diel + Season + Phase + (Diel × Season)	20	8,250.60	7.55	0.01	
Diel + Season + Phase + (Diel × Season) + (Phase × Season)	29	8,250.88	7.82	0.01	
Diel + Season	8	8,554.81	311.75	0.00	
Diel + Season + Phase	11	8,559.09	316.03	0.00	
Diel + Season + Phase + (Diel × Phase)	20	8,560.17	317.12	0.00	
Diel + Season + Phase + (Phase × Season)	20	8,562.67	319.61	0.00	
Diel + Season + Phase + (Diel × Phase) + (Phase × Season)	29	8,564.25	321.19	0.00	
Diel	5	8,599.05	356.00	0.00	
Phase + Diel	8	8,603.88	360.82	0.00	
Phase + Diel + (Diel × Phase)	18	8,606.71	363.65	0.00	
Season	5	9,686.30	1,443.25	0.00	
Phase + Season	8	9,689.37	1,446.31	0.00	
Phase + Season + (Phase × Season)	17	9,692.07	1,449.01	0.00	
Null	2	9,733.14	1,490.09	0.00	
Phase	5	9,736.89	1,493.83	0.00	

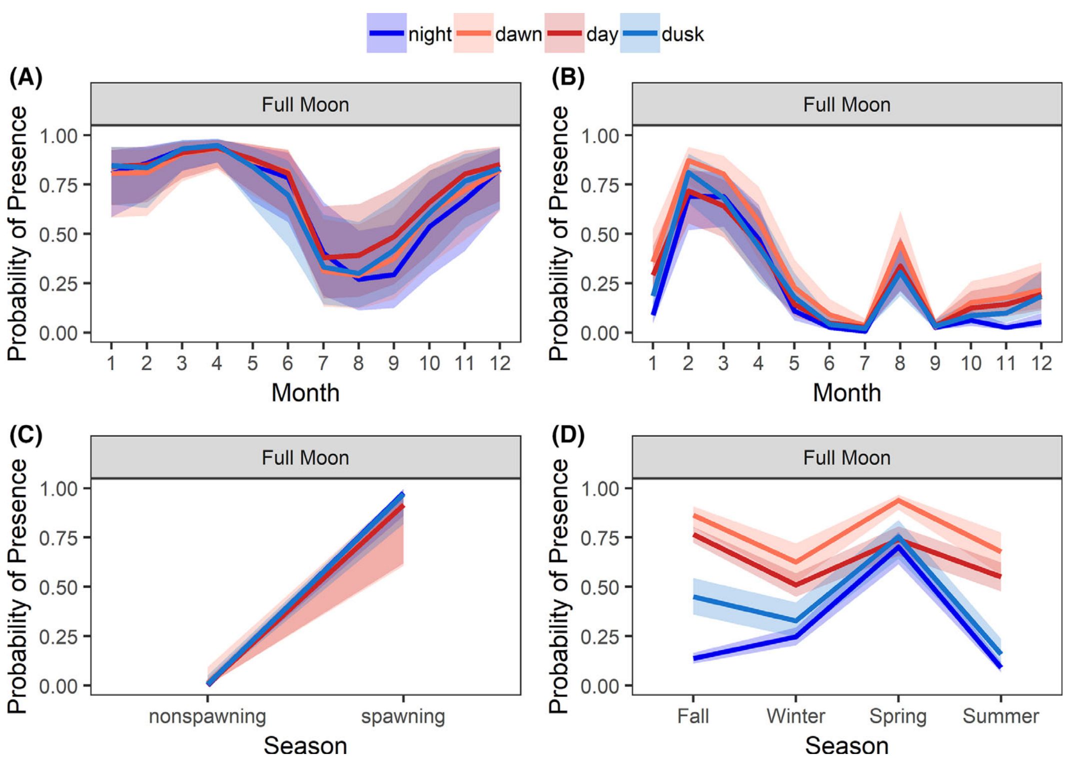

FIGURE 3. Probability estimates from the best approximating generalized linear mixed models for **(A)** Black Grouper, **(B)** Nassau Grouper, **(C)** Gag, and **(D)** Yellowfin Grouper when lunar phase is held constant at the full moon. The best approximating model for each species was chosen based on the lowest corrected Akaike's information criterion value from an iterative process. Therefore, the time frame factors are not the same across all models.

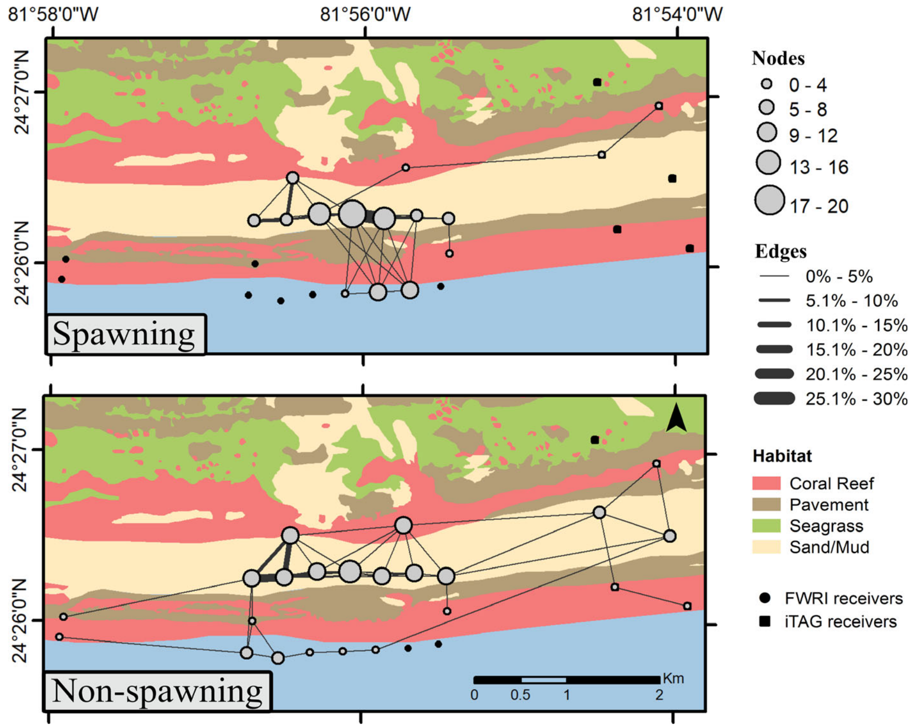

FIGURE 4. Spatial graph of grouper movements during spawning months (December–April; top panel) or nonspawning months (May–November; bottom panel) for those individuals that were spawning capable at the time of tagging ($n = 6$). Node size is proportionate to its degree, and the width of the edges is proportionate to movements between nodes versus total movements. Locations of Fish and Wildlife Research Institute (FWRI) and integrated Tracking of Aquatic Animals in the Gulf of Mexico (iTAG) receivers are shown.

methods, such as monitoring bioacoustics for grouper courtship and spawning-related sounds.

The mean 50% detection range used in the home range estimates was averaged between two habitats, which may have resulted in slight overestimation of the range in coral reef and hardbottom while underestimating the range in sand. Additionally, the receiver array design and the fact that most of the grouper were tagged outside of the main array mean that home range estimates and movements detected in this study are likely conservative. Nevertheless, as there are few published papers with home range sizes or spatial movement data for these four grouper species, we feel that our results provide beneficial information and are comparable to those of other telemetry studies. The few studies focusing on these grouper species have found either small home ranges or high site fidelity, with few movements greater than a few kilometers. Farmer and Ault (2011) reported that the mean home range of two subadult Black Grouper was 1.44 km^2. Kiel (2004) found a maximum spatial use area of 0.26 km^2 for 14 adult and subadult Gag. Bolden (2001) calculated the mean home range of 22 adult and subadult Nassau Grouper to be 0.018 km^2. There are, however, reports of individuals traveling more than 100 km, sometimes linked to a spawning aggregation (Nassau Grouper: Bolden 2000; Yellowfin Grouper: Burns et al. 2006). In our study, we did not see evidence of grouper moving large distances. The tagged grouper were not detected on any of the Florida Keys receivers located outside of WDR, but we acknowledge that they might have spent time in a nearby area just outside of array coverage. The combination of no long-distance movements and the increase in grouper presence during spawning months supports the hypothesis that there is a grouper spawning aggregation site within or near WDR.

Spatial movement graphs and home range locations suggest that different grouper species may utilize different areas of WDR. Although tagged Black Grouper represented a variety of sizes, they grow the largest compared to the other tagged grouper species and have been shown to form territories (Luckhurst 2010), which may cause the other grouper species to inhabit areas that are less frequented by Black Grouper. Habitat preferences may also be driving the partitioning of space use, as studies have shown that grouper densities are linked to structural features (Sluka et al. 2001). Due to the low sample sizes of Nassau Grouper, Gag, and Yellowfin Grouper, it is difficult to draw any generalizations about species-specific patterns. However, there is very little literature about these species' movements and habitat use in the Florida Keys,

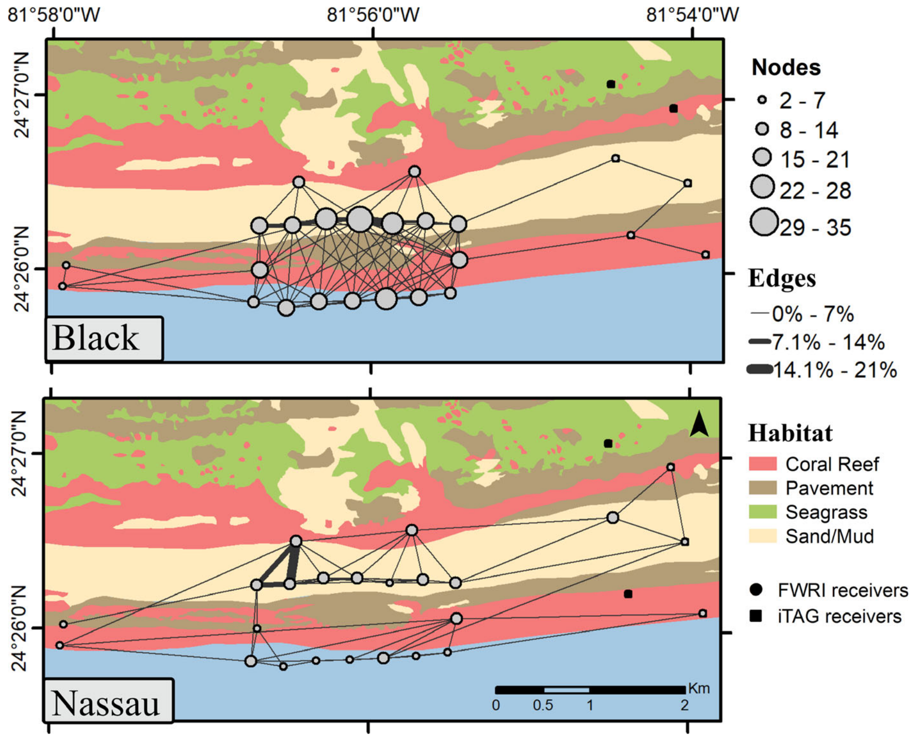

FIGURE 5. Spatial graph of grouper movements separated by species: Black Grouper ($n = 7$; top panel) and Nassau Grouper ($n = 3$; bottom panel). Node size is proportionate to its degree, and the width of the edges is proportionate to movements between nodes versus total movements. Locations of Fish and Wildlife Research Institute (FWRI) and integrated Tracking of Aquatic Animals in the Gulf of Mexico (iTAG) receivers are shown.

and results from this study will provide valuable baseline data for future work.

Although the overall sample size in this study was low, we believe that the tagged fish reflect the behavior of grouper in the lower Florida Keys. Based on biennial visual scuba surveys of hardbottom habitat in the Florida Keys for the Reef Visual Census (RVC; a multi-agency project that began in 1978), the average density of grouper species in the lower Florida Keys is low. Survey sites are randomly assigned based on habitat strata, covering low-relief hardbottom, mid-channel patch reefs, and aggregate reefs from nearshore to about 30 m deep. From 2014 to 2018 (the period of our study), 350 sites were surveyed in the lower Florida Keys, but the number of grouper observed during surveys was very low, which led to high uncertainty in density estimates for most species (Table 8). Effectively, the average density was 0 fish/176 m^2 (where 176 m^2 is the area of an RVC survey) for Nassau Grouper, Gag, and Yellowfin Grouper and 0.1 fish/176 m^2 for Black Grouper. The percentage occurrence for Nassau Grouper and Yellowfin Grouper was higher for the RVCs around our array compared to RVC sites in the rest of the lower Florida Keys, while the percentage occurrence was similar for Black Grouper and Gag (Table 8).

A large effort was required to catch the 18 grouper tagged for this study (a total of 578 h of trap soak time), and only 1 of the 10 Black Grouper was likely sexually mature. The lack of large, sexually mature individuals could be due to larger grouper preferring deeper water, but the largest Black Grouper we tagged was routinely detected at WDR for multiple years. Instead, this lack of large, mature Black Grouper may be due to the high fishing pressure at WDR. In fact, fishing has substantially changed the trophic structure of the reef fish communities in southern Florida, with most of the snapper–grouper complex fished at unsustainably high rates and with the largest-sized species being depleted more severely than the smaller-sized species (Ault et al. 2014).

A seasonal grouper closure was established in 2010 for state waters of the Atlantic Ocean and all waters of Monroe County (containing the Florida Keys) in an effort to protect grouper spawning aggregations (Recreational Grouper Seasons 2017). This closure prohibits recreational and commercial harvest of Black Grouper, Gag, Yellowfin Grouper, and seven other grouper species from January 1 to April 30. However, the closure may be simply shifting the high fishing pressure to different times of the year, such as late spring and summer when other fish species aggregate at WDR to spawn, thus still limiting the amount of spawning-capable grouper.

Four of the eight Black Grouper tagged in this study were last detected during the open grouper season (May

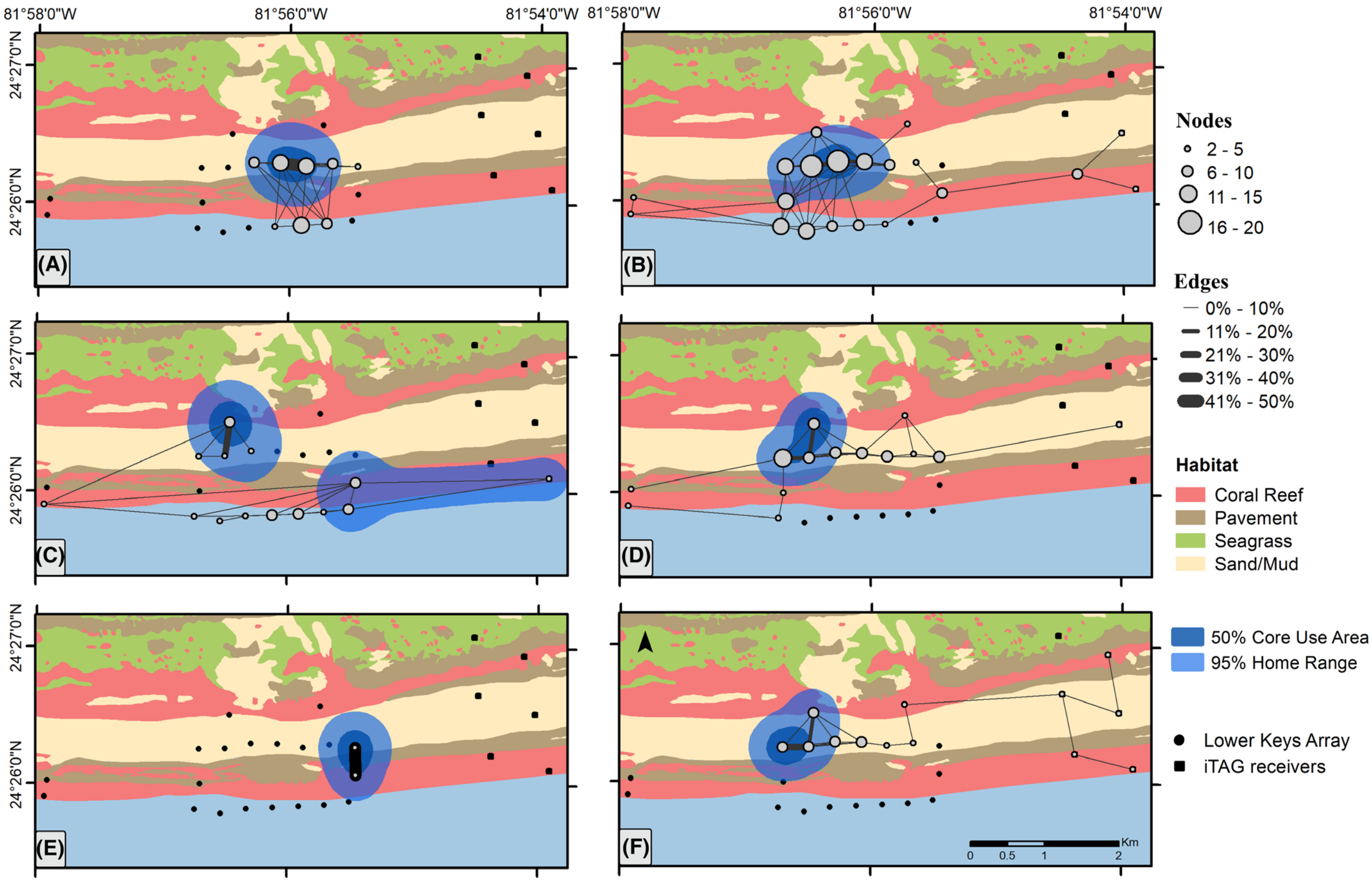

FIGURE 6. Brownian bridge 50% core use area (dark blue), 95% home range (light blue), node degree, and movements of individual grouper. All species are represented: **(A)** Black Grouper, fish 01; **(B)** Black Grouper, fish 02; **(C)** Nassau Grouper, fish 04; **(D)** Nassau Grouper, fish 10; **(E)** Gag, fish 06; and **(F)** Yellowfin Grouper, fish 09. Locations of receivers in the lower Florida Keys array and integrated Tracking of Aquatic Animals in the Gulf of Mexico (iTAG) receivers are shown.

1–December 31), and all of them were of legal size. Three of these fish (fish 07, 14, and 15) had high R_i values while they were detected and had 1–5 years left from their last detection until their tag expiration date. Similarly, both Gag and the Yellowfin Grouper had their last detections recorded during the open fishing season, with at least 1 year before tag expiration. One of the Gag (fish 08) was confirmed as harvested by an angler, who found the transmitter while cleaning the fish on July 8, 2015. The Yellowfin Grouper was detected in the same location for nearly a year before its last detection, just 7 d after the seasonal closure ended. Given the lack of movement by tagged grouper from shallower inshore receivers to deeper offshore receivers and the timing of some individuals' last detections, the lack of longer detection data and the absence of larger fish may be due to fishing pressure instead of ontogenetic habitat shifts.

Furthermore, the current minimum legal size of Black Grouper (610 mm) is less than the length at which 50% of females reach maturity (856 mm) and much less than the length at which 50% of females transition into males (1,214 mm; SEDAR 2010). The removal of mature fish during the open season and a poorly suited size limit (for Black Grouper) could be greatly limiting the spawning potential of grouper species, particularly protogynous hermaphrodites, such as the Black Grouper, Gag, and Yellowfin Grouper. Interestingly, Black Grouper presence in WDR was very high during May—a month that is not traditionally considered part of their spawning period. Although only one tagged Black Grouper was likely sexually mature, the increased presence in May is interesting, as it suggests the potential for Black Grouper to have a protracted spawning period in the Florida Keys compared to other regions.

Two grouper, fish 04 (Nassau Grouper) and fish 07 (Black Grouper), reached their length at 50% maturity over the study duration based on von Bertalanffy growth curves (Ehrhardt and Deleveaux 2007; SEDAR 2010). These two grouper were more likely to be in the WDR array during spawning months even when they were probably not yet mature, suggesting that immature individuals are following mature grouper during the spawning season

TABLE 7. Brownian bridge 95% home ranges and 50% core use areas. Grouper with less than 30 d of detection were not analyzed for home range or core use areas.

Fish ID	Species	TL (cm)	Days detected	Receiver locations visited	95% home range (km^2)	50% core use area (km^2)
01	Black Grouper	104	473	8	0.88	0.17
02	Black Grouper	54	337	20	1.01	0.16
04	Nassau Grouper	40	381	14	2.61	0.16
05	Nassau Grouper	62	115	18	1.34	0.25
06	Gag	71	104	2	0.64	0.16
07	Black Grouper	72	635	16	1.72	0.4
08	Gag	65	50	5	0.72	0.19
09	Yellowfin Grouper	57	317	13	0.78	0.15
10	Nassau Grouper	57	362	14	0.78	0.19
14	Black Grouper	80	50	9	1.37	0.14
15	Black Grouper	77	66	11	0.90	0.16
16	Black Grouper	42	530	5	0.45	0.08
17	Black Grouper	51	63	2	0.39	0.08

TABLE 8. Average density of grouper per 176 m^2 along with their associated variances from the Reef Visual Census data (CV = coefficient of variation). Percent occurrence was calculated as the number of stations in which fish were present divided by the total number of stations surveyed near our array in Western Dry Rocks (WDR) and the rest of the lower Florida Keys.

	Density			Percent occurrence	
Species	Average	SE	CV (%)	WDR	Lower Keys
Nassau Grouper	0.006	0.004	58	3	1
Black Grouper	0.105	0.015	14	11	16
Gag	0.002	0.001	70	0	0
Yellowfin Grouper	0.001	0.001	100	3	0

or that individuals are maturing at a smaller size. Nassau Grouper were found to follow Yellowfin Grouper to a spawning site after the overfishing of a local Nassau Grouper spawning aggregation site (Kadison et al. 2010), so the presence of a few older, spawning-capable individuals may not only show smaller individuals where to gather but may also influence the establishment (or re-establishment) of other species' spawning aggregations. This provides hope that an established grouper FSA can contribute to the formation or recovery of other grouper species' FSAs and that protection of one FSA could have benefits for other species.

The three grouper that were detected on fewer than 30 d and excluded from the analyses showed interesting variations in detection timing and location. Fish 03, the largest Nassau Grouper tagged, was detected primarily on the southeast side of the bar in April–May 2015 but was never heard from again. Fish 13, an adult Nassau Grouper, was detected on nearly all receivers throughout August 2015 (and like other Nassau Grouper, it rarely crossed over the bar) as well as for a few days in January 2017 on the south side of the bar. Fish 18, a subadult Black Grouper, was only detected sporadically on a single receiver north of the northern sand channel from December 2017 through March 2018. Although these grouper were not included in all analyses due to their low numbers of DDs, it is still informative to note the individual variations in movements and consideration of habitat located just outside of WDR but not within receiver coverage. These three fish were detected many days after their tagging date and were not detected on any other receivers in the Florida Keys, making tag loss or long-distance movements unlikely, but it is impossible to determine whether their low numbers of DDs were due to emigration from the coverage area, predation, or fishing pressure.

We would like to note that the rectangular array design around the bar formation and the tagging of many fish outside this array, although deemed necessary due to high boating/anchoring activity and equipment tampering, did not constitute an ideal setup for home range estimates or for the tracking of spatial movements. In an ideal world, receivers would have been placed in a gridded array over the entire WDR area to obtain highly accurate, fine-scale movements over a broad location. However, equipment, safety, and time constraints required some compromises on coverage area. Similarly, to maximize detection range but still adequately detect both the 13 Vemco V16 tags (150–162 dB) and the 5 Vemco V13 tags (147–153 dB), the VRTx receivers used in our range test were set to high power (154 dB) rather than to medium (148 dB) or very high (160 dB) power levels. A more comprehensive range test in the future, including sentinel tags, would allow for individual detection ranges of each receiver, a more thorough investigation on factors affecting signal transmission, and more robust handling of detection rates. However, we feel that the data presented in this article have been appropriately handled and interpreted within the constraints and limitations that nearly every telemetry study faces, and our results represent a baseline from which future work will fill in coverage gaps that are deemed important.

Conclusions

The results of our study suggest that the WDR area contains important habitat for adult and subadult grouper as growth-to-maturity habitat and as a potential grouper spawning aggregation site. The WDR is already known to contain a Permit FSA and multiple snapper species' FSAs, which are recognized as essential fish habitat (NOAA 1997) and important for consideration in management plans (Lindeman et al. 2000; Brownscombe et al. 2020). Future management plans involving WDR should consider the potential of a grouper spawning aggregation site in the area, especially if there is a low density of large, sexually mature grouper in the lower Florida Keys. Riley's Hump in the Dry Tortugas contains a multispecies spawning aggregation site that was nearly fished out, but it recovered once spatial protection was put in place. The success of the Florida Keys fisheries critically depends on the protection of multispecies spawning aggregations like that potentially contained at WDR. To more definitively determine whether there is a grouper spawning aggregation site in WDR, additional work incorporating technologies complementing acoustic telemetry (e.g., monitoring bioacoustics for grouper courtship and spawning sounds) should be conducted.

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SUPPORTING INFORMATION

Additional supplemental material may be found online in the Supporting Information section at the end of the article.