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Grouper source levels and aggregation dynamics inferred from passive acoustic localization at a multispecies spawning site

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ABSTRACT:

Four species of grouper (family Epinephelidae), Red Hind (*Epinephelus guttatus*), Nassau (*Epinephelus striatus*), Black (*Mycteroperca bonaci*), and Yellowfin Grouper (*Mycteroperca venonosa*) share an aggregation site in Little Cayman, Cayman Islands and produce sounds while aggregating. Continuous observation of these aggregations is challenging because traditional diver or ship-based methods are limited in time and space. Passive acoustic localization can overcome this challenge for sound-producing species, allowing observations over long durations and at fine spatial scales. A hydrophone array was deployed in February 2017 over a 9-day period that included Nassau Grouper spawning. Passive acoustic localization was used to find positions of the grouper-produced calls recorded during this time, which enabled the measurement of call source levels and evaluation of spatiotemporal aspects of calling. Yellowfin Grouper had the lowest mean peak-to-peak (PP) call source level, and Nassau Grouper had the highest mean PP call source level (143.7 and 155.2 dB re: 1 μ Pa at 1 m for 70–170 Hz, respectively). During the days that Nassau Grouper spawned, calling peaked after sunset. Similarly, when Red Hind calls were abundant, calls were highest in the afternoon and evening. The measured source levels can be used to estimate communication and detection ranges and implement passive acoustic density estimation for these fishes. © 2022 Author(s). All article content, except where otherwise noted, is licensed under a Creative Commons Attribution (CC BY) license (<http://creativecommons.org/licenses/by/4.0/>). <https://doi.org/10.1121/10.0010236>

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I. INTRODUCTION

Fish spawning aggregations (FSAs), where high densities of individuals gather at fixed times and locations for reproduction, are common among fish species (Domeier and Colin, 1997; Erisman *et al.*, 2017). Many groupers of the family Epinephelidae form transient aggregations that occur during short periods each year. These aggregations usually last from days to weeks during one or two consecutive months (Domeier and Colin, 1997). Transient FSAs provide an opportunity to efficiently estimate population size and health for solitary species, such as Nassau Grouper (*Epinephelus striatus*), that spend most of their lives separate from others of their species. They also represent the complete reproductive potential of regional populations of fishes in some areas as they are the primary source of larvae (Domeier and Colin, 1997; Sadovy and Domeier, 2005; Nemeth *et al.*,

2006). Many transient FSAs have been heavily exploited by fishing due to their high temporal and spatial fidelity (Sadovy 1994; Domeier and Colin, 1997; Heyman and Kjerfve, 2008). This has led to severe declines of many species, including Nassau Grouper, Red Hind (*E. guttatus*), Black Grouper (*Mycteroperca bonaci*), and Yellowfin Grouper (*M. venonosa*). These four species have been fished in the Caribbean, Gulf of Mexico, and Western Atlantic (Crabtree and Bullock, 1998; Tuz-Sulub *et al.*, 2006; Kadison *et al.*, 2011). In fact, Nassau Grouper and Red Hind were once the most economically valuable species throughout the Caribbean (Colin *et al.*, 1987; Sadovy, 1994).

Proper management of these four species and their FSAs requires knowledge of many factors, including the spatial and behavioral structure of mating aggregations (Shapiro *et al.*, 1993). For spatial structure, this includes short- and long-term movements and habitat use (Farmer and Ault, 2011). These grouper overlap in habitat and in some locations, such as Little Cayman, Cayman Islands, multiple species form FSAs in the same area, typically spawning either at different times of the year or locations within the area (Claro and Lindeman, 2003; Whaylen *et al.*, 2006; Heyman and Kjerfve, 2008). At this FSA, fine-scale

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movements have been observed by divers periodically during the day (Whaylen *et al.*, 2006) and continuous larger-scale movements at the resolution of 0.5 km or greater have been examined via acoustic telemetry studies, which are invasive to the fish (Whaylen *et al.*, 2006; Blincow *et al.*, 2020). The fine-scale movements before, during, and after FSAs are still relatively unknown as these other methods have not allowed for nighttime or continuous observation of aggregations at resolutions less than 0.5 km.

Passive acoustic monitoring and localization is a noninvasive method that can be used to study both fine- and large-scale aspects of the spatial distributions and movements of these grouper because males produce sound during spawning aggregations (Mann *et al.*, 2010; Schärer *et al.*, 2012a; Schärer *et al.*, 2012b; Schärer *et al.*, 2014; Wilson *et al.*, 2020). These grouper are all known to produce courtship-associated sound (CAS) or calls as part of their spawning behavior. Wilson *et al.* (2020) measured and described the acoustic features of these calls and defined the CAS call labels that we use in this study: N2, RH1, RH2, B, YF1, and YF2. Nassau Grouper is also known to produce two calls associated with aggressive or alarm behaviors (N1 and N3, respectively), referred to as agonistic calls, and Wilson *et al.* (2020) hypothesized that there might be a third call (unknown, UNK).

Passive acoustic localization can also be used to measure the source levels of these grouper sounds and potentially lead to the implementation of density estimation using passive acoustics (McDonald and Fox, 1999; Marques *et al.*, 2009; Hildebrand *et al.*, 2015) at FSAs. Estimating fish abundance from sound requires knowledge of sound source levels, propagation ranges, and information on sound production rates, which may be determined from localizations (Marques *et al.*, 2009; Locascio and Mann, 2011; Rowell *et al.*, 2017). However, there have been relatively few studies of fish source levels (Barimo and Fine, 1998; Lindström and Lugli, 2000; Sprague and Luczkovich, 2004; Širović and Demer, 2009; Locascio and Mann, 2011; Parsons *et al.*, 2013; Holt and Johnston, 2014; Erisman and Rowell, 2017) or applications of passive acoustic localization of fish sounds (Mann and Jarvis, 2004; Locascio and Mann, 2011),

which has been one of the limitations to advancing the application of passive acoustic methods to study fishes.

We studied the habitat preferences and movements of four grouper species (Red Hind, Nassau Grouper, Black Grouper, and Yellowfin Grouper) and measured the source levels of the nine call types known or presumed to be produced by these groupers using recordings collected over 9 days during a Nassau Grouper spawning event off of the west end of Little Cayman, Cayman Islands, British West Indies. We used passive acoustic localization to find the positions of the calling individuals of these four grouper species over a 6.4 km² area, where these and other species are known to form FSAs (Whaylen *et al.*, 2006). This is the first study to report measured source levels for the calls of Epinephlidae species and conduct passive acoustic localization for multiple fish species within a habitat.

II. METHODS

A. Data collection

A passive acoustic array was deployed off the west end of Little Cayman (Fig. 1) at a FSA from February 11 to February 19, 2017. The location was near the shelf edge where Nassau grouper are known to aggregate and there are sandy areas and coral relief [Fig. 2(A)]. The array consisted of three calibrated two-channel Wildlife Acoustics SM3M hydrophone recorders (Maynard, MA). An HTI-96 min hydrophone (−165 dB re: 1 V μPa^{−1} from 0.02 to 30 kHz; Long Beach, MS) was connected to each channel with either a 1 or 30 m cable. The hydrophones were deployed 0.5–1 m above the bottom in depths of 24–33 m in a hexagon pattern with 18–40 m spacing between the hydrophone pairs [Fig. 2(B)]. A 12 kHz pinger was placed near the array’s center and used as a source to synchronize the recorder clocks. The distances and compass heading within the array were measured by scuba divers and used to solve for the array geometry. To evaluate the array geometry and localization error, an uncalibrated JW Fisher 22 kHz sound source (East Taunton, MA) capable of 150–180 dB output was placed at each receiver position and nine other known locations within and outside the array (Wilson *et al.*, 2019). The positions of the

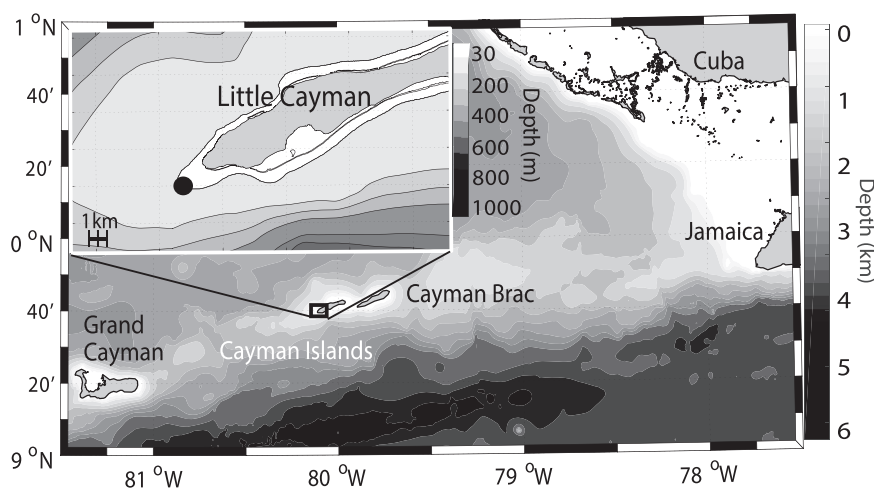


FIG. 1. A map of the Cayman Islands and the west end of Little Cayman. The location of the Cayman Islands is shown with the inset indicating the location of the acoustic array (black dot; 19.64 N, 80.12 W) at a Nassau Grouper spawning site on the west end of Little Cayman (modified from Wilson *et al.*, 2020).

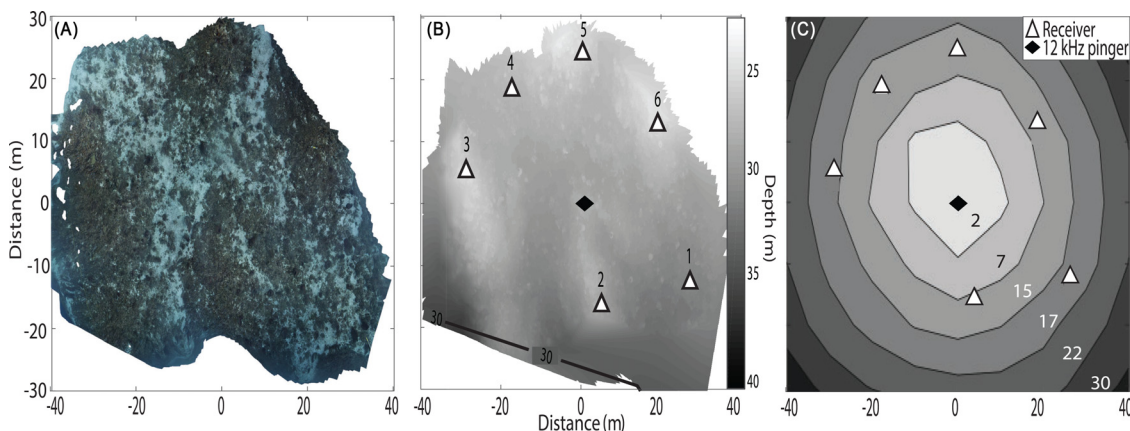


FIG. 2. (Color online) The array habitat image (A), geometry (B), and localization error (C). (A) The images collected during diver transects were stitched together to create an image of the array habitat. (B) The location of the receivers (white triangles) with their labeled number and the 12 kHz pinger (black diamond) used for synchronization are shown with the 30 m depth contour that runs parallel to the shelf edge and shaded bathymetry, where darker colors indicate deeper depths. (C) The contours show the maximum estimated localization error (m) across the array area (Wilson et al., 2019).

sound source were later estimated using the localization methods described here to evaluate the error. All of the recorders were sampling continuously at a rate of 48 kHz over the 9-day study period.

B. Passive acoustic localization

We used the time-difference-of-arrivals (TDOAs) between receivers and implemented hyperbolic localization (Spiesberger and Fristrup, 1990) with the Optimization Toolbox in MATLAB (The MathWorks, Natick, MA) to perform two-dimensional (2D) localization. A homogenous sound speed of 1541.8 ms⁻¹ was used because divers recorded constant temperatures throughout the water column during deployment and recovery of the array. Regional models of sea surface temperature and salinity (Chassignet et al., 2007; Banzon et al., 2016) were used to calculate the sound speed.

The data were decimated to 32 kHz and bandpass filtered using an elliptical filter (Table I) before signals of interest, in this case, pings or grouper calls, were manually identified on a receiver. Despite grouper calls being low frequency, 32 kHz was used to allow for better bandpass filtering while still preserving a high temporal resolution. The recorded signal from this receiver was then used as a

matched filter to detect the signal on other receivers. For grouper calls, all of the calls were manually identified on receiver 5. For pings, the receiver that was used varied. The correlation threshold used for matched filtering was determined for each signal type through empirical testing (Table I). The signal-to-noise ratio (SNR) measurements were also made to determine if the signals were detectable above the background noise (Wilson et al., 2019). The SNR was calculated for a signal band determined from a priori knowledge of the signals (Wilson et al., 2020) and a noise band of equal bandwidth and 50 Hz above the signal band. The noise was measured above the signal band because impulsive, broadband noise was common in the data and not always captured in the noise measurements before or after the signal band. When two or more other receivers met the matched filtering criteria and had a SNR greater than 3 dB, the TDOA measurements were made between all pairs of these receivers and the receiver selected for matched filtering. The TDOAs that were greater than the maximum theoretical TDOA between receivers were discarded. An initial position was estimated using the manually selected signal and two receivers with the strongest matched filter correlations. Additional receivers were added one at a time and retained for the final position estimate if they produced a new estimate

TABLE I. Descriptions of calls localized and their associated localization parameters. The species that produces each call is provided in the first column with the call label used in the study and call type shown, respectively, in the second and third columns. The localization parameters, the correlation value threshold, and the bandpass filter used to filter the signal prior to localization are listed under the columns *Correlation value* and *Bandpass filter*, respectively. The last three columns indicate the total number of calls logged and localized and the mean number of arrivals used for these localizations.

Species	Call label	Call type	Correlation value	Bandpass filter (Hz)	Total calls	Calls localized	Mean number of arrivals
Nassau	N1	Agonistic	0.2	75–250	1389	813	4.4
	N2	CAS	0.2	75–250	12978	11 146	4.8
	N3	Agonistic	0.2	75–250	1126	629	4.5
Unknown	UNK	Unknown	0.2	75–250	370	197	4.3
Red Hind	RH1	CAS	0.15	50–250	26590	10 309	4.1
	RH2	CAS	0.15	50–250	6170	2948	4.1
Black	B	CAS	0.4	50–225	1262	692	4.1
Yellowfin	YF	CAS	0.2	75–250	415	151	4.1

within a 2 m radius of the initial assessment. A Levenberg-Marquardt (LM) algorithm and multiple initial starting points were used to find the best position estimates and their least-square-error (LSE).

The localization error was evaluated by measuring the error at 15 locations within and outside of the array using a known sound source and running 3 simulation scenarios that assessed the error due to estimating 2D locations in a three-dimensional (3D) environment, TDOA measurement errors, and TDOA measurement errors with noise (Wilson *et al.*, 2019). The mean error (\pm standard deviation) for the 15 known source locations was 1.5 ± 2.2 m for positions inside the array ($n = 12$) and 3.3 ± 3.8 m for all of the positions. The 3D simulations for the depth range most groupers are expected to be within, 15 m from the approximately 35 m bottom, had a mean error of 1.1 ± 1.7 m for 2D estimates over an $80 \text{ m} \times 80 \text{ m}$ (6.4 km^2) area that spanned the array. For the same area, the 2D simulations for the TDOA measurement error showed that the localization error could range from 2 to 7 m from the center to the perimeter of the array and up to 7 m across all of the array. The simulation for the TDOA measurement error with noise had the greatest error of 16.6 ± 0.9 m inside of the array, which was driven primarily by a high error at the perimeter [Fig. 2(C)].

C. Temporal and spatial patterns of grouper calls

We manually detected and logged the occurrences of eight known call types (Mann *et al.*, 2010; Schärer *et al.*, 2012a; Schärer *et al.*, 2012b; Schärer *et al.*, 2014) and one hypothesized call type (Wilson *et al.*, 2020) produced by Nassau Grouper (N1, N2, N3, and UNK), Red Hind (RH1 and RH2), Black Grouper (B), and Yellowfin Grouper (YF1 and YF2; Fig. 3) on recordings from receiver 5 [Fig. 2(B)]. The call type and approximate start and end times of the calls were recorded using the MATLAB software package Triton (Wiggins *et al.*, 2010). The total number of logged calls per day and hour were calculated and normalized by the recording effort. Any data with noise that could mask grouper calls were disregarded and not included as part of the recording effort. For Yellowfin Grouper, the recorded calls from both call types were combined due to a low number of call occurrences. We used these totals to analyze each species' calling patterns and compared them with trends in call localizations.

We applied the localization methods to all of the logged calls. The estimated positions within the 6.4 km^2 area around the synchronization source with a LSE less than 0.15 m were used to analyze the spatial patterns and movements of the four grouper species (Table II). The localizations were grouped by hour and plotted on the bathymetry with the time of call indicated to examine the spatial trends. For Nassau Grouper, the spatial trends of agonistic calls (N1, N3, and UNK) were compared to the CAS (N2) to evaluate associated spawning patterns.

The divers observed Nassau Grouper spawning and Red Hind displaying spawning behavior near the array during

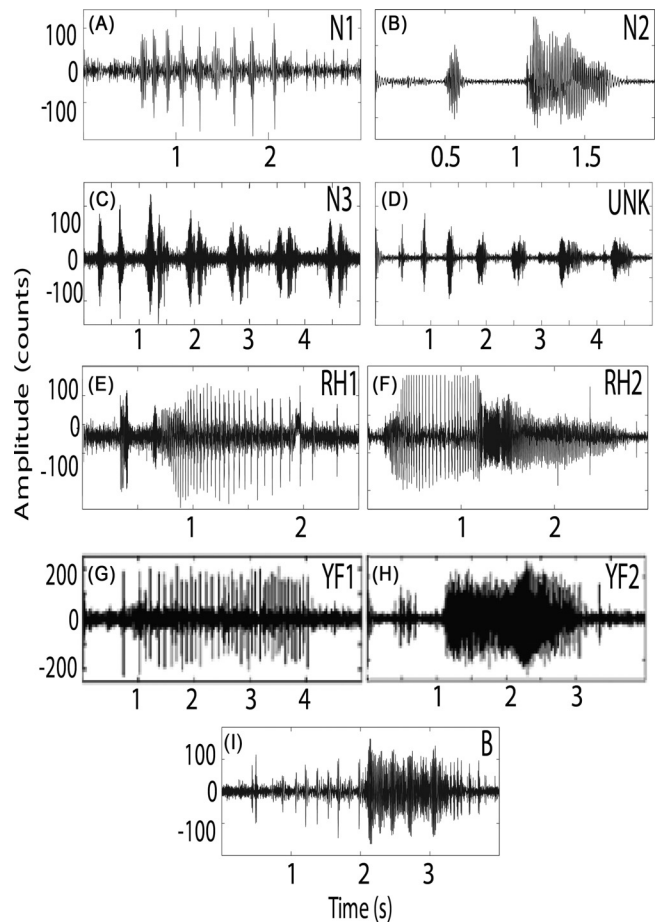


FIG. 3. Bandpass filtered time series of [(A)–(D)] three known Nassau Grouper call types (N1–N3) and one presumed call type (UNK), [(E), (F)] two Red Hind calls (RH1, left and RH2, right), [(G), (H)] Yellowfin Grouper calls (YF1, left and YF2, right), and (I) Black Grouper call B. The time series were bandpass filtered with an elliptical filter from 20 to 500 Hz. The figure has been modified from Wilson *et al.* (2020).

our deployment. Due to this, we analyzed the temporal and spatial trends for Nassau Grouper during spawning days and Red Hind during peak calling days to understand behaviors and aspects related to spawning. These behaviors and aspects included movements, changes in calling, and spatial area of aggregations. The peak calling days were defined to have a daily call rate of one standard deviation or more above the mean daily call rate of the deployment. The hourly call rates of the CAS produced by Nassau Grouper (N2) and Red Hind (RH1 and RH2) were tested for normality using Lilliefors tests and further analyzed using a one-way analysis of variance (ANOVA) and Bonferroni corrected *ad hoc* testing to determine if there were significant differences in diel calling trends during spawning and peak calling days. A significance level of 0.05 was used for all of the statistical tests.

D. Grouper source levels

Using the localized calls with the lowest LSE, we measured the root mean square (RMS) and peak-to-peak (PP) received levels, RL_{rms} and RL_{pp} , respectively, for each of the

TABLE II. The source levels of grouper call types. The call and segment type of the source level measurements are shown in the first two columns. The number of calls measured and the bandwidth of the bandpass filter used to filter calls prior to measurement are provided, respectively, in the third and fourth columns. The mean source levels (\pm standard deviation) are shown for peak-to-peak (PP) source levels, SL_{pp} , and root mean square (RMS) source levels, SL_{rms} . The source level ranges are provided in the column following the mean.

Call type	Segment	Number of calls	Bandpass filter (Hz)	Mean SL_{pp} (dB re 1 μ Pa at 1 m)	SL_{pp} Range	Mean SL_{rms} (dB re 1 μ Pa at 1 m)	SL_{rms} range
N1	Pulse	196	70–170	152.1 \pm 6.1	132.7–165.0	138.8 \pm 6.1	120.9–151.9
N2	Tone	199	70–170	155.2 \pm 5.0	139.5–165.7	139.6 \pm 5.4	124.6–153.1
N3	HB high	177	70–170	150.6 \pm 6.9	126.0–164.8	138.2 \pm 7.0	112.1–153.2
	HB low	177	70–170	148.0 \pm 6.7	124.2–162.5	133.6 \pm 6.6	107.2–148.9
UNK	Pulse	182	70–170	151.8 \pm 6.1	131.8–167.5	138.1 \pm 6.3	117.5–154.4
RH1	Pulse 1	180	150–250	148.3 \pm 4.8	136.3–162.8	135.1 \pm 4.9	123.7–150.8
	Pulse train	180	70–170	145.5 \pm 4.8	133.4–160.1	128.9 \pm 4.7	117.7–143.4
RH2	Pulse 2	165	150–250	146.0 \pm 5.1	130.3–158.7	130.4 \pm 5.0	116.9–142.8
	Tone	165	70–170	141.5 \pm 6.1	125.6–155.3	127.5 \pm 5.6	113.5–139.3
B	Tone	159	50–150	150.6 \pm 5.2	130.3–165.5	135.3 \pm 5.5	115.7–151.6
	Pulse	39	70–170	149.1 \pm 6.6	133.3–158.3	136.2 \pm 6.5	118.6–144.6
YF		133	70–170	143.7 \pm 6.1	124.5–157.3	127.8 \pm 6.2	107.6–142.2

known or presumed grouper call types (Table II). All of these calls are composed of various low-frequency segments described as pulses (present in calls N1, N2, RH1, RH2, B, and YF2), heartbeat pulses (N3), tones (N2, RH2, B, and YF2), and pulse trains (RH1, RH2, and YF1; Wilson *et al.*, 2020).

For each call type, the received levels were measured either for a single segment (N1, N2, UNK, and combined YF1 and YF2) or multiple segments if the call type was suspected of having segments with different received levels (N3, RH1, RH2, and B). The RMS measurements were calculated using the portion of the call or call segment that contained 5%–95% of the total energy between the estimated start and end times (Wilson *et al.*, 2020). The examples of the latter were the low and high heartbeat pulses of one Nassau Grouper call (N3) and Red Hind pulses, pulse trains, and tones. For calls with repeated segments, the segment with the highest received level was used for these measurements.

The decimated data from each receiver were bandpass filtered using an elliptical filter (Table I) and visually examined to select the arrival with the greatest SNR or least interference to measure RL_{rms} and RL_{pp} . The unfiltered, decimated selected arrival was then bandpass filtered using a fourth-order Butterworth filter that had negligible loss across the frequency band of interest. The RMS and PP source levels, SL_{rms} and SL_{pp} , respectively, were calculated from these measured received levels using the localized position of the call and spherical spreading assumption for the transmission loss as the water depth was comparable to the distance across the array.

We calculated the means and standard deviations of SL_{rms} and SL_{pp} for each call type or segment. A one-way ANOVA with Bonferroni corrections was used to find significant differences among SL_{pp} after testing each distribution for normality using a Lilliefors test. Due to the number of Yellowfin Grouper source level measurements, only 133 measurements were used for these statistical tests. Additionally, the Black Grouper pulse, a call segment that is not always present in this call type, was excluded from this analysis because the sample size was too small.

We qualitatively compared the mean SL_{rms} for each call type with the peak frequencies and durations of these calls reported by Wilson *et al.* (2020) to examine trends between call characteristics and source levels, of groupers. In addition, we contrasted the SL_{rms} results to other studies of fish species that reported source levels, along with call frequency and duration characteristics (Barimo and Fine, 1998; Širović and Demer, 2009; Locascio and Mann, 2011; Parsons *et al.*, 2013; Erisman and Rowell, 2017).

III. RESULTS

A. Temporal and spatial patterns of grouper calls

During the week following the February 2017 full moon, we recorded over 20 000 grouper calls. There was an order of magnitude more Nassau Grouper and Red Hind calls than Black and Yellowfin Grouper calls. Red Hind, Black, and Yellowfin Grouper calls increased over the deployment period with both Red Hind and Black Grouper calls peaking on the night of the third-quarter moon, the last night with recordings (Fig. 4). Nassau Grouper spawning was observed from February 14 to 17, and Nassau Grouper calling peaked on February 15, five days after the full moon. The mean number of Nassau Grouper CAS (call N2 in Fig. 3) per hour from February 14 to 17 was significantly higher from 19:00 to 20:00 compared to the mean number of calls on the days prior and after [$F_{47,137} = 11.84$, $p < 0.01$; Fig. 5(A)]. The number of Red Hind calls was significantly higher from 16:00 to 20:00 during February 17–19 compared to the previous days, February 11–16 ($F_{47,137} = 12.74$, $p < 0.01$). We recorded the highest number of calls for Nassau Grouper and Red Hind during the 19:00 h [Fig. 5(B)].

The localized Nassau Grouper CAS (N2) indicated two areas of increased calling activity during peak calling days: an area between receivers 3 and 4 in the northwest (NW) of the array and receivers 1 and 6 on the east side of the array [Fig. 6(A)].¹ Both areas featured a sandy bottom located between coral relief. Generally, throughout the day, there

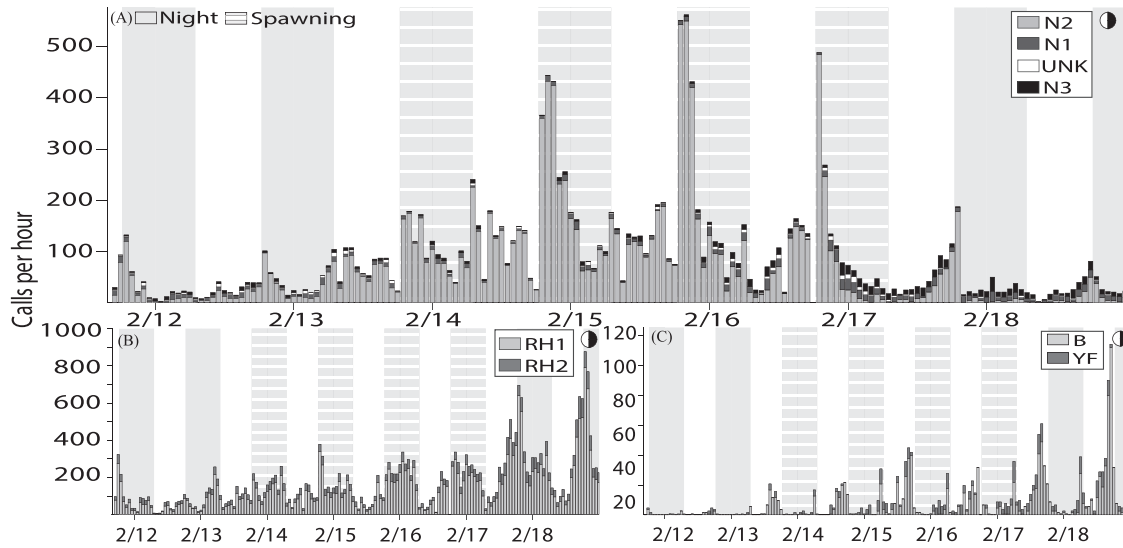


FIG. 4. The hourly call totals normalized by effort for (A) known or presumed Nassau Grouper (N1, N2, N3, and UNK), (B) Red Hind (RH1 and RH2), and (C) Black (B) and combined Yellowfin Grouper (YF) call types. Each bar represents the effort-normalized number of calls that occurred each hour with call types marked in different colors. The gray background columns show the time between sunset (18:20) and sunrise (06:49) with the striped gray showing the nights that Nassau Grouper spawning was observed. The figure was modified from Wilson *et al.* (2020).

were more calls localized in the NW area. There were very few localized calls during the hour around sunset, approximately 17:30–18:30 [Fig. 6(A)]. This is the same time that spawning was observed 30–100 m from the array along the

shelf break to the west. However, localized calls were abundant at both areas during peak calling after sunset and extended across a 10–20 m wide zone between these sandy areas [Fig. 6(A)]. Call detections in the area decreased around midnight and remained low until an hour or two before sunrise.

In the days before peak calling and spawning, localized Nassau Grouper agonistic calls had spatial patterns similar to CAS. These agonistic calls occurred sporadically throughout the day and were localized more often near receivers 1 and 2 or receivers 3 and 4 [Fig. 6(B)] without strong temporal patterns in their occurrences. The daily count of agonistic calls increased slightly over the recording period; the fewest number of calls, 158, occurred on February 12 compared to 531 calls on February 17.

Throughout the deployment, localizations of Red Hind CAS (RH1 and RH2) indicated high call activity at two areas within the array: one on the western side and another on the eastern side of the array (Fig. 7).¹ Compared to Nassau Grouper, Red Hind had more calls occurring between receivers 2 and 3, and these calls extended outside the array into deeper areas between the 30 and 40 m depth contour (Fig. 7). On February 15, Red Hind calls within the array nearly ceased around the hours that Nassau Grouper spawning occurred (approximately 17:30–18:30), and most calls were localized centrally in the array or west of receiver 2 [Fig. 7(A)]. On February 18, calls were more common in the area west of receiver 2 prior to sunrise and across the entire array around sunset. There were relatively few Red Hind calls localized in the study area for a couple of hours following sunrise [approximately 6:30–8:30; Fig. 7(B)].

Black and Yellowfin Grouper calls and localizations indicated that these species did not likely remain long within the array area. We localized some calls throughout the day sporadically, but these localized calls had no apparent

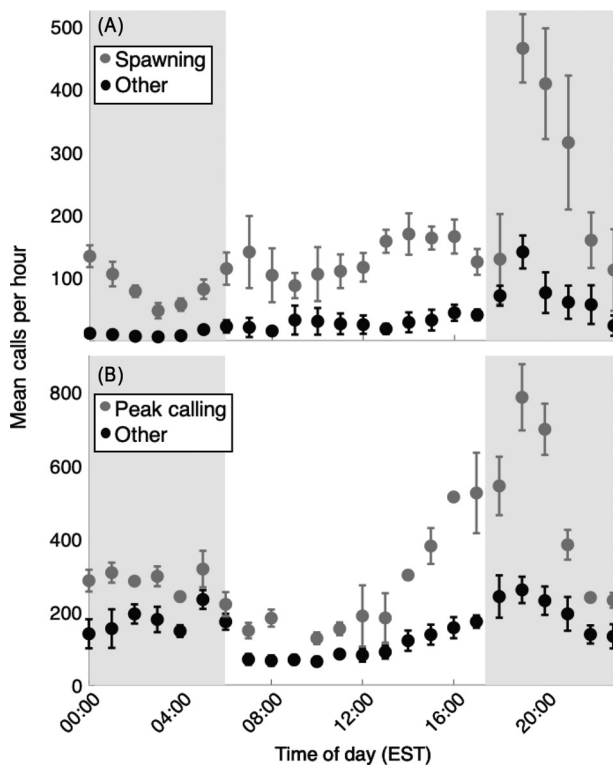


FIG. 5. The mean calls per hour for courtship associated sounds for (A) Nassau Grouper (N2) and (B) Red Hind (RH1 and RH2 combined). Calls observed on spawning days, February 14–17, for Nassau Grouper or peak calling days, Feb. 17–19, for Red Hind are indicated by the gray dots and all of the other days are shown in black. The bars show the standard error, and the gray shaded areas indicate the time between sunset (18:20) and sunrise (06:49).

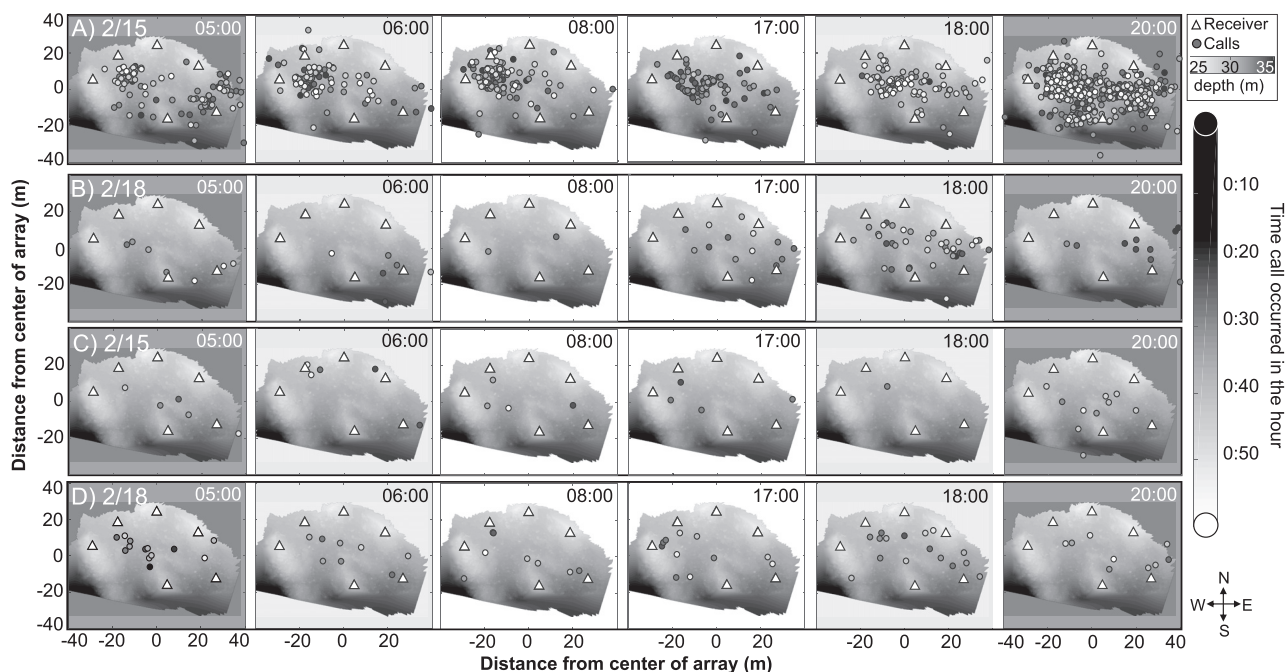


FIG. 6. Six hours of localized Nassau Grouper calls for (A) CAS (N2) on a spawning day (February 15) and (B) a non-spawning day (February 18), and (C) agonistic calls (N1, N3, and UNK) on February 15 and (D) February 18. The hours before, during, and two hours after sunrise and sunset are shown to highlight patterns during these times. The colored circles in each panel show one hour of call locations with the start time labeled in the top-right. The circle's color indicates when it was produced with darker colors depicting earlier and lighter colors depicting later in the hour. The background color of each panel reflects either the time between sunset (18:20) and sunrise (06:49; dark gray), the hour of sunrise or sunset (light gray), or the time between sunrise and sunset (white). The white triangles mark the receiver locations, the black line shows the 30 m depth contour, and the array bathymetry varies from 25 m in light gray to 35 m in dark gray in all of the panels. The figure was modified from Wilson et al. (2019).

temporal patterns. The highest hourly call localization rates were 54 and 8 calls per hour for Black and Yellowfin Grouper, respectively (Fig. 8).

B. Grouper source levels

The mean PP source levels of calls ranged from 143.7 dB to 155.2 dB re 1 μ Pa from 70 to 170 Hz, respectively, for Yellowfin and Nassau Grouper calls. The highest call source level for Red Hind was 148.3 dB re 1 μ Pa from 150 to 250 Hz and for Black Grouper, the highest call source level was 150.6 dB re 1 μ Pa from 50 to 150 Hz. The largest range of SL_{pp} was measured for known or presumed Nassau Grouper

calls, which varied from 124.2 dB for N3 to 167.5 dB for UNK segments (Fig. 9, Table II). There were significant differences between the mean source levels of the call types and segments ($F_{12,2108} = 112.11$, $p = 0$), including Nassau Grouper's CAS call N2, which were significantly higher than all other source levels ($p < 0.005$). For the call types with SL measurements for two segment types (i.e., N3, RH1, RH2, and B), Red Hind call RH1 was the only call with significantly different source levels between segments ($p = 0.002$, 95% confidence interval (CI) = [0.78, 4.89]; Fig. 10, Table II).

The maximum mean RMS source levels for each grouper call type with Yellowfin Grouper call types combined generally decreased with an increasing mean peak frequency

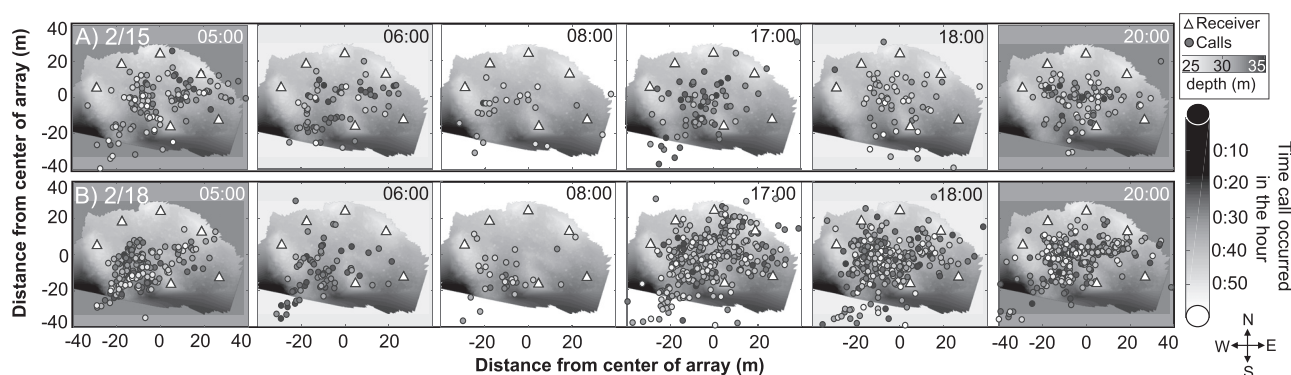


FIG. 7. Six hours of localized Red Hind CASs (RH1 and RH2) on (A) a Nassau Grouper spawning day (February 15) and (B) a Red Hind peak calling day (February 18). The colored circles in each panel show one hour of call locations with the start time labeled in the top-right. The figure colors and markings are the same as those in Fig. 6. The figure was modified from Wilson et al. (2019).

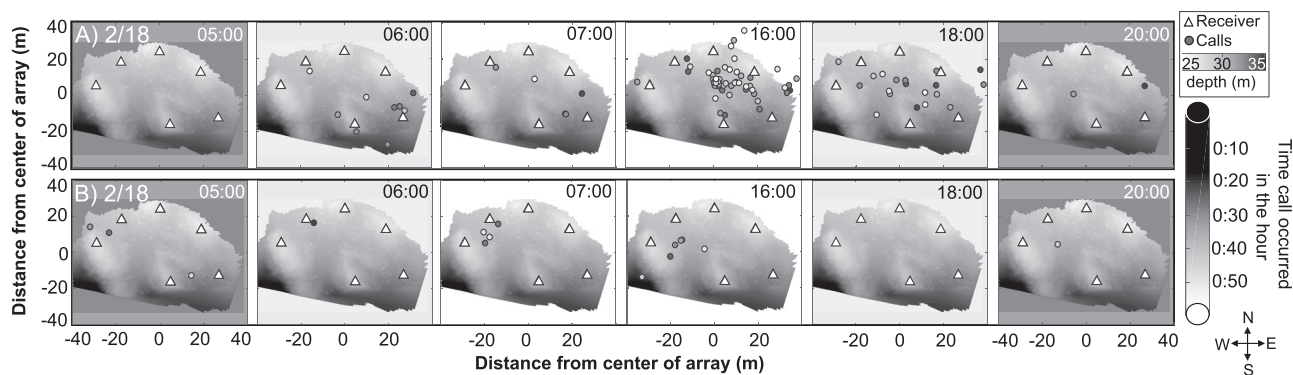


FIG. 8. Six hours of localized calls on February 18 for (A) Black Grouper and (B) Yellowfin Grouper. The colored circles in each panel show one hour of call locations with the start time labeled in the top-right. The figure colors and markings are the same as those in Fig. 6.

and duration [Figs. 11(A) and 11(B)]. The mean source level decreased as the mean frequency increased for all Nassau Grouper calls, and most of the call type mean source levels decreased with increasing mean duration as well. This was not the case for Red Hind, whose source levels were almost the same despite differences in frequency and duration. Similarly, when comparing the results of the source levels of all four grouper with other fish families, there appeared to be no relationship between source level and frequency or duration. The SL_{rms} ranged from 110 to 167 dB re $1 \mu Pa$ for peak or fundamental frequencies below 400 Hz and over durations from 0.1 to 3.5 s [Figs. 11(C) and 11(D)].

IV. DISCUSSION

Passive acoustic localization revealed different behavioral patterns, including calling and movement, for Nassau

Grouper and Red Hind at a multispecies FSA area near the west end of Little Cayman. The Nassau Grouper CAS (N2 calls) per hour was higher on spawning days and significantly higher after sunset. The estimates from divers indicated that Nassau Grouper densities increased in this area leading up to spawning. This suggests that the elevated call rates on spawning days may be due to higher fish densities. However, the significant increase in N2 calls after sunset is likely associated with spawning behavioral changes. Spawning was observed during sunset when very few Nassau Grouper calls were localized within the array, presumably because fish moved outside the array to the spawning area at the shelf edge several tens of meters away. The increase in localized calls at night indicates Nassau Grouper returning to the shallower bottom habitat after spawning. Most of the Nassau Grouper calls were localized to the sandy bottom areas between coral patches, locations where divers often reported

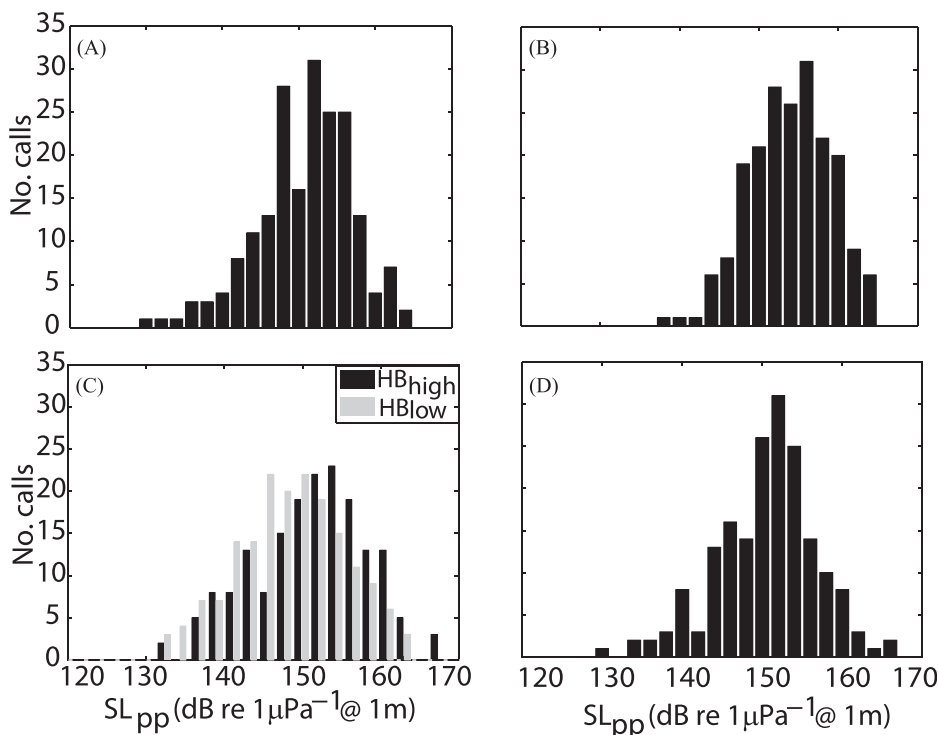


FIG. 9. The distribution of measured PP source levels (SL_{pp}) for Nassau Grouper call segments (A) N1 pulses, (B) N2 tones, (C) N3 heartbeat low (HB low) and high (HB high) pulses shown in gray and black, respectively, and (D) UNK pulses. The measurements were made for more than 177 calls for each call type, and calls were bandpass filtered between 70 and 170 Hz.

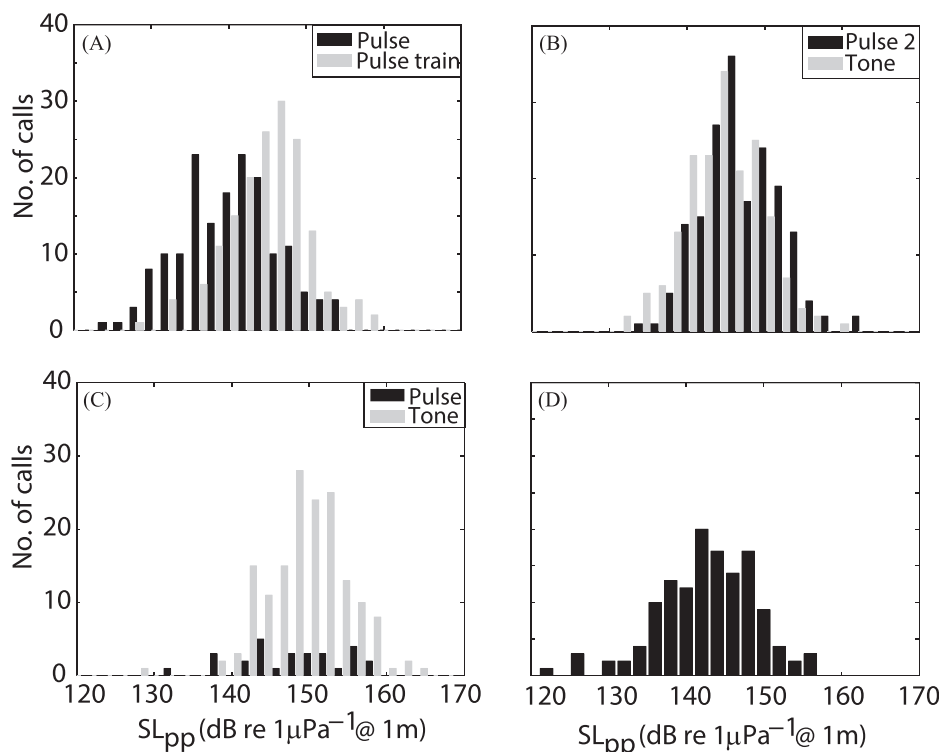


FIG. 10. The distribution of measured PP source levels (SL_{pp}) for other Epinephelid calls, including Red Hind call segments (A) RH1 first pulse (black) and pulse train (gray), (B) RH2 pulse before tone (black) and tone (gray), Black Grouper call segments (C) B pulse (black) and tone (gray), and Yellowfin Grouper (D) YF pulses and tones combined. The measurements were made for more than 133 calls for each call and segment type except Black Grouper pulses ($n = 39$). Red Hind and Black Grouper pulses were bandpass filtered between 150 and 250 Hz and 50 and 150 Hz, respectively. All other call types and segments were bandpass filtered between 70 and 170 Hz.

seeing these fish during the days prior to spawning. In sandy habitats, Nassau Grouper’s spatial distributions can be influenced by cleaner stations (Sluka *et al.*, 1999). Thus, the preference toward the sandy areas in this study may be due to cleaner behaviors.

The localization and calling trends of Red Hind suggest that spawning territories may have formed in this area by the third-quarter moon on February 18 with significant increases in calling in the evening hours (16:00–20:00), which is a characteristic of spawning calling patterns (Mann *et al.*, 2010). Red Hind spawning was not visually confirmed, but spawning behaviors have been observed in this area during Nassau Grouper spawning in previous years (Whaylen *et al.*, 2006). Therefore, it is possible that Red Hind spawning occurred during the last night of this study, February 19, or sometime afterward as their calling increased over our monitoring period. Red Hind spawn between the third-quarter and new moon elsewhere in the Caribbean (Shapiro *et al.*, 1993). The three areas within the array that had high call activity may be different male territories. Male Red Hind form territories with harems of one or more females during spawning aggregations (Shapiro *et al.*, 1993). In Puerto Rico, different Red Hind spawning aggregations are separated by hundreds of meters (Shapiro *et al.*, 1993) and in the U.S. Virgin Islands, an aggregation was estimated to span a 70×140 m area (Nemeth *et al.*, 2007). Hence, we believe that the observed calling activity and these hypothesized male territories are likely part of a single aggregation that ranged beyond our 70×55 m array.

Similar to Nassau Grouper, the localizations showed that Red Hind calling also nearly stopped within the array during some hours. However, unlike Nassau Grouper, this occurred

around sunrise for Red Hind, when spawning is not known to occur. During this time, the decrease in calls is likely due to a reduction in Red Hind call rates rather than fish leaving the detectable area. Red Hind aggregations and territories can move over a spawning period, but these movements occur on the order of days not hours (Shapiro *et al.*, 1993). There was no dedicated effort to closely observe their behavior at this site, thus, the details of Red Hind spawning cannot be confirmed. While we did not attempt to track individuals from these localizations, such an analysis could determine territorial boundaries for Red Hind as males are known to defend their territories, frequently swimming along the borders while producing calls (Mann *et al.*, 2010).

Low numbers of CAS for Yellowfin and Black Grouper were localized within the array each day, indicating that they regularly moved through this area during the spawning season. Yellowfin and Black Grouper are known to spawn near this array location after Nassau Grouper spawn. Yellowfin Grouper aggregate approximately 0.5 km northeast of this site (Semmens, 2018). However, the exact location(s) of the Black Grouper aggregation remains unknown. Still, they display spawning behaviors in this area around this time of year (Whaylen *et al.*, 2006), and pair spawning has been observed in deeper water near the site (Semmens, 2018). The calling trends at this site in 2015 and 2017 and a site farther north in 2016, near the Yellowfin Grouper spawning location, indicated all four species were present at each site and suggest spawning-related movements of Nassau Grouper between sites (Wilson *et al.*, 2020). This study confirms previous diver observations that Black and Yellowfin Grouper also move within the larger FSA area during the spawning season.

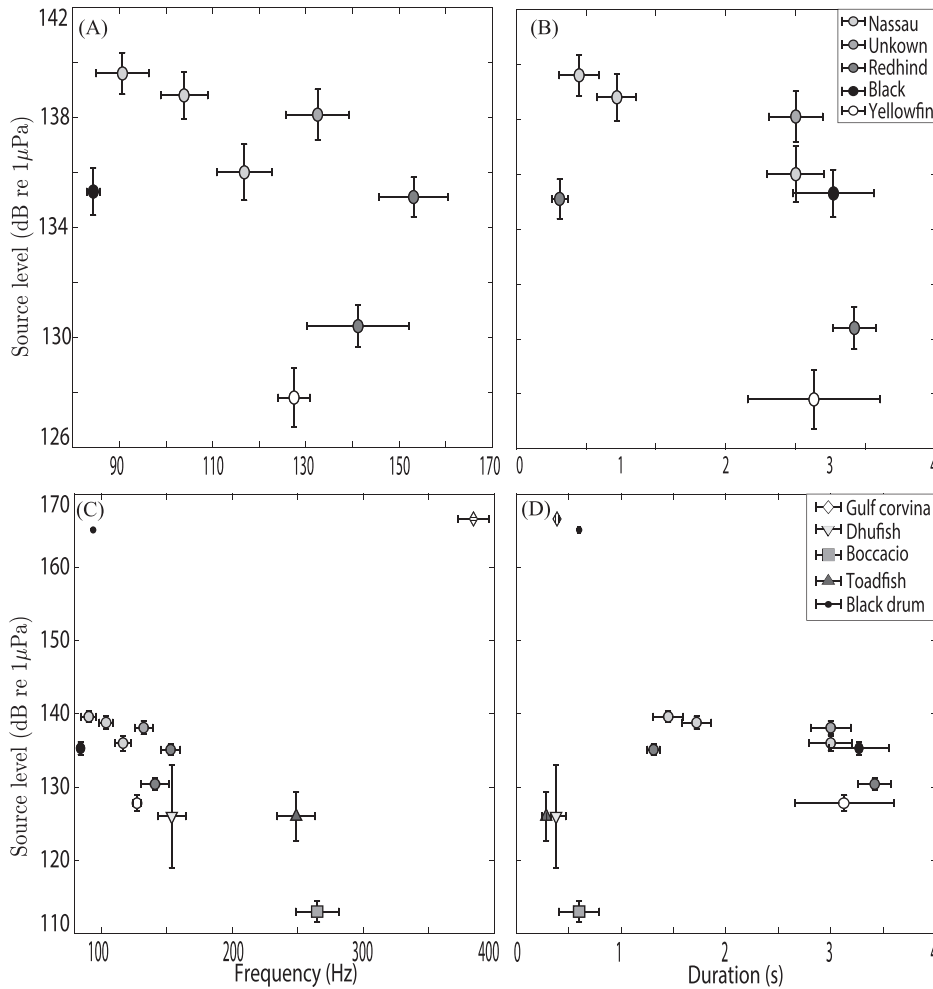


FIG. 11. The maximum mean RMS source level (SL_{rms}) for the nine known or presumed grouper call types are shown and compared to the mean (A) peak frequency and (B) duration of calls. Grouper call measurements are marked by colored circles with light gray indicating measurements for the known or presumed Nassau Grouper calls, dark gray for Red Hind, white for Yellowfin Grouper, and black for Black Grouper. These grouper SL_{rms} are plotted with the SL_{rms} measurements previously reported for Gulf Corvina (Erisman and Rowell, 2017; white diamond), Dhufish (Parsons et al., 2013 light gray downward triangle), Boccacio (Širović and Demer, 2009; dark gray square), Toadfish (Barimo and Fine, 1998; dark gray upward triangle), and Black Drum (Locascio and Mann, 2011; black dot) and compared to the (C) mean peak or fundamental frequency and (D) mean duration. The vertical and horizontal bars show the 95% CI of the standard error for the SL measurements and either the peak of the fundamental frequency or duration.

The spatial ecology of the spawning grouper described here has implications for fisheries management. The movement information that we have provided may serve to help appropriately size marine protected areas aimed at multispecies spawning sites. Knowledge of the spatial distribution of the aggregation and migratory paths to and from spawning aggregations has been emphasized for management (Shapiro et al., 1993; Sadovy 1994; Erisman et al., 2017; Blincow et al., 2020). The movements to, from, and within the spawning area over the full duration of the spawning period and the nature of species interactions need to be considered to properly manage the entirety of these multispecies FSAs. Unfortunately, we could not estimate the full spatial area of the aggregation as it extended beyond the array area. A more extensive acoustic array would be necessary for such estimates to be obtained. However, Nassau Grouper are already protected in all of the Cayman Islands by an inclusive no-take closure from December to April, which has been in place since 2016 (Cayman Islands, 2016), and this study confirms the importance of such large spatial closures for this species and other grouper species. However, there are currently no fishing regulations for Red Hind, Black, and Yellowfin Grouper in the Cayman Islands.

We have provided the first report of source level measurements for Epinephelid calls using estimated positions.

The measured maximum received levels of the grouper calls were comparable to previous reports for these species (Mann et al., 2010; Schärer et al., 2012a; Schärer et al., 2012b; Schärer et al., 2014), and the estimated source levels were in the range of other known fish source levels (Barimo and Fine, 1998; Lindström and Lugli, 2000; Sprague and Luczkovich, 2004; Širović and Demer, 2009; Locascio and Mann, 2011; Parsons et al., 2013; Holt and Johnston, 2014; Erisman and Rowell, 2017). There was no apparent relationship between species size and source levels; Red Hind, a dwarf grouper (Sluka et al., 1999), had source levels comparable to or higher than the other three larger species. Yellowfin Grouper source levels were the lowest, but this measurement may be biased. This species had the lowest number of calls detected. Due to this, lower SNR calls were used for the receive level measurements, and this could contribute to lower signal measurements and source level estimates. For some fish species, source level is correlated with the size and acoustic properties of sounds such as frequency, duration, or pulse rate (Parsons et al., 2013). These results suggest that such relationships between size and acoustic properties may not hold across all fish species. However, measurements should be made in the same manner for all species to assess this accurately.

Many factors can contribute to errors in the position estimates and, therefore, the source levels. They include

uncertainty in receiver positions, environmental properties (e.g., sound speed, bottom type) and propagation effects, acoustic properties of the signal, the number of arrivals, and the SNR of arrivals used for localization, ambient and impulsive noise, and the presence of other signals (Carter, 1987; Spiesberger and Fristrup, 1990; Wiggins *et al.*, 2013). Little Cayman's currents are variable and can be strong (Molinari *et al.*, 1981; Whaylen *et al.*, 2004). Along with tides, they can produce flow that creates strumming noise in passive acoustic recordings. Some of our receivers, especially receivers 2 and 3, were prone to this noise due to their proximity to the shelf edge. As a result, many calls were localized with only three or four arrivals instead of all six. Last, grouper calls have similar frequencies and overlap in bandwidth (Wilson *et al.*, 2020), thus, calls occurring at or near the same time could result in significant localization errors. However, call overlap was not typical for the majority of the calls or arrivals.

Using the mean distance of calls from the receiver and the position errors reported in Wilson *et al.* (2019), the absolute source level measurement error was estimated to be as great as 2.3 dB at the center and 10.4 dB near the perimeter. Many more calls were localized inside the array than at the perimeter; therefore, the source level error is expected to be closer to 2 dB for these measurements. This expected error is lower than the measured source level variability (25.9–41.5 dB for all call types), suggesting that actual variability in fish source levels may contribute more to the observed range than measurement error. The directionality of these sounds is unknown, but it may explain some of the measurement variability. For example, Oyster Toadfish (*Opsanus tau*) produce directional sound variations of 3–6 dB (Barimo and Fine, 1998), and groupers may have similar variations.

With accurate source levels fish abundance can be estimated using passive acoustic density estimation methods developed for marine mammals as long as the average sound production rate and detection probability are also known (McDonald and Fox, 1999; Marques *et al.*, 2009; Hildebrand *et al.*, 2015). Previous studies have evaluated the relationship between the number of detected calls, measured sound pressure levels, and estimates of fish aggregation densities (Rowell *et al.*, 2012; Rowell *et al.*, 2017). However, we are not familiar with any studies where the full distance approach was applied. Little Cayman and this multispecies spawning site may be a good testing place for this approach as density estimates for this Nassau Grouper aggregation are known (Stock *et al.*, 2021; Waterhouse *et al.*, 2020). The main challenge would be the estimation of sound production rates, but it may be possible to estimate these using concurrent acoustic tagging and passive acoustic localization. Estimating fish densities via passive acoustics could enable long-term and continuous monitoring of fish density within an area. With the aid of automated detection and classification (Ibrahim *et al.*, 2018a; Ibrahim *et al.*, 2018b), real-time density estimates may be possible as well.

The ranges over which spawning aggregations can be detected using passive acoustics are not known for these fishes. If we assume 90 dB re 1 μ P ambient noise (Wenz 1962) for the 100 Hz bandwidths used for these source level measurements (70–170 Hz, 50–150 Hz, and 150–250 Hz) and the mean source levels we measured, the detection ranges for these grouper calls are estimated to be 0.3–1 km, assuming spherical spreading and no bottom effects. The latter may not be a realistic assumption for groupers, which often remain within a few meters from the bottom. During this study, calls produced near the center of the array were often not detected on all of the receivers separated by 50 m or less. Additionally, very few calls were detected when Nassau Grouper were observed spawning approximately 30–100 m away from the array. However, it is unknown whether calling ceases during spawning. A previous study in 2015 and 2016 placed hydrophones approximately 300 m from the Nassau Grouper spawning aggregation and did not detect the spawning-related calling peak observed in this study (Wilson *et al.*, 2020). Due to this, we believe that 0.3 km is the upper detection range for these grouper calls at this site in Little Cayman. If the hearing sensitivity of these groupers were known, these source levels could be used to estimate their communication ranges. As anthropogenic noise continues to rise in marine environments (Slabbekoom *et al.*, 2010; Radford *et al.*, 2014), given the already short detection range for these calls, it will be critical for fisheries managers to understand the fish communication ranges to assess the potential impacts of noise appropriately.

In addition to source level estimation, passive acoustic localization provides valuable observations that could address many questions about grouper ecology and fish acoustic communications. Passive acoustic localization has commonly been used to study group dynamics (Quick and Janik, 2008; Guazzo *et al.*, 2017), habitat preferences (Frankel *et al.*, 1995; Yack *et al.*, 2013), sound propagation (Stafford *et al.*, 1998; Širović *et al.*, 2007), sound production and swimming rates (Janik, 2000), and, in some cases, individual properties and behaviors (Van Parijs and Clark, 2006; Sousa-Lima and Clark, 2008) of marine mammals. For our localizations of grouper, further analysis of Nassau Grouper and Red Hind may allow for individual habitat use or territoriality at the spawning site to be assessed. It is also possible that individuals that are simultaneously calling and moving to be isolated, enabling the measurement of swimming speeds for these species. Isolation of individual calls would also allow examining of intraspecies variation of sound production and evaluation whether acoustic features of fishes could be a possible proxy for male fitness (Amorim *et al.*, 2015). Intraspecies variation in calls may allow for individual recognition and monitoring, similar to what can be accomplished with dolphin and their signature whistles (Caldwell *et al.*, 1970; Kershenbaum *et al.*, 2013; Sayigh *et al.*, 1999). Localization of calls in 3D rather than in 2D would improve the accuracy and precision of call positions and source level measurements while providing depth

information about the spatial structure and dynamics of grouper aggregations. 3D localization was not used in this study due to insufficient array depth aperture and a high number of unusable arrivals and TDOAs. Grouper tend to be benthic, therefore, 2D approximations are still informative. However, 3D localization could be achieved by placing additional receivers at different depths throughout the water column.

The use of 2D passive acoustic localization in this study has revealed new information about the spatial and temporal patterns of calling of four grouper species at a multispecies FSA in Little Cayman, including the spawning of Nassau Grouper. Localizations indicated Nassau, Black, and Yellowfin Grouper movement in and out of the array area, suggesting movements over the larger area of the FSA site and periods when call rates decrease for Red Hind and Nassau Grouper. The decrease in call rates for Red Hind is likely the result of sound production decreasing. For Nassau Grouper, the decrease was partly due to moving outside the array's detectable area for spawning, but there was also likely a decrease in sound production during spawning. Source level measurements of the calls produced by these four species showed that species size was not correlated with source levels. It remains unknown whether individual size correlates with source levels within species. The upper limit of detection ranges for these grouper calls was 0.3 km and may be less based on empirical results. This study's methods and results can be further expanded to address other fisheries science and management questions. More information about the spatial dynamics of aggregations, communication ranges of fishes, and the parameters that could lead to passive acoustic density estimation methods and individual monitoring would enable fisheries managers to better develop and assess management strategies.

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¹See supplementary material at <https://www.scitation.org/doi/suppl/10.1121/10.0010236> for a movie of all N2 call localization for February 15, 2017, and a movie of all Red Hind call localizations for February 18, 2017.

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