

Fish sound production and acoustic telemetry reveal behaviors and spatial patterns associated with spawning aggregations of two Caribbean groupers

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ABSTRACT: Regional abundances of Nassau grouper *Epinephelus striatus* and yellowfin grouper *Mycteroperca venenosa* have declined due to overfishing of their spawning aggregations, prompting permanent and seasonal fisheries closures in the US Virgin Islands (USVI). As both species produce sounds associated with reproductive behaviors (courtship-associated sounds; CAS), passive acoustic and acoustic telemetry methods were used to determine temporal patterns of reproductive activity, site usage, and fish movements in order to assess the effectiveness of current management strategies at 2 marine protected areas (MPAs) in the USVI: the Grammanik Bank (GB) and Hind Bank Marine Conservation District (MCD). Patterns of sound production and ultrasonic acoustic tag detections showed that both species formed spawning aggregations from January through May at the GB, highlighting the current seasonal regulations (1 February to 30 April) as insufficient for protecting spawning stocks during the entire reproductive season. Acoustic tagging confirmed connectivity between the GB and MCD and exposed the broad extent of habitat used, including non-protected areas, during the spawning season. Spawning did not likely occur within the MCD, but the MPA did support abundances of calling individuals during spawning periods, indicating that both species produce CAS away from their spawning sites. This finding coupled with the detection of routine migrations between spawning and non-spawning sites presents a potential mechanism to lead conspecifics to the aggregation site and thereby increase reproductive fitness and spawning output.

KEY WORDS: Nassau grouper · *Epinephelus striatus* · Yellowfin grouper · *Mycteroperca venenosa* · Passive acoustics · Ultrasonic acoustic tagging · Fish movement patterns · Marine protected area

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INTRODUCTION

A broad diversity of fishes, represented by 20 tropical fish families and nearly 170 species, has been reported to spawn in aggregations (Sadovy de Mitcheson & Colin 2012). Spawning aggregations

occur when fish congregate at discrete sites over a short period of time and during specific seasonal and lunar periods to release gametes, constituting an annual event that often represents their sole opportunity for reproduction and contribution to recruitment (Domeier & Colin 1997). Highly pre-

dictable in space and time, spawning aggregations are vulnerable to overfishing (Sadovy & Domeier 2005), which disrupts synchronized spawning, decreases mean length, reproductive output, and spawning stock biomass and may lead to extirpation and possible regional species extinction (Beets & Friedlander 1992, Sadovy & Figuerola 1992, Sadovy 1994, Aguilar-Perera & Aguilar-Dávila 1996, Coleman et al. 1996, Matos-Caraballo 1997, Giménez-Hurtado et al. 2005, Aguilar-Perera 2006, Sadovy de Mitcheson et al. 2012, Sadovy de Mitcheson & Erisman 2012). In many cases, reef fish aggregations have disappeared prior to our understanding a species' reproductive requirements.

One of the best known examples of a species that has experienced local population collapse due to overfishing of aggregations is the Nassau grouper *Epinephelus striatus* (Sadovy 1997, Cornish & Eklund 2003, Sadovy & Domeier 2005, Aguilar-Perera 2006, Sadovy de Mitcheson et al. 2012), which is currently listed as Endangered by the International Union for the Conservation of Nature (IUCN; www.iucnredlist.org), and proposed as threatened under the US Endangered Species Act. In recent decades, the majority of known Nassau grouper aggregations in the tropical western Atlantic have disappeared, and the remaining have decreased significantly in number of individuals (Sadovy & Eklund 1999, Sala et al. 2001, Aguilar-Perera 2006, Sadovy de Mitcheson et al. 2008). The yellowfin grouper *Mycteroperca venenosa* is another large aggregating species that often utilizes the same aggregation sites as Nassau grouper (Olsen & LaPlace 1979, Whaylen et al. 2004, Nemeth et al. 2006b, Heyman & Kjerfve 2008) and is currently listed as Near Threatened by the IUCN due to heavy fishing pressure and habitat destruction, although there is limited information on the status of the species and aggregations throughout its range (Brule & Garcia-Moliner 2004).

Protection of spawning aggregations has typically focused on seasonal or area closures, which target the most common spawning times and locations known to fishers. Many fish spawning aggregation (FSA) sites are used by multiple species either simultaneously or sequentially (Whaylen et al. 2004, Nemeth et al. 2006b, Heyman & Kjerfve 2008). While some marine protected areas (MPAs) have produced population recovery (Beets & Friedlander 1999, Nemeth 2005), others have been ineffective, resulting in continued population decline for target species, possibly due to inadequate design or lack of enforcement (Eklund et al. 2000, Nemeth et al. 2006a, 2007, Rhodes & Tupper 2008, Rhodes et al. 2014). In a

review of 17 MPAs implemented to protect FSA sites, Grüss et al. (2014) reported that only 43% had positive conservation effects on target species. One of the major impediments to designing effective MPAs for FSA protection is a lack of understanding of the complex patterns of behavior and movement associated with spawning aggregations.

Recent application of ultrasonic telemetry and passive acoustics has greatly aided our understanding of the behaviors associated with spawning aggregations, especially for groupers (Epinephelidae). Acoustic tagging studies, which utilize an array of acoustic receivers and fish tagged with acoustic transmitters, have been used to evaluate MPA design (Chapman et al. 2005) and determine home range, site fidelity, diel movements, and large and small-scale migration patterns (Heupel et al. 2010, Hitt et al. 2011). For groupers, acoustic tags have been used to estimate the timing of aggregation formation, spawning frequency, as well as arrival, departure, and residency times (Zeller 1998, Semmens et al. 2007, Starr et al. 2007, Rhodes & Tupper 2008, Rhodes et al. 2012). Ultrasonic telemetry has also revealed accurate patterns of spawning seasonality, use of migratory corridors, and other complex behaviors that may increase the vulnerability of groupers during the spawning season (Starr et al. 2007, Rhodes et al. 2012). However, because individual tagged groupers do not participate in all spawning months and can skip entire spawning seasons (Nemeth 2005), patterns of grouper abundance at spawning aggregation sites and use of MPAs over the spawning season have not been fully documented.

The use of passive acoustics, which can record courtship-associated sounds (CAS) produced by some grouper species at spawning aggregations, such as Nassau and yellowfin groupers (Schärer et al. 2012a,b), is a promising technology to monitor aggregation dynamics and has certain advantages over ultrasonic telemetry. Passive acoustic methods generate large datasets with minimal effort (Myrberg 1997, Luczkovich & Sprague 2002, Rountree et al. 2006, Luczkovich et al. 2008a, Mann et al. 2008) that can be used to locate spawning aggregation sites (Luczkovich et al. 1999, 2008b, Walters et al. 2009, Rowell et al. 2011) and monitor site usage, reproductive behavior, and aggregation presence and residency duration (Locascio & Mann 2008, Mann et al. 2009, 2010, Nelson et al. 2011, Schärer et al. 2012a,b, 2014). When calibrated, passive acoustics can also assess relative and absolute changes in spawning stock abundance at high temporal resolution (Rowell et al. 2012, Marques et al. 2013). In groupers, sound

production levels and rates have been observed to reflect relative fish abundance, aggregation formation, courtship behaviors, and spawning activity through comparisons to underwater visual surveys and passive video recordings (Rowell et al. 2012, Schärer et al. 2012a,b, 2014).

In this study, passive acoustic recordings were integrated with results of ultrasonic acoustic tagging of Nassau and yellowfin groupers to examine the temporal relationship of grouper CAS to movement patterns between spawning and non-spawning sites and to examine how these combined technologies might elucidate the complex and elusive behaviors associated with spawning aggregations. We specifically tested the hypothesis that frequency of detections of fish tagged with acoustic transmitters and frequency of fish CAS would show a positive relationship at the spawning site but a neutral or weak relationship at a non-spawning site. We expected that the strongly synchronized behaviors of aggregation formation would result in a tight coupling of movement and CAS patterns at the spawning site but that the dispersal of groupers over large areas of reef would decouple this relationship away from the spawning site. The combined technologies were also used to determine whether the current temporal and geographic protection measures are optimal for protecting spawning stocks of these species.

MATERIALS AND METHODS

Study sites

Passive acoustic and telemetry studies were conducted within the Grammanik Bank (GB) and Hind Bank Marine Conservation District (MCD), 2 MPAs which are located 10 km south of St. Thomas, US Virgin Islands (USVI), along the southern edge of the Puerto Rican Bank (Fig. 1). The GB covers 1.5 km² and includes mesophotic coral reef banks dominated by *Orbicella* spp. (formerly *Montastraea* spp.), hard bottom sparsely colonized with isolated coral colonies and sponges, and sand channels at depths of 30 to 50 m (Herzlieb et al. 2006, Smith et al. 2008). The benthic composition of the MCD (41 km²) includes extensive mesophotic coral reefs, colonized hard bottom habitat, sand channels, and algal plains at depths of 30 to 60 m (Smith et al. 2010). The GB and MCD boundaries are separated by 2 km of unprotected mesophotic coral reefs at their closest proximity. Since 2005, the GB has been closed to fishing from 1 February until 30 April to protect a Nassau

and yellowfin grouper FSA site (Federal Register 2005). This closure has resulted in initial recovery of spawning stocks of both species (Nemeth et al. 2006b, Kadison et al. 2010, 2011). The MCD was declared a year-round no-take area in December 1999 through a cooperative effort between the Caribbean Fishery Management Council and local fishermen to protect deep coral reefs and improve fishery resources (Federal Register 1999, Nemeth & Quandt 2005). Within the MCD is a known red hind *Epinephelus guttatus* FSA site (Beets & Friedlander 1999, Nemeth 2005). Regulations enacted at this MPA have resulted in increases in fish size, numbers, and landings of red hind (Nemeth 2005). The MCD also supports an FSA of tiger grouper *Mycteroperca tigris* but not Nassau or yellowfin grouper (R. S. Nemeth unpubl. data).

Study species

Nassau grouper *Epinephelus striatus* form FSAs over a 7 to 10 d period in relation to the full moon, with peak spawning occurring during a specific 2 to 4 d period (Colin 1992, Domeier & Colin 1997, Whaylen et al. 2004, Heyman & Kjerfve 2008). The spawning season for Nassau grouper historically occurred from November through July with variation in timing and duration among locations: November to February in the Bahamas (Colin 1992, Cushion et al. 2008), December to March in Belize (Starr et al. 2007, Heyman & Kjerfve 2008), December to January in Mexico (Aguilar-Perera 2006), January to February in the Cayman Islands (Bush & Ebanks-Petrie 1994), January to April in Jamaica (Thompson & Munro 1978), and June to July in Bermuda (Domeier & Colin 1997). Spawning periodicity is assumed to be fixed at the site level; however, in the USVI, a newly formed Nassau grouper FSA at the GB has been found to occur from February through April (Nemeth et al. 2006b) in contrast to December through February for an aggregation extirpated in the 1970s at a nearby site (Olsen & LaPlace 1979). Given the Endangered status of Nassau grouper, the species is protected year-round in the USVI through permanent no-take regulations.

Yellowfin grouper *Mycteroperca venenosa* spawning occurs following the full moons of January through May with some regional variability: February to May in Jamaica (Thompson & Munro 1978), March to May in Mexico (Tuz-Sulub et al. 2006), February to April in the USVI (Nemeth et al. 2006b), January and April to May in Cuba (García-Cagide &

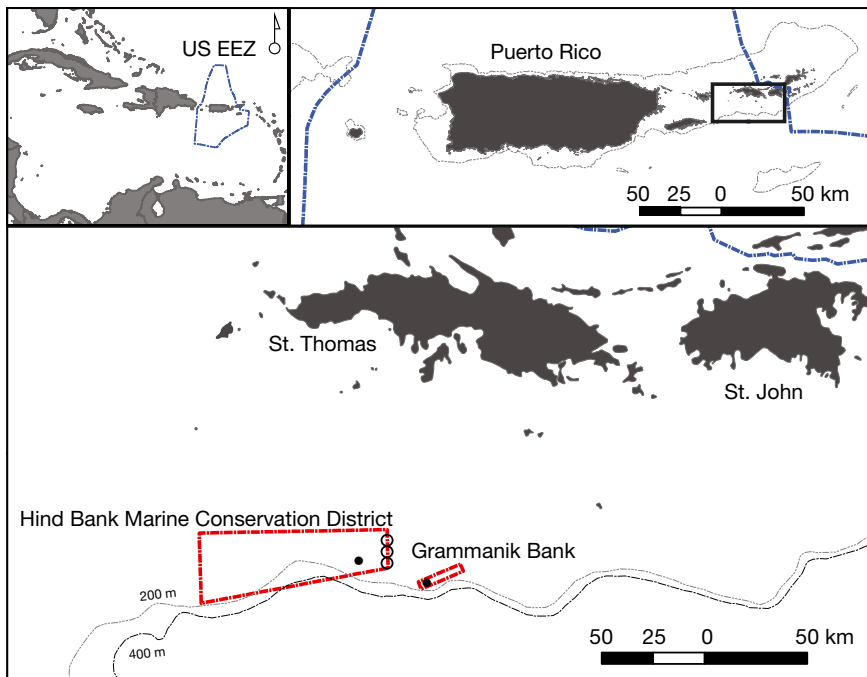


Fig. 1. US Caribbean Exclusive Economic Zone (US EEZ; blue) and location of the seasonal Grammanik Bank (GB) and permanent Hind Bank Marine Conservation District (MCD) marine protected areas (red). Closed circles signify locations with both passive acoustic and acoustic telemetry receivers. Open circles indicate locations with only acoustic telemetry receivers

García 1996), February to April in the Bahamas (Cushion et al. 2008), January to April in Belize (Heyman & Kjerfve 2008), and January to May in Puerto Rico (Schärer et al. 2012a). Aggregation formation and presence occurs over a 1 wk period for each respective spawning event (Heyman & Kjerfve 2008, Schärer et al. 2012a). In the USVI, the yellowfin grouper fishery is seasonally closed from February through April to protect spawning stocks.

Passive acoustic recordings

Passive acoustic studies were conducted using DSG-Ocean long-term acoustic recorders (DSG; Loggerhead Instruments) deployed at 2 fixed locations within the GB and MCD prior to Nassau and yellowfin grouper spawning seasons in 2011 and 2012 (Fig. 1). The fixed passive acoustic sampling stations were approximately 6 km apart, including a 3 km stretch outside of the MPAs. Sounds produced by Nassau and yellowfin groupers were recorded at the center of the Nassau and yellowfin grouper FSA site in the GB (Nemeth et al. 2006b) and simultaneously at a red hind FSA site (Nemeth 2005) within the MCD. The species-specific CAS are distinctive in duration, peak frequency, and tonal characteristics and are easily distinguished from each other audibly and visually in spectrograms and oscillograms (Schärer et al. 2012a,b; Fig. 2).

The DSG units were self-contained in cylindrical PVC housings, consisting of a single hydrophone (sensitivity = -186 dBV μPa^{-1} ; frequency range 2 to 37 kHz), micro-computer, circuit board, and 24 D-cell alkaline batteries. The DSG board integrated an additional 20 dB gain and was calibrated with a $0.1 V_{\text{peak}}$ frequency sweep from 2 Hz to 100 kHz. The DSGs, which were coated with antifouling paint, were attached to subsurface anchored buoy lines 2 m above the seafloor at 40 m depth. Ambient noise was recorded for a period of 20 s every 5 min from 20 January until 31 May 2011 and 17 November 2011 until 31 May 2012. Files were digitized at a sample rate of 9523 Hz and 10000 Hz during the first and second deployments, respectively, onto 32 GB removable secure digital high capacity (SDHC) flash memory cards.

Acoustic analyses were adopted from previous studies that established a methodology to quantify grouper CAS and calculate relative fish density (Rowell et al. 2012, Schärer et al. 2012a,b, 2014, Appeldoorn et al. 2013). Upon DSG retrieval, files were converted to .wav files and examined manually. CAS of Nassau and yellowfin groupers with high signal to noise ratios, i.e. distinguishable from background ambient noise, were identified visually and audibly for each 20 s file with the aid of spectrograms. Manually counted CAS were summed per day for each species at each site and multiplied by 15 to account for the sampling interval, resulting in

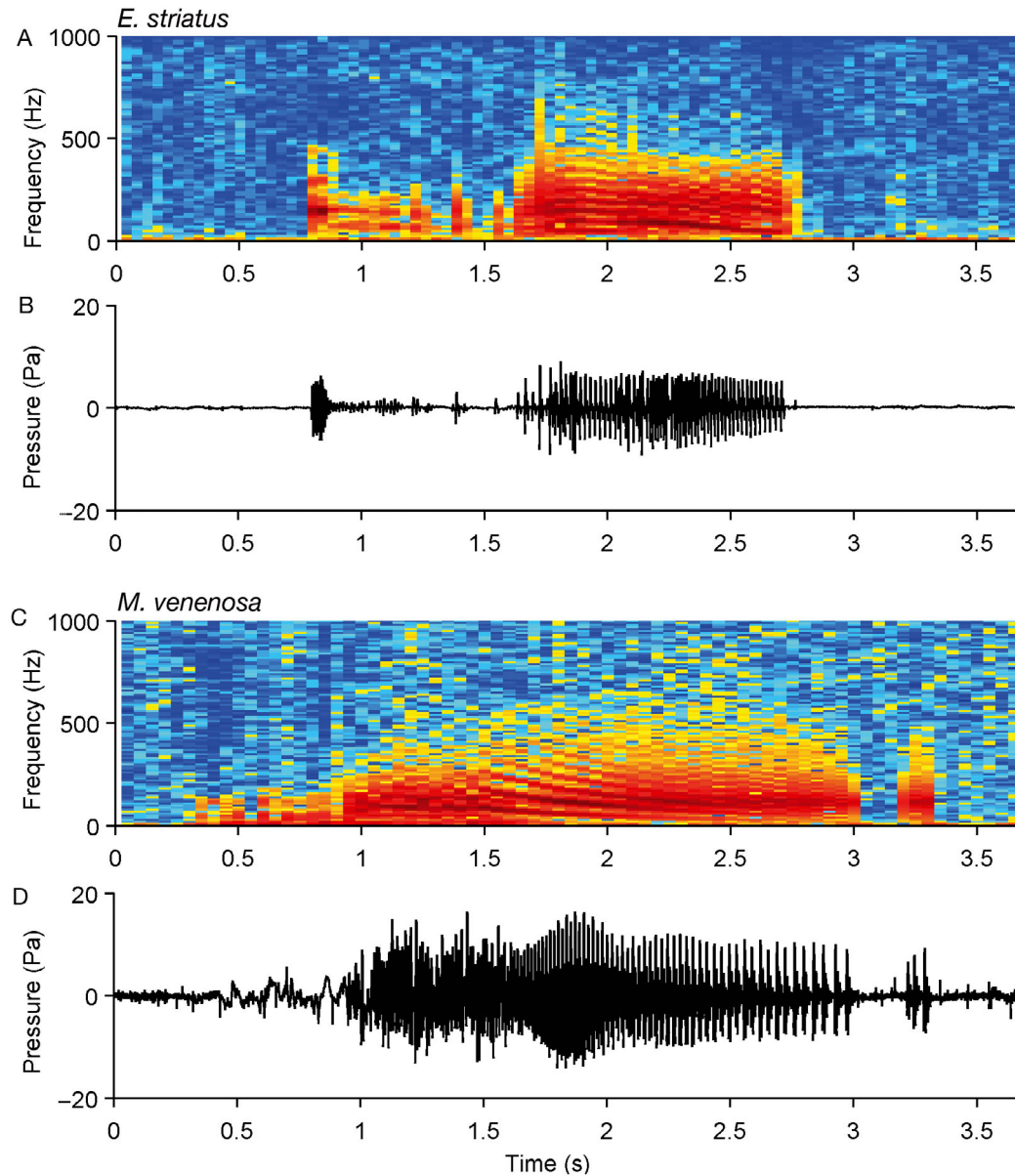


Fig. 2. Spectrograms and ocollograms of individual courtship-associated sounds (CAS) of (A,B) Nassau grouper *Epinephelus striatus* and (C,D) yellowfin grouper *Mycteroperca venenosa*

an estimate of total CAS d^{-1} at each site. Time series of total CAS d^{-1} were created to determine temporal patterns of peak and elevated CAS levels during each lunar cycle (full moon to full moon). Days with the highest total CAS during each full moon period were identified as days of peak CAS for each species. Periods of elevated CAS were defined as days in which CAS totals were greater than or equal to half the peak CAS total for each lunar cycle. Comparisons of the timing of peak CAS and the start and end of elevated CAS of yellowfin grouper relative to lunar cycle (i.e. days after full

moon, DAFM) at spawning (GB) and non-spawning (MCD) locations were each analyzed with a 2-way ANOVA with DAFM as the dependent variable and year (2011 vs. 2012) and DSG location (GB vs. MCD) as independent variables, and months of spawning season with CAS peaks treated as replicates (i.e. MCD: January to May 2011 [n = 5] and February to May 2012 [n = 4]; GB: January to May 2011 [n = 5] and January to May 2012 [n = 5]). Nassau grouper did not show distinctive CAS peaks at MCD in either year; therefore, it was excluded from this analysis.

Ultrasonic telemetry

To examine the relationship between grouper CAS and movement patterns, ultrasonic telemetry data were analyzed from a separate fish tracking study carried out from 2007 to 2012 (Nemeth et al. 2009, Nemeth 2012, Kobara et al. 2013). Telemetry data were analyzed from 5 acoustic receivers (Vemco model VR2 and VR2W) moored at the 2 DSG locations and 3 additional sites 600 m apart along the eastern boundary of the MCD (Fig. 1). Receivers were range tested in 2007, and detection distance of acoustic transmitters (V16, Vemco) ranged from 300 to 500 m. Although maximum detection ranges likely varied from day to day depending upon environmental conditions and habitat complexity (Farmer et al. 2013), the present study primarily focused on the presence/absence of groupers at the 2 DSG locations and MCD eastern boundary. Receiver moorings were constructed of a poured concrete block, 0.95 cm polypropylene line, and two 20 cm polystyrene floats. Receivers were attached to mooring lines with stainless steel clips approximately 15 to 20 m above the bottom at depths of 30 to 50 m to maximize detection ranges (Farmer et al. 2013). Acoustic receivers were wrapped in electrical tape to minimize biofouling, which usually consisted of filamentous green algae and occasionally encrusting sponges, hydroids, or small bivalves. Data were downloaded approximately every 6 mo.

Between 2007 and 2010, 216 Nassau grouper and 284 yellowfin grouper were caught in fish traps at the GB site, measured to total length (cm), and gender determined using light abdominal pressure and ultrasound imaging (Whiteman et al. 2005). A total of 25 Nassau grouper and 21 yellowfin grouper were surgically implanted with an acoustic transmitter (Vemco model V-16-4H) and subsequently released by divers at the same location. There was no statistical difference in fish length between acoustically tagged fish and a subsample of each spawning population (Nassau: tagged = 62.6 cm, $n = 25$ vs. population sample = 63.5 cm, $n = 216$, Kruskal-Wallis test, $H = 0.362$, $p = 0.55$; yellowfin: tagged = 74.8 cm, $n = 21$ vs. population sample = 74.4 cm, $n = 284$, Kruskal-Wallis test, $H = 0.039$, $p = 0.84$). The transmitter ping rate for 2007 and 2008 was 45 s and for 2010 was 60 s, which allowed tags to transmit for 17 and 40 mo, respectively.

Acoustic transmitter detections of tagged Nassau and yellowfin groupers were quantified at the locations of the 5 acoustic receivers. The number and percentage of tagged individuals detected annually

were calculated, where percentages included all fish tagged in the current year plus fish tagged in previous years that were still believed to be detectable based on life expectancy of acoustic transmitters (i.e. 17 mo for 2007 and 2008 tags, 40 mo for 2010 tags). Tag detections at the GB and 3 MCD eastern boundary receivers were used to determine the number of tagged individuals that migrated between the GB and MCD protected areas, as well as the number of trips made per month and season. The amount of time spent outside MPA boundaries was calculated by subtracting the last time a fish was detected at the GB receiver from the first detection at one of the MCD eastern boundary receivers, and vice versa. If multiple trips were taken by a fish, these times were averaged across all months and years to obtain a single value for each fish's westward and eastward trips between MPAs, and these data were used for statistical analysis. Differences in time spent outside the MPA boundaries between species (westward and eastward trips included together) and differences between westward and eastward swim times between the GB and MCD eastern boundary receivers for each species were compared using Kruskal-Wallis non-parametric ranks test.

Detections at the GB and MCD (i.e. DSG locations) were used to determine the number of individuals that migrated between the spawning site and non-spawning site, swim times associated with these migrations, residency duration, as well as the number of months individuals were present at the GB FSA site. Maximum swim speeds for Nassau and yellowfin groupers were calculated by averaging the shortest acoustic detection time interval of each fish between DSG locations. Differences in maximum swim speed between species were tested with a non-parametric Kruskal-Wallis ranks test using the maximum swim speed for each fish.

Relationship between grouper CAS and tag detections

Acoustic transmitter detections of Nassau grouper at the locations of the DSG instruments during the 2011 and 2012 spawning seasons were summed each day for comparison to total CAS d^{-1} . Time series of total CAS and tag detections d^{-1} from the GB and MCD were tested for autocorrelation and subsequently first differenced to mitigate its effects. Cross correlations were performed to determine the statistical relationship between first differenced time series of total CAS and tag detections d^{-1} for each site

and year. For time series that did not show strong autocorrelation (i.e. total CAS and tag detections d^{-1} at the MCD), additional cross correlations were performed on time series that were not first differenced.

RESULTS

Passive acoustic recordings

CAS of Nassau and yellowfin groupers were recorded each month during 2 consecutive spawning seasons at the GB and MCD, with yellowfin grouper totals exceeding those of Nassau grouper (Figs. 3 & 4). At the GB, Nassau grouper sound production peaked with lunar periodicity during the months of January through May, with limited CAS during the months of November and December in the second season (Fig. 3). Daily CAS totals peaked on average 8 DAFM (range = 3–12 DAFM) in both years, with elevated totals extending between 1 and 12 DAFM (Table 1). The highest numbers of Nassau grouper CAS occurred from January through April 2011 and February through May 2012. Days of peak CAS for yellowfin grouper were recorded during the months of January through May in both years at the GB with marked lunar periodicity (Fig. 3). Monthly sound production peaked on average 8 DAFM (range = 5–9 DAFM), with elevated totals from 4 to 12 DAFM (Table 1).

At the MCD, Nassau grouper CAS were less frequent than at the GB (Fig. 4). Nassau grouper CAS were detected during January through May 2011 and November 2011 through May 2012; however, no peak or elevated patterns were discernible in relation to the lunar cycle but loosely matched similar temporal patterns as yellowfin grouper sound production at the MCD (Fig. 4). The majority of CAS in 2012 was recorded in the months of February through May as seen at the GB. Yellowfin grouper sound production at the MCD was concentrated around the full moons of January through May 2011 and February through May 2012 with lower CAS totals than at the GB (Fig. 4). CAS peaked about 5 DAFM (range = 1–7 DAFM), with elevated totals occurring 1 d before the full moon to 10 DAFM (Table 2). On average, the timing of yellowfin grouper sound production at the MCD occurred significantly earlier in each lunar phase than at the GB and was consistent among years (Table 3). Elevated CAS levels at the MCD started, peaked, and ended 2.9, 2.4, and 1.7 d earlier than at the GB, respectively.

Ultrasonic telemetry

Nassau grouper were acoustically tagged in 2007 ($n = 10$), 2008 ($n = 9$), and 2010 ($n = 6$). The number of acoustically tagged Nassau grouper detected each year, including fish tagged in previous years, was as follows: 2007 ($n = 10$ of 10, 100%), 2008 ($n = 15$ of 19, 79%), 2009 ($n = 8$ of 10, 80%), 2010 ($n = 7$ of 8, 88%), 2011 ($n = 4$ of 9, 44%), and 2012 ($n = 3$ of 7, 43%), where percent refers to the number of transmitters that could have been detected, based on battery life-span, had all fish returned to the spawning site. Yellowfin grouper were acoustically tagged in 2007 ($n = 9$), 2008 ($n = 8$), and 2010 ($n = 4$), and the number of transmitters detected was as follows: 2007 ($n = 9$ of 9, 100%), 2008 ($n = 12$ of 17, 70%), 2009 ($n = 2$ of 8, 25%), and 2010 ($n = 4$ of 4, 100%). Despite the 40 mo life span of the 2010 acoustic transmitters, yellowfin grouper tagged in 2010 were not detected at the GB spawning site in subsequent years.

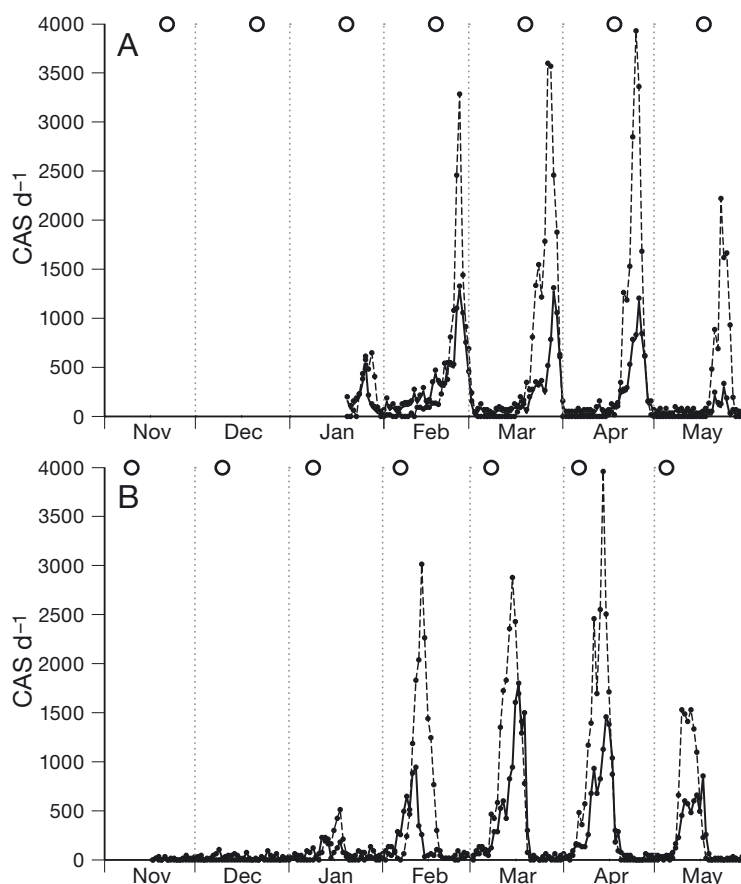


Fig. 3. Total estimated courtship-associated sounds (CAS) d^{-1} of Nassau grouper *Epinephelus striatus* (solid line) and yellowfin grouper *Mycteroperca venenosa* (dashed line) at the Grammanik Bank (GB) from (A) 20 January to 31 May 2011 and (B) 17 November 2011 to 31 May 2012.

O: full moon

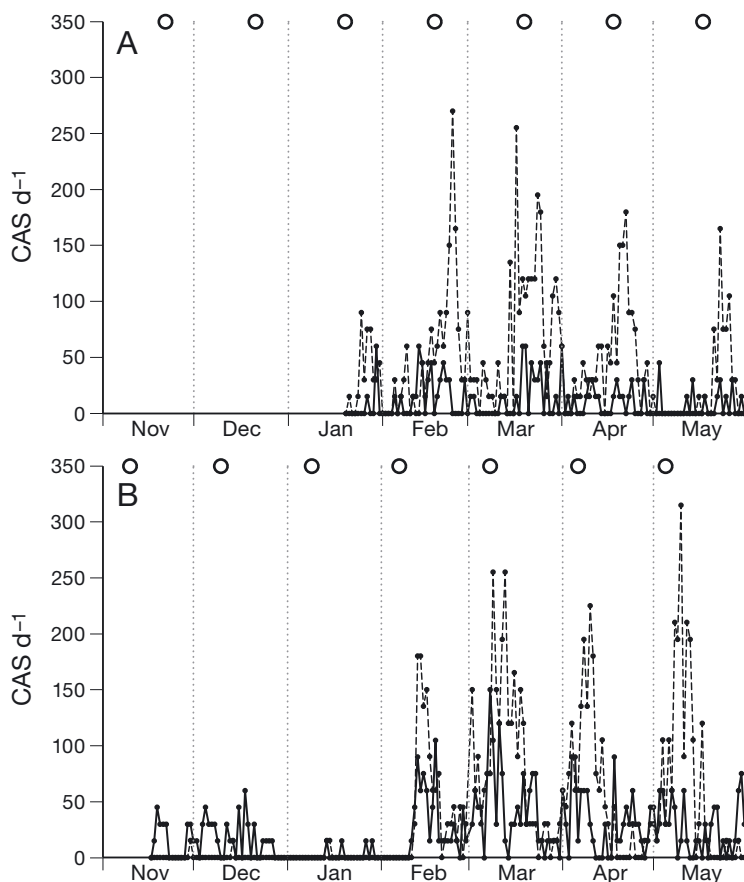


Fig. 4. Total estimated courtship-associated sounds (CAS) d^{-1} of Nassau grouper *Epinephelus striatus* (solid line) and yellowfin grouper *Mycteroperca venenosus* (dashed line) at the Hind Bank Marine Conservation District (MCD) from (A) 20 January to 31 May 2011 and (B) 17 November 2011 to 31 May 2012. O: full moon

Tracking grouper movement patterns using acoustic transmitters from 2007 to 2012 showed that 64.0% ($n = 16$) of Nassau grouper and 76.2% ($n = 16$) of yellowfin grouper migrated from the GB spawning aggregation site and crossed the eastern MCD boundary (Fig. 5). Nassau grouper spent an average of 3 consecutive spawning months (3.4 ± 1.43 SD, $n = 25$, range = 1–6 mo) at the GB spawning site and averaged 1.5 trips mo^{-1} or 4.5 trips during the spawning season (range = 2–11 trips per season). Nearly all tagged yellowfin grouper (87.5%) were detected only 1 spawning month at the GB spawning site but swam between the GB and MCD boundary an average of 5 times mo^{-1} (range = 2–9 trips per season). At maximum swim speeds, Nassau grouper (0.56 m s^{-1}) and yellowfin grouper (0.58 m s^{-1}) covered the distance between the GB and MCD boundary through unprotected waters in only 1.5 h, but typically averaged 11 h (maximum = 72 h) and

6 h (maximum = 21 h), respectively. There was no difference between species in maximum swim speed (Kruskal-Wallis test, $H = 0.42$, $p = 0.52$) nor in the amount of time spent in unprotected waters during the spawning season (Kruskal-Wallis test, $H = 0.23$, $p = 0.64$). On average, both species tended to spend less time in unprotected waters during eastward migrations to GB from the MCD than during westward trips to the MCD from the GB (Nassau grouper = 3.5 vs. 16.5 h, Kruskal-Wallis test, $H = 4.10$, $p < 0.05$; yellowfin grouper = 4.5 vs. 7.5 h, Kruskal-Wallis test, $H = 0.99$, $p = 0.32$). The shorter amount of time spent in unprotected waters swimming toward the spawning site suggests that groupers were swimming faster on average or taking a more direct route than when swimming away from the spawning site.

More than half of all groupers tagged at the GB between 2007 and 2010 (14 Nassau = 56%, 15 yellowfin = 71.4%) were also detected at the MCD receiver (i.e. DSG2 location; Fig. 5), a distance of approximately 6 km. Average time from the GB to MCD DSG location was 8.5 h (range = 2.5–26 h) for Nassau grouper and 19 h (range = 3–42 h) for yellowfin grouper. Nassau and yellowfin grouper transmitters were in the detection range of this acoustic receiver an average of 1 h ($n = 11$, range = 11 min to 3.5 h) and 40 min ($n = 13$, range = 1 min to 4 h), respectively. The short period of time both species spent at the DSG2 location within the MCD (Fig. 5) indicated that most groupers were not residents at this location but moved through the area quickly and continued sound production. After crossing into the MCD or departing the DSG2 location, Nassau and yellowfin groupers that swam outside the detection range of the acoustic array were undetected over a period of 6 to 19 h (mean 12.2 h) and 4 to 31 h (mean 14.5 h), respectively, before being redetected at either the DSG2 or MCD boundary receivers (Fig. 5).

Relationship between grouper CAS and tag detections

Detections from 3 Nassau grouper, but none of the yellowfin grouper, occurred during the DSG recording periods in 2011 and 2012. Daily and monthly patterns of Nassau grouper CAS showed remarkable similarity to acoustic transmitter detections in 2011 and 2012 at the GB (Fig. 6). Significant cross correlations between first differenced CAS and tag detections d^{-1} occurred around a lag of 0 d in both years at

Table 1. Timing of peak and elevated courtship-associated sounds (CAS) of Nassau grouper *Epinephelus striatus* and yellowfin grouper *Mycteroperca venenosa* recorded at the Grammanik Bank (GB) from 20 January to 31 May 2011 and 17 November 2011 to 31 May 2012. DAFM: days after full moon

Year	Month	Peak total CAS	Date of peak	DAFM	Dates of elevated total CAS	DAFM
<i>Epinephelus striatus</i>						
2011	Jan	540	26 Jan	7	25–26 Jan	6–7
	Feb	1290	26 Feb	8	25–28 Feb	7–10
	Mar	1275	29 Mar	11	28–30 Mar	10–12
	Apr	1170	26 Apr	8	24–28 Apr	6–10
	May	300	24 May	7	21 May 24–25 May	4 7–8
2012	Jan	225	12 Jan	3	12–14 Jan 17–18 Jan	3–5 8–9
	Feb	945	12 Feb	5	8–12 Feb	1–5
	Mar	1800	17 Mar	9	15–19 Mar	7–11
	Apr	1455	15 Apr	9	11 Apr 13–17 Apr	5 7–11
	May	855	17 May	12	10–17 May	5–12
<i>Mycteroperca venenosa</i>						
2011	Jan	645	28 Jan	9	25–29 Jan	6–10
	Feb	3285	26 Feb	8	25–26 Feb	7–8
	Mar	3600	27 Mar	9	27–30 Mar	9–12
	Apr	3930	25 Apr	7	24–26 Apr	6–8
	May	2220	23 May	6	23–25 May	6–8
2012	Jan	510	18 Jan	9	16–18 Jan	7–9
	Feb	3015	14 Feb	7	12–15 Feb	5–8
	Mar	2880	15 Mar	7	12–17 Mar	4–9
	Apr	3960	14 Apr	8	11 Apr 13–15 Apr	5 7–9
	May	1530	10 May 13 May	5 8	10–15 May	5–10

Table 2. Timing of peak and elevated yellowfin grouper *Mycteroperca venenosa* courtship-associated sounds (CAS) recorded at the Hind Bank Marine Conservation District (MCD) from 20 January to 31 May 2011 and 17 November 2011 to 31 May 2012. DAFM: days after full moon; negative values indicate days before full moon

Year	Month	Peak total CAS	Date of peak	DAFM	Dates of elevated total CAS	DAFM
2011	Jan	90	25 Jan	6	25 Jan	6
	Feb	270	24 Feb	6	27–28 Jan	8–9
	Mar	195	24 Mar	6	23–25 Feb 17 Mar	6–8 –1
	Apr	180	22 Apr	4	19–25 Mar 18 Apr	1–7 0
	May	165	23 May	6	20–24 Apr 23 May 26 May	2–6 6 9
2012	Feb	180	13 Feb 14 Feb	6 7	13–17 Feb	6–10
	Mar	255	9 Mar	1	9–10 Mar	1–2
			13 Mar	5	12–13 Mar	4–5
	Apr	225	10 Apr	4	7–11 Apr	1–5
	May	315	10 May	5	8–10 May 12–13 May	3–5 7–8

the spawning site (Fig. 6). At the MCD, no significant cross correlations were found between first differenced time series around a lag of 0 d (Fig. 7). However, a weak significant cross correlation was observed between time series that were not corrected for autocorrelation. These results supported the hypotheses that frequency of CAS and frequency of acoustic detections would show a positive relationship at the spawning site but a neutral or weak relationship at a non-spawning site.

DISCUSSION

The GB is a known location of Nassau and yellowfin grouper FSAs in the USVI (Nemeth et al. 2006b, Kadison et al. 2010). A significant temporal relationship was found between time series of Nassau grouper CAS and acoustic tag detections at the spawning site but not at the non-spawning site. The patterns in CAS and movement data suggest that the MCD and the area between MPAs serve as critical habitat, including important migratory corridors during the spawning season and that both species are currently vulnerable to incidental fishing mortality in non-protected areas.

CAS and acoustic detections increased simultaneously after each full moon for both Nassau grouper and yellowfin grouper at the GB spawning aggregation site. As sound production measurements reflect relative grouper density and reproductive behaviors that precede spawning (Rowell et al. 2012, Schärer et al. 2012a, Appeldoorn et al. 2013), patterns of peak and elevated CAS corresponded to changes in relative fish abundance and likely the timing of spawning. The strong positive relationship between sound production and transmitter detections at the GB supported our primary hypothesis, but also suggests that movement patterns of individually tagged groupers represent, fairly

Table 3. Results of 2-way ANOVA comparing start, peak, and end of elevated courtship-associated sounds (CAS) of yellowfin grouper *Mycteroperca venenosa* relative to mean days after full moon (DAFM) between years (2011 vs. 2012) and sites (GB: Grammanik Bank, MCD: Hind Bank Marine Conservation District), with summary of mean DAFM \pm SE for each variable at each site. Significant ($p < 0.05$) values are highlighted in **bold**

Variable	Source	df	SS	MS	F	p
Start of CAS	Year	1	5.956	5.956	1.123	0.306
	Site	1	40.262	40.262	7.592	0.015
	Year \times Site	1	1.062	1.062	0.200	0.661
	Error	15	79.550	5.303		
	Summary:	MCD: 3.08 ± 0.772 , GB: 6.00 ± 0.728				
Peak of CAS	Year	1	0.144	0.144	0.123	0.730
	Site	1	26.544	26.544	22.687	<0.001
	Year \times Site	1	0.144	0.144	0.123	0.730
	Error	15	17.550	1.170		
	Summary:	MCD: 5.42 ± 0.363 , GB: 7.80 ± 0.342				
End of CAS	Year	1	1.176	1.176	0.446	0.515
	Site	1	13.600	13.600	5.152	0.038
	Year \times Site	1	0.424	0.424	0.160	0.694
	Error	15	39.600	2.640		
	Summary:	MCD: 7.40 ± 0.545 , GB: 9.10 ± 0.514				

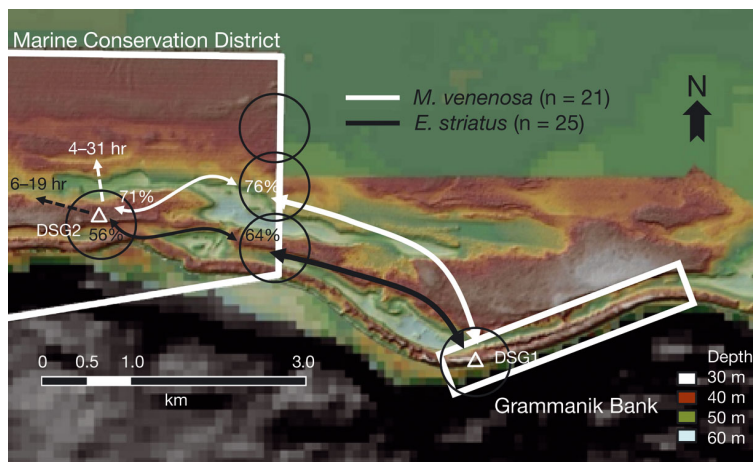


Fig. 5. Summary of migration pathways showing movements of yellowfin grouper *Mycteroperca venenosa* and Nassau grouper *Epinephelus striatus* between the Grammanik Bank (GB) spawning site and the eastern boundary of the Hind Bank Marine Conservation District (MCD) and the passive acoustic recorder location within the MCD. Black circles represent acoustic telemetry receivers with 400 m detection radius. Triangles: passive acoustic recorder locations at the GB (DSG1) and MCD (DSG2). Percentages indicate % of yellowfin and Nassau grouper that were tagged at GB and were also detected at receivers along the eastern boundary of the MCD and at the DSG2 location. Dashed arrows indicate hours that Nassau (black) and yellowfin (white) groupers were not detected on acoustic arrays

accurately, the general population movement patterns at the spawning site. Moreover, the behavior and movement patterns of the adult spawning population can also be inferred from a small sample size of acoustically tagged groupers, assuming they are representative (i.e. sex ratio, mean length), as in this study, of the larger spawning population.

Acoustic detections revealed that 64 and 76.2% of the tagged Nassau and yellowfin groupers repeatedly entered and migrated through the MCD on a daily basis. Grouper CAS were also recorded at the MCD, a non-spawning site, up to 6 km away from the GB but showed a decoupled relationship with acoustic detections for Nassau grouper. Acoustic tracking in this and previous studies have shown that groupers undergo frequent movements to and from their respective aggregation sites (Starr et al. 2007, Nemeth 2009, 2012, Rhodes et al. 2012, Kobara et al. 2013). Why groupers expend the energy to migrate 10 km or more on a regular, often daily, basis during the week of spawning may be related to certain required activities, such as foraging or visiting cleaning stations away from the spawning site or to occupy habitats that provide better protection from predation (Samoilys 1997, Rhodes & Sadovy 2002, Semmens et al. 2006, 2007, Nemeth et al. 2006a). Alternatively, since groupers display home site fidelity (Beets & Hixon 1994, Lembo et al. 1999, Kaunda-Arara & Rose 2004) and return to their territories after spawning (Waschkewitz & Wirtz 1990, Rhodes et al. 2012), individuals who have non-spawning territories close to the spawning site may frequently revisit their home territories to reduce the risk of displacement.

Since the locations of FSA sites are thought to be learned behaviors passed from one generation to the next (Warner 1988, Colin 1996), the extensive, often daily, movements of Nassau and yellowfin groupers combined with ongoing sound production may facilitate attraction of conspecific adults and recruit naïve first-time spawners to the FSA site (Nemeth 2012). Conspecific attraction could serve

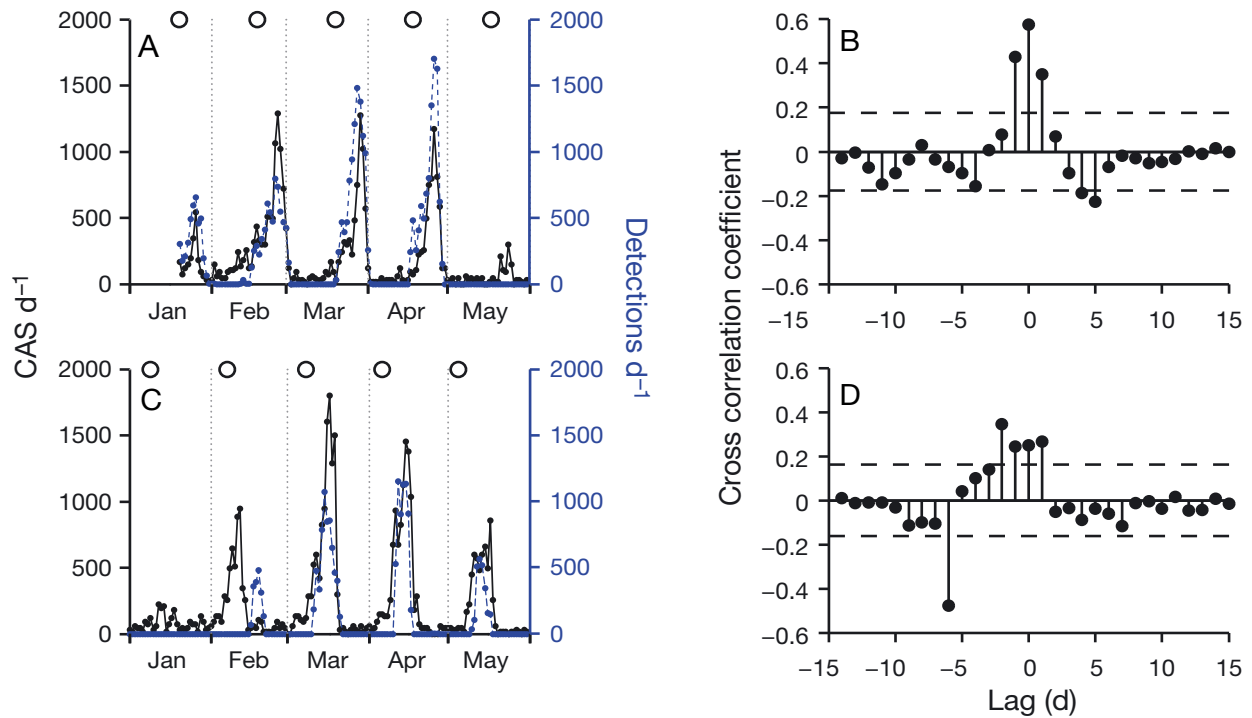


Fig. 6. (A,C) Time series of total courtship-associated sounds (CAS) (black solid line) and acoustic tag detections d^{-1} (dashed blue line) of Nassau grouper *Epinephelus striatus* at the Grammanik Bank (GB) in (A) 2011 and (C) 2012, and (B,D) cross correlations of first differenced time series of total CAS and acoustic tag detections d^{-1} in (B) 2011 and (D) 2012. Dashed black lines in (B,D): 95% confidence limits

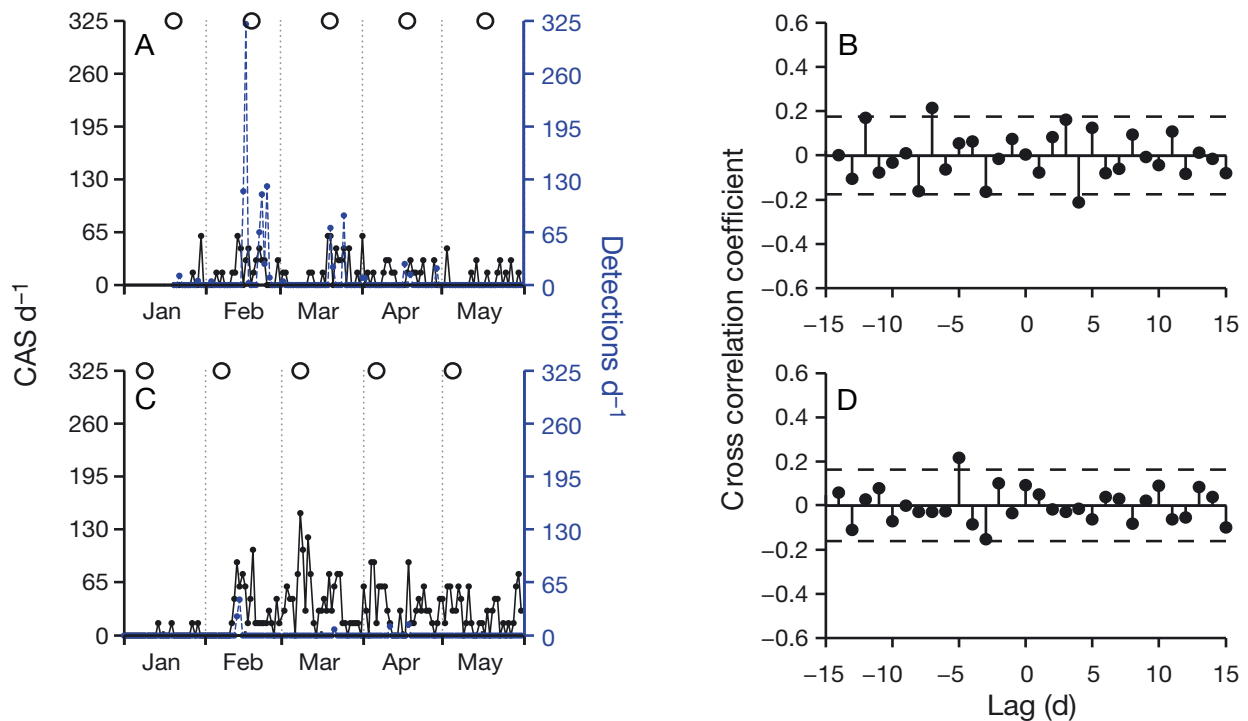


Fig. 7. (A,C) Time series of total courtship-associated sounds (CAS) (black solid line) and acoustic tag detections d^{-1} (dashed blue line) of Nassau grouper *Epinephelus striatus* at the Hind Bank Marine Conservation District (MCD) in (A) 2011 and (C) 2012, and (B,D) cross correlations of first differenced time series of total CAS and acoustic tag detections d^{-1} in (B) 2011 and (D) 2012. Dashed black lines in (B,D): 95% confidence limits

as a mechanism to increase mate encounter rates, enhance mate choice, and improve fertilization success (Molloy et al. 2012). The strongest evidence supporting this hypothesis is that initial and elevated yellowfin grouper CAS within the MCD were recorded nearly 3 d before CAS began at the GB (i.e. fish are calling before they reach the spawning site). More importantly, yellowfin grouper CAS terminated 1.7 d earlier in the lunar phase at the MCD than at the GB, which coincided with when spawning has been observed (i.e. 6–10 DAFM; R. S. Nemeth unpubl. data). This pattern suggests that groupers are actively calling in a large staging area (sensu Nemeth 2012) around the spawning site just before and during aggregation formation but shift their acoustic behaviors and abundance close to the GB aggregation site (i.e. courtship arena) during peak spawning. Distinct CAS patterns by yellowfin grouper at the MCD suggest that their staging areas extended a distance of at least 6 km around the spawning aggregation site (i.e. the distance between the GB and MCD DSGs), whereas the lower Nassau grouper CAS totals at the MCD location suggest a relatively smaller staging area or lower abundance for this species. Moreover, groupers spent less time swimming to reach the GB spawning site, suggesting that movement was more directed and synchronized toward the spawning site whereas fish were less directed or slower when swimming away from the spawning site.

Since yellowfin grouper are more abundant than Nassau grouper at the GB spawning aggregation site (Nemeth et al. 2006b, Kadison et al. 2011), differences in species-specific CAS totals likely corresponded to differences in relative abundance. Higher CAS levels of yellowfin grouper within the MCD also suggested a greater abundance of yellowfin grouper away from the spawning site relative to Nassau grouper. However, the consistency of the relationship of sound production to relative abundance (fish density) or reproductive behaviors over different months and years has not been fully established for different grouper species (Appeldoorn et al. 2013). For example, concentrations of peak Nassau grouper CAS shifted at both sites from January through April in 2011 to February through May in 2012, but similar temporal shifts were not observed for yellowfin grouper at the GB. Annual temporal shifts in peak abundance have been documented for the red hind (Mann et al. 2010, Rowell et al. 2012) and appear to be influenced by the actual timing of the full moons relative to the preferred spawning month (Nemeth et al. 2007). During this study, the full moons occurred about 10 d earlier in each calendar month in 2012

than 2011 (i.e. 9 January 2012 vs. 19 January 2011) and may have influenced monthly differences between years. Water temperature at the GB ranged between 25.5 and 27.0°C at 40 m depth during the 2011 and 2012 spawning season in both years (R. S. Nemeth unpubl. data) and thus likely had little influence on grouper abundance patterns. Successive monitoring should indicate whether this is a long-term trend or simply variation with respect to the monthly timing of the full moons. If the latter, monitoring should also lead to a predictive relationship, as determined for red hind (Nemeth et al. 2007), that could be incorporated into conservation and management strategies.

Management of fish stocks with complex reproductive strategies requires knowledge that incorporates both temporal and spatial variation in spawning seasonality and habitat use. Here, Nassau grouper aggregated over a 5 mo spawning season (January to May), which differs from other studies that found Nassau grouper to primarily aggregate during the months of December through March in the tropical North Atlantic and Caribbean (Colin 1992, Bush & Ebanks-Petrie 1994, Aguilar-Perera 2006, Starr et al. 2007, Heyman & Kjerfve 2008). Nemeth et al. (2006b) first documented this shift in Nassau grouper spawning seasonality from other locations in the Caribbean, including the former aggregation in the USVI (Olsen & LaPlace 1979). It has been suggested that during the process of recovering from near regional extinction, Nassau grouper have reformed a spawning aggregation at the GB and may have mimicked yellowfin grouper site selection and seasonality (Nemeth et al. 2006b). Future long-term acoustic monitoring can determine whether this temporal shift and extended spawning season at the GB will continue or return to the historic and traditional spawning season as the Nassau grouper population continues to recover.

Current protections at the MCD and GB and for Nassau and yellowfin groupers may be allowing gradual spawning population recovery (Nemeth & Quandt 2005, Nemeth et al. 2006b, Kadison et al. 2010). However, recordings of CAS and acoustic tracking revealed that both species utilized broad mesophotic reef areas during the spawning season and highlighted the importance of the area between MPAs, which remains open to fishing during susceptible reproductive periods, as essential habitat and migratory corridors for a majority of their population. A continuation and expansion of passive acoustic and ultrasonic telemetry monitoring will be important to define the range of essential reproductive and migra-

tory habitat for Nassau and yellowfin groupers and determine whether the current geographic limits of the GB and MCD should be expanded or modified to ensure the complete protection of spawning stocks, which may be necessary for full recovery and maintenance of these aggregations. The current 3 mo (February through April) GB area and yellowfin grouper fishery closures do not encompass the more extensive spawning period documented for either species in this study and therefore do not prevent incidental catch mortalities outside of the protected areas or season. To prevent fishing mortality during spawning periods and assist population recovery, year round protection should continue for Nassau grouper and the MCD, while the GB and yellowfin grouper protection should be expanded to a minimal closure from January until the end of May. Given similar declining trends of global and regional grouper populations (Sadovy de Mitcheson et al. 2012), incorporating acoustic methodologies into monitoring programs can greatly enhance management practices and MPA design.

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