Sounds associated with reproductive behavior of the black grouper (Mycteroperca bonaci)

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ORIGINAL PAPER

Sounds associated with the reproductive behavior of the black grouper (*Mycteroperca bonaci*)

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Abstract Passive acoustic and synchronous video recordings were made at two spawning aggregation sites to study the sounds associated with reproductive behaviors of *Mycteroperca bonaci*. A characteristic sound was produced during courtship displays involving behaviors commonly observed for groupers of this genus at aggregations. The sound has a short pulsing section followed by a longer tonal portion with a mean peak frequency below 100 Hz. Courtship-associated sounds were quantified over one spawning season at Mona Island, Puerto Rico. Most of the daily sound production occurred during a period of 2 h prior to sunset. The highest rates of sound production lasted for a period of 10 days with lunar periodicity over three consecutive months coincident with the reported season of reproduction. Passive acoustics provide a tool to measure the variability of the reproductive activity of *M. bonaci* over time and may provide a method to evaluate current strategies designed to protect multi-species spawning aggregations that are critical for the recovery of threatened groupers.

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Introduction

The black grouper, *Mycteroperca bonaci* (Poey, 1860), is one of the largest groupers in the western Atlantic and is considered near-threatened by IUCN (Ferreira et al. 2008) due to declining trends in population abundances. It is a highly targeted fishery species throughout its range from southeast USA to southern Brazil (Heemstra and Randall 1993). The black grouper is a protogynous hermaphrodite (García-Cagide and García 1996; Brulé et al. 2003) that forms transient spawning aggregations (Domeier and Colin 1997), which have been described from Bermuda, Belize, Colombia, Brazil and Florida (Crabtree and Bullock 1998; Eklund et al. 2000; Ferreira-Teixeira et al. 2004; Heyman and Kjerfve 2008; Luckhurst 2010; Bent 2012). The reproductive biology and ecology of black grouper involves migrations of adults from a larger area to one site for spawning, aggregating at higher than usual densities during various days (Ferreira-Teixeira et al. 2004; Luckhurst 2010).

As with many other grouper species, the combination of slow maturation, typical hermaphroditism and formation of fish spawning aggregations (FSA) makes the black grouper populations exceedingly vulnerable to the effects of fishing. Various known FSAs of other grouper species have ceased to form due to unsustainable fishing (Sala et al. 2001; Rhodes and Sadovy 2002; Sadovy and Domeier 2005; Aguilar-Perera 2006; Matos-Caraballo et al. 2006), and the protection of FSAs is imperative in order to conserve remaining grouper populations. In order to achieve this, the dynamics of FSAs must be better understood to protect this critical life stage. With this information, seasonal and spatial fisheries management strategies, as well as monitoring programs to determine changes in spawning stock during FSAs, can be designed more effectively.

Fishes are known to produce sounds associated with reproductive behaviors, territorial defense, competition for food or when threatened (Gannon 2008), and various groupers have species-specific sounds related to reproductive behaviors (Lobel 1992; Mann et al. 2010; Nelson et al. 2011; Schärer et al. 2012a, b). The Nassau grouper relies on the combination of bilateral muscles and the air bladder to produce sound (Hazlett and Winn 1962), which during reproductive displays the males typically produce to gravid females at spawning time (Schärer et al. 2012b). An increase in the rate of these particular courtship-associated sounds (CAS) indicates intensification of behaviors that precede spawning (Colin 1992; Archer et al. 2012). At least one species related to the black grouper, the yellowfin grouper (*Mycteroperca venenosa*), has been documented to produce higher rates of CAS during peak spawning (Schärer et al. 2012a).

Courtship-associated sound production provides a quantifiable variable to measure reproductive activity that is nondestructive, relatively easy to collect and less vulnerable to short-term variations in abundance than visual counts. Variations in sound production provide an indicator of changes in abundance and reproductive activity of the spawning stock (Rowell et al. 2012). Passive acoustic monitoring can be used to develop methods to estimate population density or abundance as long as the behavioral context of sound production is well understood (Marques et al. 2013). During spawning aggregations, this method provides a potential alternative to assess threatened fish populations such as the black grouper that are otherwise difficult to quantify outside FSAs.

The purpose of this study was to characterize the sound produced by the black grouper during courtship displays at FSA sites. We analyzed video and hydrophone recordings at two FSA sites in Puerto Rico to ascertain the sound of black grouper during reproductive behaviors. The physical characteristics and temporal variability of these sounds were analyzed from a long-term (6 months) passive acoustic record. It is expected that monitoring CAS will help elucidate the temporal dynamics of black grouper FSAs and more accurately define the spawning season at this location.

Methods

Study sites

Bajo de Sico (BDS) is an offshore seamount located at 67.43°W and 18.22°N in the Mona Passage, 27 km west of Puerto Rico. At BDS, the seafloor <100 m depth covers approximately 11 km^2 (Fig. 1). The black grouper study site at BDS is located within a seasonal no-take zone (NTZ) designated by the Caribbean Fishery Management Council (CFMC) and the Puerto Rico Department of Natural and Environmental Resources where current regulations prohibit fishing of reef fishes during 6 months (October 1–March 31).

Mona Island (MI) is a carbonate island that covers 55 km^2 of emergent land surrounded by 27 km^2 of insular submerged platform located at 67.89°W and 18.09°N, approximately 72 km west of Puerto Rico (Fig. 1). The black grouper FSA is located within a year-round NTZ that extends one nautical mile from the island's shore in Puerto Rican jurisdiction waters. Both FSA sites are located near the shelf break where depths range from 30 to 200 m, and the main habitats are rock promontories, reef walls and reef slopes covered by sponges, algae, gorgonians and isolated colonies of plating corals.

Courtship behavior and sound identification

Video and audio recordings of black grouper were conducted with closed circuit rebreather and open circuit diving at BDS and MI, Puerto Rico, from 2011 to 2013. Courtship displays of black grouper were recorded in situ with an HD video camera held by divers as well as with autonomous video and audio recorders deployed on the seafloor without the presence of divers (for a full description of equipment, see Schärer et al. 2012a, b). The autonomous recorder was deployed at BDS on February 18, 2012 and February 4, 2013, while at MI, it was deployed on March 14, 2012 and April 19, 2012.

Sounds produced during black grouper courtship displays were isolated from audio–video recordings to identify the species-specific CAS. Each time two or more black groupers were visible in video files, the audio record starting 10 s before until 10 s after their presence was listened to with noise-canceling headphones. All sounds produced during that time period were visually inspected by looking at the spectrograms of the audio portion in Adobe Audition (version 3) software by focusing on the frequency bands lower than 1,000 Hz. The audio associated with the courtship displays was isolated and extracted for identification purposes.

Sound characterization

In order to quantify and characterize black grouper CAS extracted from video files, audio-only files were collected with a digital spectrogram recorder (DSG-Ocean, Loggerhead Instruments) deployed at MI from November 2011 to June 2012. The DSG sampling schedule was programmed to record audio during 20 s every 5 min. The MI site has been surveyed for groupers by conducting underwater visual surveys during February and March since 2007. During these surveys, up to eight black groupers were documented

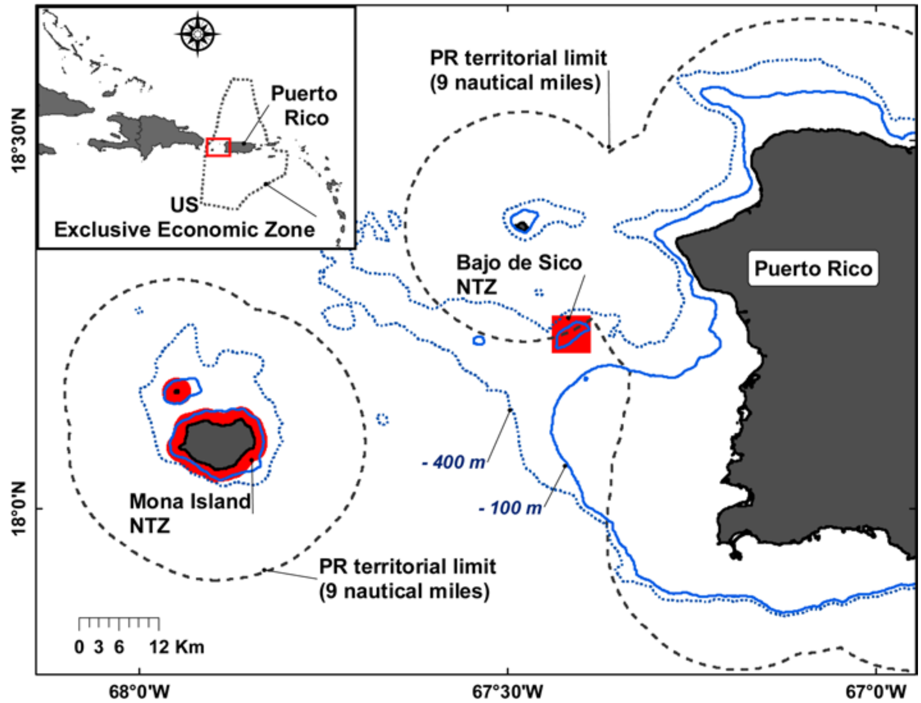

Fig. 1 Map of the study sites located within two no-take zones (NTZ) in the Mona Passage west of Puerto Rico

in reproductive condition (distended abdomen and color phases associated with reproduction).

Black grouper sounds from the DSG with high signal-to-noise ratios were analyzed and characterized with a custom MATLAB program (HotWav). HotWav applied a high-pass filter at 30 Hz and a low-pass filter at 500 Hz, with 5 Hz of resolution, and calculated peak frequency, duration, 6 dB bandwidth and maximum received sound level (dB re 1 μPa_{rms}) for each sound. A total of 36 CAS calls with high signal-to-noise ratios were used for characterization. Oscillogram and spectrogram figures were generated in MATLAB with a fast Fourier transform size of 1,024 points for the spectrogram.

Temporal patterns in sound production

The occurrence of black grouper CAS was quantified from the long-term deployment of the DSG recorder to determine temporal patterns in sound production. Sounds associated with black grouper from MI's long-term recording were counted by visual and audible detection in Ishmael 2.0 (CIMRS Bioacoustics Lab) from spectrograms generated with a Hamming window and frame size of 2,048 samples. Black grouper CAS were summed for each hourly block and each day. Daily totals were multiplied by 15 to account for the sampling schedule, yielding an estimate of total CAS days^{-1} at MI.

In order to determine monthly peaks in black grouper CAS production and the residence patterns at the aggregation, the median CAS days^{-1} was compared between months for the complete deployment. The months with days of twice as many as the mean CAS days^{-1} (defined as peak days of sound production) were considered peak months of reproductive behavior. Peak periods of CAS production with respect to the lunar cycle were identified by comparing CAS days^{-1} in relation to days after full moon pooling the data of January, February and March, which had higher counts of CAS. The median CAS days^{-1} was compared between days to determine lunar patterns. Diel patterns in sound production were identified by classifying each black grouper sound from the complete long-term deployment into the hour period it occurred and then calculated the proportion of calls during that time period. Count data were tested statistically for differences in hourly, daily and monthly patterns with the nonparametric Kruskal–Wallis test ($\alpha = 0.05$).

Results

Courtship behavior and sound identification

Videos of the FSA showed interactions among groups of 2–5 black groupers at both MI and BDS. On two occasions, they were recorded with handheld video in courtship displays with one fish in the whitehead phase at the time of sound production (online resource file ESM_1). This behavior included one individual swimming sideways and shaking the body laterally (twitching) while emitting the sound. Additional video recorded with the autonomous system at BDS (February 2013) showed two black groupers approached closely by a third, which twitched as the sound was perceived (online resource file ESM_2). This behavior was observed high in the water column on this occasion, but divers also observed it near the seafloor and along the shelf break at 20–40 m depth. Spawning rushes were not observed at any time during the dives or in autonomous recordings. Sounds were detected during each one of the courtship displays recorded; therefore, consistent relationship between the sound production and the courtship display led us to define it as an important part of reproductive behavior.

Sound characterization

The sound produced by the black grouper (online resource file ESM_3) was low in frequency (<100 Hz) and is composed of a series of pulses followed by a longer tonal section (Fig. 2). Not all signals included the discrete pulses prior to the tonal section; however, the tonal section was always very similar in form as depicted in spectrograms and oscillograms. Mean peak frequency was 83.5 ± 8.6 Hz ($N = 36$) ranging from 67 to 96 Hz. Mean 6 dB bandwidth was 6.1 ± 2.7 Hz ($N = 36$), ranging from 1.8 to 16.5 Hz. Overall sound duration averaged 4.3 ± 1.3 s with a minimum of 2.4 s and maximum of 7.9 s, and maximum received sound level was 131.3 dB re 1 μPa_{rms}.

Temporal patterns in sound production

Long-term passive acoustic recordings from MI revealed elevated numbers (over 50 CAS $days^{-1}$) of black grouper sounds from January through May. During January, February and March, the number of CAS $days^{-1}$ reached more than 100 with a maximum of 225 CAS $days^{-1}$ on February 17, 2012. The mean monthly values of CAS $days^{-1}$ were highest in February followed by March and then January (Fig. 3). The mean CAS $days^{-1}$ was 4.3 times higher in February than November, and the difference between monthly medians was significant (Kruskal–Wallis test, H25 = 30.5, $P = 0.000$). Higher mean values of CAS $days^{-1}$ were detected between 5 and 16 days after full moon, with a distinct, peak 10 days after full moon (Fig. 4) that was repeated in January and February, but distinct in March. A sharp drop in CAS was detected 11 days after full moon during January and February. Differences in median CAS $days^{-1}$ for days after full moon were also

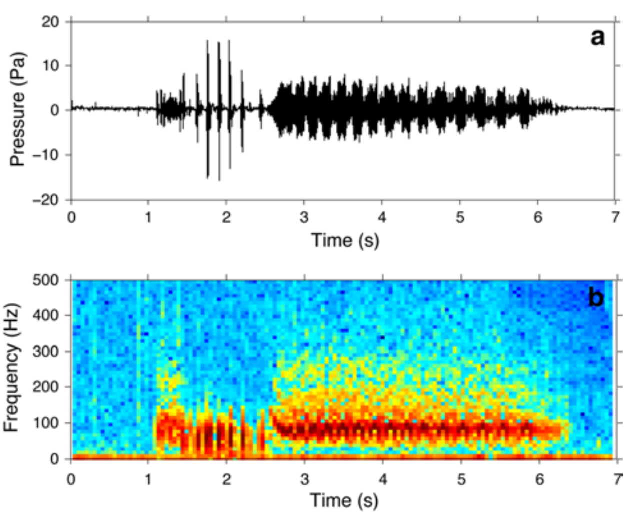

Fig. 2 **a** Oscillogram and **b** spectrogram (fast Fourier transform size = 1,024 points) of sound produced by *M. bonaci*. *Colors* indicate relative sound intensity; *blue* indicates low, and *dark red* is high

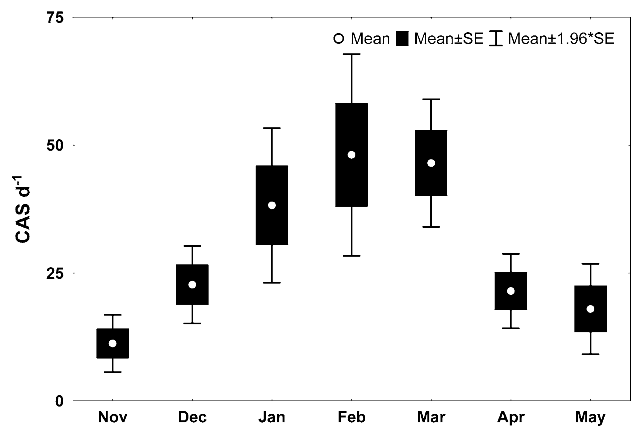

Fig. 3 Mean number of courtship-associated sounds per day (CAS $days^{-1}$) by month for *M. bonaci* during long-term DSG deployment at Mona Island, Puerto Rico (November 2011–May 2012)

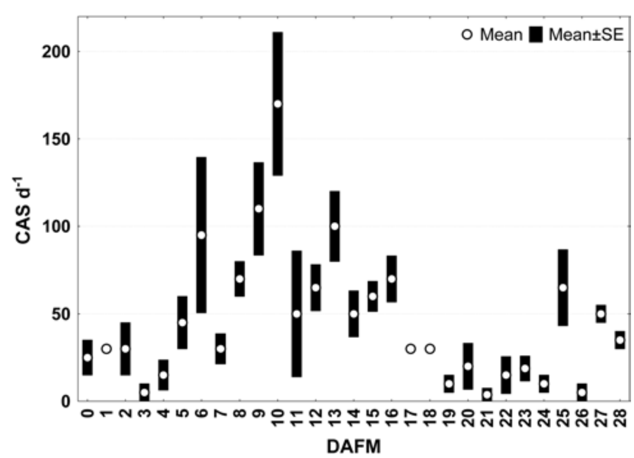

Fig. 4 Mean number of courtship-associated sounds per day (CAS $days^{-1}$) during days after the full moon (DAFM) for *M. bonaci* of the 3 months of highest sound production (January–March 2012) at Mona Island, Puerto Rico

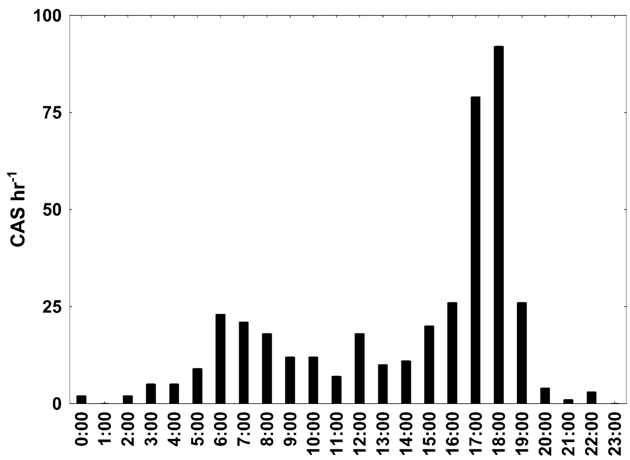

Fig. 5 Total courtship-associated sounds (CAS hours^{-1}) of *M. bonaci* by hour interval during long-term DSG deployment at Mona Island, Puerto Rico ($N = 406$)

statistically significant (Kruskal–Wallis test, H25 = 65.1, $P = 0.0001$). Hourly trends in sound production (Fig. 5) revealed the highest proportion of total daily calls at 1700 and 1800 hours with 19.5 % and 22.7 %, respectively ($N = 406$ CAS).

Discussion

Video and audio recordings of black grouper during this study revealed sound associated with the interaction of whitehead phase individuals with conspecifics during courtship displays that have been described at FSAs prior to spawning (Luckhurst 2010). Although black grouper had previously been described as capable of producing a thumping or a pulse train sound (Tavolga 1960; Fish and Mowbray 1970), another distinct sound is described here and associated with courtship displays during spawning aggregations. Other groupers are also known to produce sound during courtship or territorial displays at spawning aggregations (Mann et al. 2009, 2010; Nelson et al. 2011; Schärer et al. 2012a, b). The whitehead color phase is exhibited by male *M. bonaci* and more individuals were observed in this color phase during dusk when spawning was observed in Belize (Paz personal communication). This whitehead color pattern of black grouper intensified during courtship displays and is analogous to the white-head color phase of tiger (*Mycteroperca tigris*) and yellowfin groupers or the bicolor phase in Nassau grouper (*Epinephelus striatus*), which are known to be an expression of sexual dimorphism and imminent spawning at FSAs (Colin 1992; Sadovy et al. 1994; Tuz-Sulub et al. 2006; Archer et al. 2012; Schärer et al. 2012a). The CAS during the whitehead display of black grouper suggests males are exhibiting to females and spawning is forthcoming.

Courtship and spawning sounds have been described for various reef fishes including various groupers (Mann et al. 2010; Nelson et al. 2011; Schärer et al. 2012a, b) and one species of hamlet, *Hypoplectrus unicolor* (Lobel 1992). The sounds described for the groupers are species-specific and distinguishable based on physical characteristics such as peak frequency, range of frequency, shape of the spectrogram and pulse pattern, from other coral reef fishes such as squirrelfishes (Winn et al. 1964) and damselfishes (Myrberg 1972). Sounds previously described for the black grouper have been associated with prodding or disturbance as a series of pulses (Tavolga 1960) similar to the pattern of the alarm call made by *E. striatus* (Schärer et al. 2012b). It was once proposed that the sound of the black grouper was generated by contact between the opercula and gill covers against the body producing a low-pitched thump (Tavolga 1960). It is likely that the sound production mechanism is from the swim bladder analogous to that described for *E. striatus* (Hazlett and Winn 1962) due to the similarity in pulsing and tonal combination.

Black grouper sound structure is comparable to the CAS of yellowfin grouper, which is composed of a short series of pulses followed by a tonal portion of similar duration (Schärer et al. 2012a). For the black grouper CAS, the range of peak frequency was between 67 and 96 Hz, while for yellowfin grouper, it is slightly higher, ranging from 101 to 132 Hz (Schärer et al. 2012a). The lower peak frequency for the black grouper signal is expected due to their larger body and hence bigger swim bladder that should produce a lower frequency sound. At the BDS spawning aggregation site, black grouper co-occurred with Nassau grouper with only a few yellowfin present during the reproductive season.

Although both of these species have similar reproductive behaviors and courtship displays, the differences in sound characteristics may serve as a proximate cue to species discrimination or sexual determination within a species. Black grouper co-occur with Nassau grouper and sometimes yellowfin grouper at spawning aggregation sites (Smith 1972; Sala et al. 2001; Whaylen et al. 2004; Heyman and Kjerfve 2008; Schärer et al. 2012b), and although the ranges of peak frequency of black, yellowfin and Nassau groupers overlap slightly, the duration and sound structure are notably different. Sound can provide an additional method of species, mate or individual recognition at spawning aggregations that substitutes visual communication after dusk when spawning is known to occur (Luckhurst 2010; Schärer et al. 2012a).

The reported spawning season for black grouper extends from December to March, with peak spawning in February (Eklund et al. 2000; Brulé et al. 2003; Heyman and Kjerfve

2008), except in Bermuda where it is between June and August (Luckhurst 2010). In Puerto Rico, spawning was reported during February (Erdman 1956), while patriarchal fishermen suggest that spawning aggregations may extend from January to May (Ojeda-Serrano personal communication). Current regulations, which apply only within the US Caribbean Exclusive Economic Zone (beyond the Puerto Rico territorial limit), prohibit the take of black grouper along with a suite of grouper species from February 1 to April 31 of each year. In this study, the temporal patterns of CAS suggested three monthly peaks in reproductive behaviors, from January to March during 2012 at MI, suggesting that the first spawning peak was unprotected by current seasonal regulations. Further research will help determine whether this pattern is consistent over time and applicable to other locations, which is critical information for the most effective implementation of management regulations and to guarantee the protection of *M. bonaci* spawning aggregations.

Peak days of black grouper abundance at FSAs occurred 5–14 days after full moon in Belize (Heyman and Kjerfve 2008), and a similar pattern (6–16) was detected at MI using passive acoustic monitoring. Spawning of black groupers occurs at dusk (Paz personal communication), and our results demonstrated diel patterns of sound production consistent with the spawning rush observation. Most of the CAS were detected between 1700 and 1800 hours, just prior to sunset (~1830 hours). However, it is unknown whether the CAS are directly associated with spawning since no spawning rushes were observed during this study.

Passive acoustic techniques utilized to record the CAS of black grouper provided a reliable method to detect their presence and reveal differences in the temporal patterns of reproductive behavior. Passive acoustic monitoring could be applied to locate and detect residence patterns of groupers at FSAs, which is essential for designating management actions and accentuating enforcement efforts. In addition, the understanding of sound production during reproductive behaviors provides a tool to evaluate the effectiveness of management strategies designed to protect multi-species spawning aggregations. In this study, the data collected revealed that it is essential to adapt the timing of seasonal protections and monitor the reproductive aggregations of grouper populations.

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