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Sound Production and Mechanism in the Giant Sea Bass, *Stereolepis gigas* (Polyprionidae)

Larry G. Allen¹, Emily S. Ladin¹, and Timothy J. Rowell²

This study provided a first detailed description of the acoustic calls and the possible sound production mechanism in the Giant Sea Bass (*Stereolepis gigas*). Passive acoustic (hydrophone) recordings of Giant Sea Bass sounds were made of three mature individuals (40–45 kg) held in a circular 17,000 l seawater tank isolated from other fish species. Four basic sounds plus combinations were identified from the tank recordings when fish were present and were encountered on numerous occasions throughout the study. We classified the basic sounds as two types of pulses (A and B), short bursts, and long bursts, and combinations of short and long bursts. Mean peak frequencies of the four sound types were less than 39 Hz, while mean durations ranged from 67 ms to 545 ms, depending on sound type. We also obtained and dissected two mature, adult Giant Sea Bass to describe the morphology of a putative sound production mechanism. Five putative sonic muscles were discovered between each of the first six pleural ribs of the male examined. These five massive muscles (=obliquus superioris?) unite ribs 3 to 9 and were found at the level of the deep hypaxial musculature. The identification of these sounds and accompanying sonic mechanism marks the first occurrence of sound production in the family of wreckfishes (Polyprionidae). This knowledge of the acoustic characteristics increases our ability to document the presence, activity, and possibly the abundance of this critically endangered species at spawning sites.

THE Giant Sea Bass (*Stereolepis gigas*) is the largest teleost and only megacarnivore found in the California kelp bed community, ranging from the Gulf of California to Humboldt Bay (Miller and Lea, 1972), but is most common south of Point Conception (Allen and Andrews, 2012). It forms spawning aggregations during the summer months (July–September; Shane et al., 1996). Giant Sea Bass are often found in kelp forests on rocky reefs as adults, while juveniles are found at sandy bottom areas (Domeier, 2001). These large, demersal teleosts reach lengths greater than 2 m, weights greater than 200 kg, ages of up to 76 years, and are apex predators (Horn and Ferry-Graham, 2006; Allen and Andrews, 2012; Hawk and Allen, 2014; Chabot et al., 2015; House et al., 2016; Allen, 2017).

Like many apex predators, Giant Sea Bass grow slowly and are easily overfished. At the end of the 1920s, the commercial fishing fleet out of San Pedro, California was growing and began fishing (gill netting and hand lining) Giant Sea Bass, often targeting their spawning aggregations in the summer months. This practice led to nearly complete demise of the Giant Sea Bass fishery off California by 1934 (Crocker, 1937). Since 1934, the only appreciable commercial landings of this species were from off Baja California. Their commercial landings and populations continued to decrease until 1982 when the Mexican government prohibited the commercial take of Giant Sea Bass from Mexican waters. In that same year, the California Department of Fish and Game placed a complete moratorium on the recreational and commercial catch that was limited to two fish and later to one fish per trip. In fact, the population of this species dwindled so rapidly during the 20th century that they are now on the International Union for Conservation of Nature (IUCN) Red List as a critically endangered species (Musick et al., 2000; Cornish, 2004). In 1990, the voters of California passed Proposition 132, which banned all gill netting from in-shore

waters and up to three miles off shore. Its implementation in 1994 was effective (Pondella and Allen, 2008), and the population now appears to be in the early stages of recovery (Allen, 2017).

Actual spawning (i.e., release of gametes) of the Giant Sea Bass has not been observed directly in the field, but the available evidence suggests that spawning occurs just after dusk during the summer months. Confirmation of spawning at or near the aggregation site of Twin Rocks, Catalina Island, California was obtained through DNA barcoding with COI primers of Giant Sea Bass eggs sampled from Goat Harbor, Catalina Island, California (Clark and Allen, 2018).

Sound production is a common behavior observed in soniferous (sound producing) fishes during courtship and reproduction (DeMartini and Sikkell, 2006; Aalbers and Drawbridge, 2008; Mann et al., 2009; Erisman and Rowell, 2017). Sounds produced by fishes are also used for the development of spawning aggregations (Gilmore, 2003), to signal reproductive readiness (Connaughton and Taylor, 1996), and for gamete release (Lobel, 2002). Thus, the identification of new sounds and their behavioral contexts is a priority for fish bioacousticians (Rountree et al., 2006). In a recent study, we demonstrated that Giant Sea Bass are among these soniferous fishes (Clark and Allen, 2018). As part of that study, we concluded that Giant Sea Bass produced booming sounds, which were often associated with aggressive behavior, but may also be associated with spawning activity. This booming sound was verified in the field as being produced by Giant Sea Bass with paired video and audio recordings on three occasions. These low frequency “booms” ranged from 50 to 80 Hz (Clark and Allen, 2018). A detailed documentation of the repertoire of sounds made by Giant Sea Bass should lead to future assessments of the locations of aggregations, the timing of spawning, and

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perhaps the number of spawning individuals (Rowell et al., 2012, 2017).

Fine and Parmentier (2015) described multiple mechanisms for sound production in fishes. Many of these use sonic muscles that vibrate the swimbladder. Extrinsic muscles extend from external structures to the swimbladder, while intrinsic muscles attach exclusively to the bladder wall. Sonic muscles are among the fastest found in fishes and typically drive the swimbladder to produce one sound cycle per contraction. Extrinsic muscles are present in many fish species and typically originate on various bones on the skull (but also epineurals, ribs, pectoral girdles, and vertebral bodies) and insert on the swimbladder or on a bone or tendon connected to the swimbladder (Fine and Parmentier, 2015).

Herein, we 1) describe the sounds produced by Giant Sea Bass in captivity before and during spawning events to infer what sounds they make in spawning aggregations in the wild and 2) describe the basic anatomy of the putative sound production mechanism of the Giant Sea Bass. The detection, *in situ*, of known spawning related sounds should be the key to verifying both the locations and timing of spawning, and future recordings of received levels of sound production by the species at identified locations may provide an alternative method to assess spawning stock sizes of this endangered but recovering species. Lastly, this information should allow us to complete the description of the courtship and mating behavior of this ecologically and economically important species.

MATERIALS AND METHODS

Characterization of new sounds.—Passive acoustic (hydrophone) recordings of Giant Sea Bass sounds were made of three mature Giant Sea Bass (one male and two females, 40–45 kg) held in a circular 17,000 l seawater tank at the Southern California Marine Institute's Fish Harbor Laboratory, Terminal Island, California isolated from other fish species. All collecting and handling of the animals followed California State University Northridge's Animal Care Protocol (#1617-006a) and specimens were collected under California State Fish and Wildlife Collecting Permit #00032.

A continuously recording underwater hydrophone (Soundtrap 202: Ocean Instruments^{NZ}; sensitivity -172.7 dBV μPa^{-1}) was suspended 35 cm below the surface near the center of the circular tank from 2000–2400 h from 1 June 2019 through 30 August 2019. Files were digitized at a sample rate of 96 kHz. The Giant Sea Bass began spawning in late June as evidenced by fertilized eggs appearing in the egg collector the morning after. This allowed us to examine the sounds being produced by the Giant Sea Bass both before, during, and after three successful spawnings centered on the spawning dates of 28 June, 31 July, and 12 August 2019. We closely analyzed recordings from before, during, and after the spawn day for 27–28 June, 1–2 August, and 11–13 August 2019. We also made control hydrophone recordings in the same tank containing no fish on the evenings of 10–11 December 2019 to ensure that the sources of sounds recorded during fish presence were not attributable to ambient sounds originating from the tanks or surrounding terrestrial environment.

To identify possible sounds produced by Giant Sea Bass, spectrograms of recordings were generated in Raven Pro 2.0

(Bioacoustics Research Program, Cornell University, Ithaca, NY; FFT length = 8,192 points) and inspected visually and aurally in 60 s windows across a frequency bandwidth of 0–2 kHz. Upon locating sounds that differed from ambient noise recorded in the tanks and putatively were produced by Giant Sea Bass, we extracted, saved, and analyzed each sound using Matlab (The Mathworks). Sounds were grouped based on similarities in structure and analyzed for temporal and spectral characteristics. We generated oscillograms of each extracted file to estimate the duration of each identified sound. Pressure spectral density levels (dB re: $1 \mu\text{Pa}^2 \text{Hz}^{-1}$; FFT length = 96,000 points = 1 s, Hanning window with length = 96,000, FFT overlap of 0%) of sounds were calculated to estimate their peak frequencies and 3 dB and 6 dB bandwidths (Hz), which provide information about the distribution of acoustic pressure as a function of frequency.

Morphology of sound mechanism.—Two mature, adult Giant Sea Bass were obtained and dissected for this portion of the study. The first specimen (a 1.3 m male) was a beach stranding off La Jolla, California on 18 April 2015. The fish was originally frozen, thawed, and a necropsy was performed on 28 April 2015. The second specimen was caught by hook and line off the San Onofre kelp bed on 29 August 2017. The 1.4 m female with ripe ovaries died in captivity at the Southern California Marine Institute, Terminal Island, California. We performed its necropsy shortly thereafter on 31 August 2017. We dissected the left thoracic section of each specimen removing the epaxial and hypaxial musculature, exposing the vertebrae and pleural rib region. Sequential photographs were taken during the dissections for documentation and intercostal muscle tissue was examined and preserved in 10% formalin. The suspected sonic muscle tissue was sent for histological sectioning to Pacific Pathology, Inc., San Diego, California. The hematoxylin and eosin sections were subsequently examined under 100x power using a compound microscope to verify tissue type.

RESULTS

Characterization of sounds.—Four basic sounds plus combinations were identified from the tank recordings when fish were present and were encountered on numerous occasions throughout the study. We classified the basic sounds as two types of pulses (A and B), short bursts, and long bursts, and combinations of short and long bursts (Fig. 1). Mean peak frequencies of the four sound types were less than 39 Hz, while mean durations ranged from 67 ms to 545 ms, depending on sound type (Table 1). Short bursts were similar to the sounds we earlier characterized as “booms” (Clark and Allen, 2018) although the peak frequencies were lower in the tank than in the wild. The short and long bursts along with their combinations are new to the Giant Sea Bass sound repertoire and only occurred during spawning events (the eve and night of spawn verified by fertilized egg collection). None of the four sound types were recorded in the absence of fish during control recordings.

Morphology of sonic mechanism.—Five putative sonic muscles were discovered between each of the first six pleural ribs of the male examined (Fig. 2). These five massive muscles (=obliquus superioris?) unite ribs 3 to 9 and were found at the level of the hypaxial musculature. Histological examination confirmed this tissue to be striated muscle tissue with

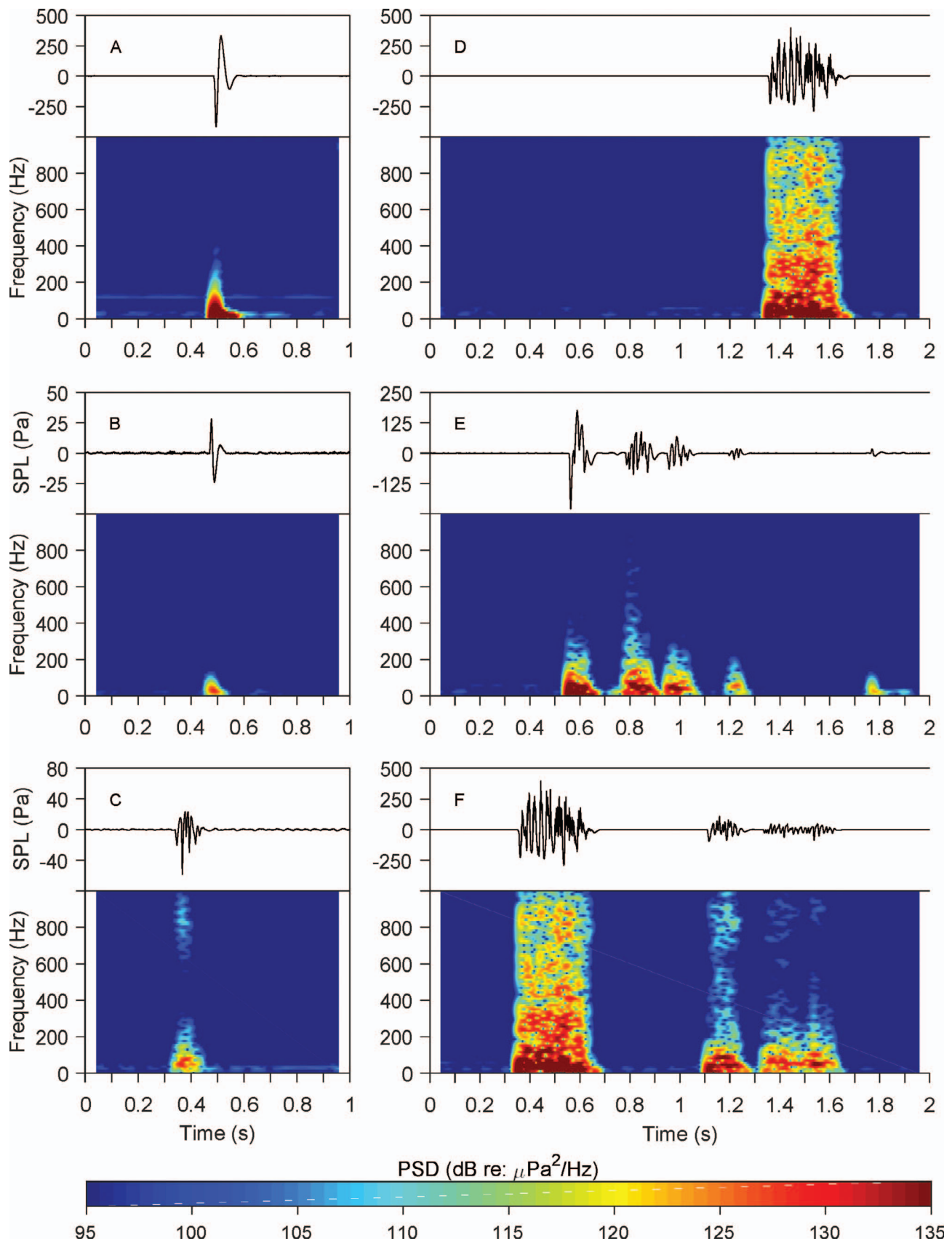


Fig. 1. Oscillograms (top panels) and spectrograms (bottom panels; Kaiser window, fast Fourier transform (FFT) length = 8192 points, overlap = 99%) of sounds detected in tanks with Giant Sea Bass: (A) Pulse A, (B) Pulse B, (C) Short Burst, (D) Long Burst, (E) Short Burst combination, (F) Long Burst combination. PSD, pressure spectral density level; SPL, sound pressure level.

Table 1. Characterization statistics of four types of sounds detected in tanks housing Giant Sea Bass (*Stereolepis gigas*).

	Mean \pm CI ₉₅	n	Min	Max
Pulse A				
Duration (ms)	82.9 \pm 8.1	25	55.1	132.3
Peak frequency (Hz)	17.8 \pm 1.7	25	9	26
3 dB bandwidth (Hz)	23.1 \pm 2.2	25	14	33
6 dB bandwidth (Hz)	32.6 \pm 2.9	25	17	51
Pulse B				
Duration (ms)	67.2 \pm 8.8	8	57.2	97.3
Peak frequency (Hz)	22.6 \pm 1.8	8	19	26
3 dB bandwidth (Hz)	25.5 \pm 1.8	8	21	29
6 dB bandwidth (Hz)	37.0 \pm 3.3	8	30	46
Short burst				
Duration (ms)	122.3 \pm 11.9	9	84.2	145.2
Peak frequency (Hz)	38.4 \pm 14.8	9	9	78
3 dB bandwidth (Hz)	16.0 \pm 3.4	9	11	25
6 dB bandwidth (Hz)	23.3 \pm 4.6	9	15	34
Long burst				
Duration (ms)	545.9 \pm 241.5	10	140.9	1477.3
Peak frequency (Hz)	31.5 \pm 9.2	10	16	58
3 dB bandwidth (Hz)	5.3 \pm 3.1	10	1	17
6 dB bandwidth (Hz)	10.9 \pm 9.5	10	2	52

elongate multinucleate cells with striations (Fig. 2). These extrinsic muscles were notably missing from the verified, mature female that was examined post-mortem. The pleural ribs were rostro-posteriorly flattened, canted, and found to sit directly adjacent and parallel to the lateral wall of the swimbladder. Further, the ribs were hinged to their respective vertebrae (3 to 8), allowing the ribs to pivot and deform the swimbladder. The muscle fibers of the tissue run obliquely between the ribs, originating on the posterior edge of the leading rib and inserting more distally on the anterior margin of following rib.

Manual traction of these ribs and muscles pulled ribs 2 to 6 medially and rostrally. No corresponding muscle tissue was found originating on the head and inserting on the ribs of either mature fish examined.

DISCUSSION

This study provided a first detailed description of the acoustic calls in the Giant Sea Bass. These fish sounds were recorded as fish swam freely within the relatively large space and included two kinds of pulses, short bursts, long bursts, and combinations of short and long bursts. The seawater tank presented an unnatural setting to document the sounds that the relatively large Giant Sea Bass make, including gamete release. The acoustic properties of the fish sounds were potentially impacted by the artificial setting and did not represent a free-field acoustic environment. However, our recordings of the same tank during the same time periods in the absence of all fish allowed us to characterize the sounds made by the fish versus those from ambient sources. We found no clear cases of the reverberation, cancellation, or augmentation expected of close-boundary processes and conclude that these were minimized in the large circular tank and the high sensitivity of the hydrophones.

Giant Sea Bass calls were recorded from both non-spawning and spawning periods in the study tank. The

two types of pulse sound and short bursts were previously recorded in the field and described low “booms.” Such low frequency sounds of peak frequency below 60 Hz have also been recorded for a co-occurring species of California sciaenid, the White Seabass (*Atractoscion nobilis*). Aalbers and Drawbridge (2008) concluded that boom sounds in White Seabass lacked harmonics and were lower in frequency than any other recorded sounds, and peak energy occasionally extended down into the human infrasonic range (<20 Hz). They asserted that the spectral characteristics of booms were consistent with hydrodynamic pressures generated by rapid movement through the water accompanied by an opening of the mouth. The same may be true of the booms produced by the Giant Sea Bass both in the tank and the field, but we never observed Giant Sea Bass opening their mouths when these pulses were recorded and simultaneously observed on video in our tank or field studies. The pulses made by Giant Sea Bass share more similarities with the “thud” sound made by White Seabass (Aalbers and Drawbridge, 2008). They concluded that White Seabass produced single and multiple pulse-trains during courtship and drumrolls and thuds during spawning. The regular pulse repetition rates and harmonic intervals of White Seabass single and multiple pulse-trains were consistent with sonic muscle contractions and the resonant response of the gas bladder (Sprague et al., 2000). We believe that the sophisticated sound producing mechanism (see below) found in Giant Sea Bass is also capable of making these low frequency sounds similarly to the way a concert bass drum makes such low frequency sounds (Fletcher and Bassett, 1978).

The short and long burst calls recorded only during times of spawning in the tank in the present study are new to the sound repertoire of Giant Sea Bass. These burst calls share similarities with the pulse-trains in White Sea Bass (Aalbers and Drawbridge, 2008). However, the bursts of the Giant Sea Bass were typically shorter in duration and lower in frequency than the pulse-trains of White Sea Bass. These characteristic differences should allow the sounds made by these two species to be distinguished in the field.

In Giant Sea Bass, we found a mechanism involving sonic muscles between pivoting ribs that were extrinsic and directly adjacent to the swimbladder. Generally, extrinsic sonic muscles have their origins on various bones on the skull but also on the pectoral girdle, ribs, or epineurals (Fine and Parmentier, 2015) and insert on the swim bladder or on a structure that attaches to the swim bladder. Sonic muscles of red drum (*Sciaenops ocellatus*) are bilaterally symmetrical muscles that originate on the abdominal hypaxial musculature inserting on a central tendon that attaches to the dorsal swim bladder. Alternatively, extrinsic muscles can also insert between two bones, one of which is connected to the swimbladder via ligaments or connective tissue (Parmentier et al., 2011) as is the case with the Giant Sea Bass mechanism.

The sonic mechanism proposed for Giant Sea Bass is unique and appears to be most similar to that found in chaetodontids (*Heniochus chrystomus*; Parmentier et al., 2011). *Heniochus chrystomus* possesses five massive muscles between the ribs (*obliquus superioris* 2) that are capable of compressing the swimbladder with the movements of a total of ten articulated ribs (ribs 3 to 7 on each side) likely play a role. Likewise, the five massive muscles between the ribs

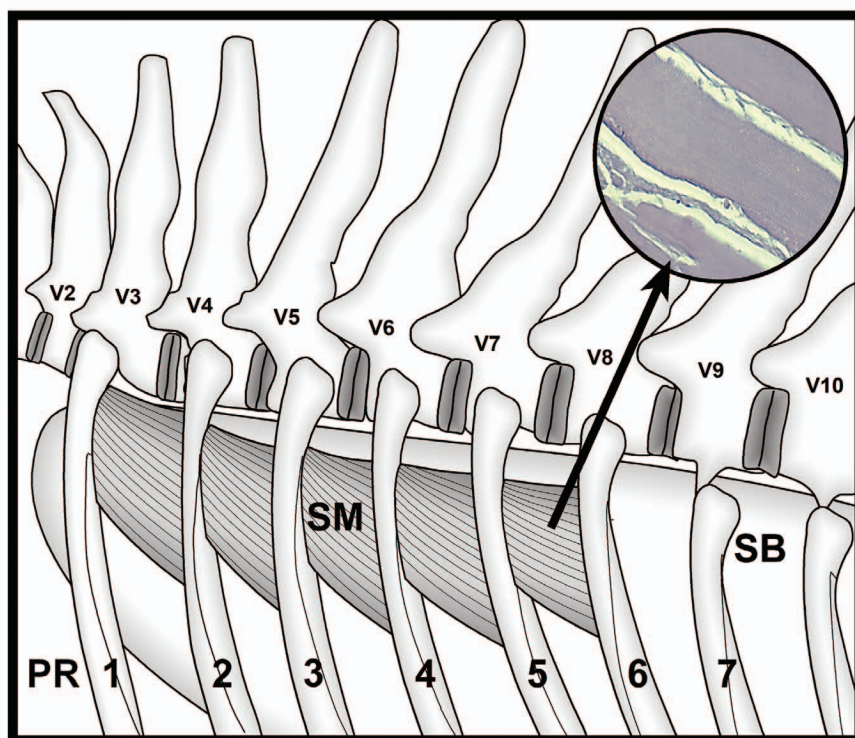
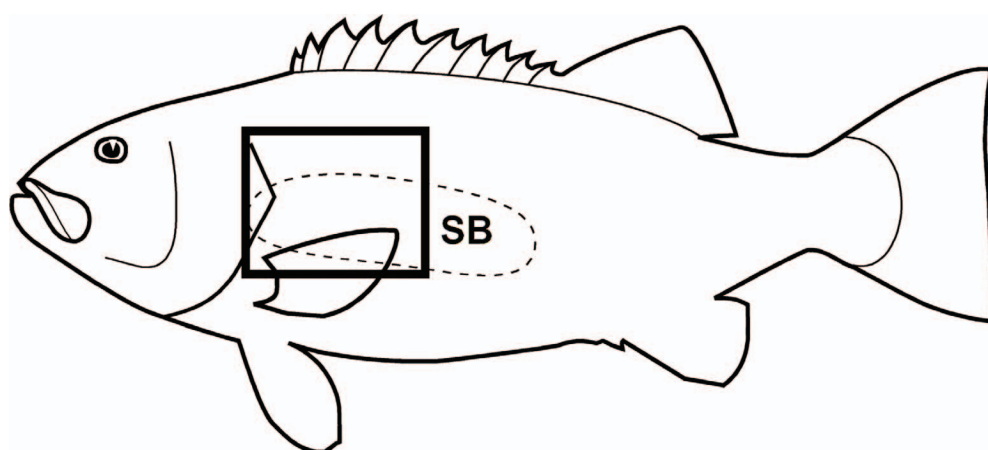


Fig. 2. Diagrammatic representation of putative sonic apparatus in male Giant Sea Bass (*Stereolepis gigas*) based on dissections. PR = pleural rib; SB = swimbladder; SM = putative sonic muscles; V = vertebra; numbers = bone series identification; (inset) histological hematoxylin and eosin stained section of striated muscle.

found in Giant Sea Bass should be able to compress the swimbladder, and the movements of a total of 12 articulated ribs (ribs 1 to 6 on each side) likely play a drumming role. One notable difference in the morphology between the sonic mechanism in *Heniochus* and that described herein for Giant Sea Bass is the absence of muscles originating on the cranium and inserting on the first rib that is found in *Heniochus*.

In conclusion, our findings represent the first lab confirmation and detailed documentation of the repertoire of sounds made by Giant Sea Bass. Identification of these Giant Sea Bass sounds and accompanying sonic mechanism also marks the first occurrence of sound production in the family of wreckfishes (Polyprionidae). Knowledge of the acoustic characteristics increases our ability to document the presence, activity, and possibly the abundance of this critically endangered species at spawning sites. Continued efforts to catalogue the sounds and behaviors of species like Giant Sea Bass will increase our ability to monitor and understand fish behaviors.

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University Northridge all provided funding to support this research.

LITERATURE CITED

- Aalbers, S. A., and M. A. Drawbridge. 2008. White seabass spawning behavior and sound production. *Transactions of the American Fisheries Society* 137:542–550.
- Allen, L. G. 2017. GIANTS! Or . . . the return of the kelp forest king. *Copeia* 105:10–13.
- Allen, L. G., and A. H. Andrews. 2012. Bomb radiocarbon dating and estimated longevity of Giant Sea Bass (*Stereolepis gigas*). *Bulletin of the Southern California Academy of Sciences* 111:1–14.
- Chabot, C. L., H. A. Hawk, and L. G. Allen. 2015. Low contemporary effective population size detected in the Critically Endangered giant sea bass, *Stereolepis gigas*, due to fisheries overexploitation. *Fisheries Research* 172:71–78.
- Clark, B. L., and L. G. Allen. 2018. Field observations on courtship and spawning behavior. *Copeia* 106:171–179.
- Connaughton, M. A., and M. H. Taylor. 1996. Drumming, courtship, and spawning behavior in captive weakfish, *Cynoscion regalis*. *Copeia* 1996:195–199.
- Cornish, A. 2004. *Stereolepis gigas* IUCN 2009. IUCN Red List of Threatened Species, version 2009.1.
- Croker, R. S. 1937. Black Sea Bass. *In*: Bureau of Commercial Fisheries. The Commercial Fish Catch of California for the Year 1935. California Department Fish and Game, Fishery Bulletin 49:76–77.
- DeMartini, E. E., and P. C. Sikkell. 2006. Reproduction, p. 483–523. *In*: The Ecology of Marine Fishes: California and Adjacent Waters. L. G. Allen D. J. Pondella, and M. H. Horn (eds.). University of California Press, Berkeley, California.
- Domeier, M. L. 2001. Giant Sea Bass, p. 209–211. *In*: California's Marine Living Resources: A Status Report. W. S. Leet, C. M. Dewees, R. Klingbeil, and E. Larson (eds.). Agriculture and Natural Resources Communication Services, University of California, Oakland, California.
- Erisman, B. E., and T. J. Rowell. 2017. A sound worth saving: acoustic characteristics of a massive fish spawning aggregation. *Biology Letters* 13:20170656.
- Fine, M. L., and E. Parmentier. 2015. Mechanisms of fish sound production, p. 77–126. *In*: Sound Communication in Fishes. Animal Signals and Communication, Vol. 4. F. Ladich (ed.). Springer, Vienna.
- Fletcher, H., and I. G. Bassett. 1978. Some experiments with the bass drum. *Journal Acoustic Society America* 64:1570–1576.
- Gilmore, R. G., Jr. 2003. Sound production and communication in the spotted seatrout, p. 177–195. *In*: Biology of the Spotted Seatrout. S. A. Bortone (ed.). CRC Press, Boca Raton, Florida.
- Hawk, H., and L. G. Allen. 2014. Age and growth of the Giant Sea Bass, *Stereolepis gigas*. California Cooperative Fisheries Investigation Reports 55:1–7.
- Horn, M. H., and L. A. Ferry-Graham. 2006. Feeding mechanisms and trophic interactions, p. 387–410. *In*: The Ecology of Marine Fishes: California and Adjacent Waters. L. G. Allen, D. J. Pondella, II, and M. H. Horn (eds.). Univ. California Press, Berkeley.
- House, P. H., B. L. Clark, and L. G. Allen. 2016. The return of the king of the kelp forest: distribution, abundance, and biomass of Giant Sea Bass (*Stereolepis gigas*) off Santa Catalina Island, California, 2014–2015. *Bulletin of the Southern California Academy of Sciences* 115:1–14.
- Lobel, P. S. 2002. Diversity of fish spawning sounds and the application of passive acoustic monitoring. *Bioacoustics* 12:287–288.
- Mann, D. A., J. V. Locascio, F. C. Coleman, and C. C. Koenig. 2009. Goliath grouper *Epinephelus itajara* sound production and movement patterns on aggregation sites. *Endangered Species Research* 7:229–236.
- Miller, D. J., and R. N. Lea. 1972. Guide to the coastal marine fishes of California. California Department of Fish Game, Fishery Bulletin 157:140.
- Musick, J. A., M. M. Harbin, S. A. Berkeley, G. H. Burgess, A. M. Eklund, L. Findley, R. G. Gilmore, J. T. Golden, D. S. Ha, G. R. Huntsman, J. C. McGovern, S. J. Parker, S. G. Poss, E. Sala . . . S. G. Wright. 2000. Marine, estuarine, and diadromous fish stocks at risk of extinction in North America (exclusive of Pacific salmonids). *Fisheries* 25:6–30.
- Parmentier, E., K. S. Boyle, L. Berten, C. Brié, and D. Lecchini. 2011. Sound production and mechanism in *Heniochus chrysostomus* (Chaetodontidae). *Journal of Experimental Biology* 214:2702–2708.
- Pondella, D. J., II, and L. G. Allen. 2008. The decline and recovery of four predatory fishes from the Southern California Bight. *Marine Biology* 154:307–313.
- Rountree, R. A., R. G. Gilmore, C. A. Goudey, A. D. Hawkins, J. J. Luczkovich, and D. A. Mann. 2006. Listening to fish: applications of passive acoustics to fisheries science. *Fisheries* 31:433–446.
- Rowell, T. J., D. A. Demer, O. Aburto-Oropeza, J. J. Cota Nieto, J. R. Hyde, and B. E. Erisman. 2017. Estimating fish abundance at spawning aggregations from courtship sound levels. *Scientific Reports* 7:3340.
- Rowell, T. J., M. T. Schärer, R. S. Appeldoorn, M. I. Nemeth, D. A. Mann, and J. A. Rivera. 2012. Sound production as an indicator of red hind density at a spawning aggregation. *Marine Ecology Progress Series* 462:241–250.
- Shane, M. A., W. Watson, and H. G. Moser. 1996. Polyprionidae: giant sea basses and wreckfishes, p. 873–875. *In*: The Early Stages of Fishes in the California Current Region. H. G. Moser (ed.). California Cooperative Oceanic Fisheries Investigations (CalCOFI) Atlas No. 33. Allen Press Inc., Lawrence, Kansas.
- Sprague, M. W., J. J. Luczkovich, R. C. Pullinger, S. E., Johnson, T. Jenkins, and H. J. Daniel III. 2000. Using spectral analysis to identify drumming sounds of some North Carolina fishes in the family Sciaenidae. *Journal Elisha Mitchell Scientific Society* 116:124–145.