Transactions of the American Fisheries Society 137:542–550, 2008

DOI: 10.1577/T04-058.1

[Article]

White Seabass Spawning Behavior and Sound Production

SCOTT A. AALBERS*[1]

Hubbs–SeaWorld Research Institute, 2595 Ingraham Street, San Diego, California 92109, USA; and Department of Biology, California State University–Fullerton, 800 North State College Boulevard, Fullerton, California 92834, USA

MARK A. DRAWBRIDGE

Hubbs–SeaWorld Research Institute, 2595 Ingraham Street, San Diego, California 92109, USA

Abstract.—White seabass *Atractoscion nobilis* (family Sciaenidae) form transient spawning aggregations in the spring and summer throughout southern California and northern Baja California, Mexico. Although spawning activity has been linked with sound production in other sciaenid fishes, the function and acoustic characteristics of white seabass sounds have not previously been identified. We described the spawning behavior and characterized the sounds generated by 62 white seabass maintained within the seminatural conditions and free-field acoustic environment of a net-pen moored in Catalina Harbor, California. In addition to visual observations, video and audio recordings were made during periods of peak spawning activity in 2001–2003. The physical characteristics of white seabass sounds were described and illustrated with sonogram, waveform, and power spectrum displays. Gravid females were identifiable during courtship and spawning by shifts in behavior and the development of dark bars across the dorsal region. During spawning, 1–9 males tightly surrounded a gravid female and the resultant pack shuddered in unison as gametes were simultaneously broadcast into the water column. Five distinct types of sound were produced by white seabass: single and multiple pulse trains during courtship, drumrolls and thuds during spawning, and booms during yawning and burst swimming. During the actual release of gametes, a rapid succession of overlapping drumroll and thud sounds resulted in identifiable spawning chants lasting 7–55 s. Consistent physical, behavioral, and acoustical patterns during courtship and spawning indicated that white seabass utilize visual, tactile, and sonic cues to communicate their reproductive state.

The white seabass *Atractoscion nobilis* is an economically important member of the family Sciaenidae (croakers and drums) that ranges primarily from San Francisco, California, to Magdelena Bay, Baja California, Mexico (Vojkovich and Reed 1983); an isolated population occurs in the northern Gulf of California. White seabass larvae have been found between Santa Rosa Island, California, and Magdelena Bay from April through August (Moser et al. 1983), indicating that spawning activity occurs throughout the southern extent of the species' range. Historically, commercial and recreational fisheries targeted the transient spawning aggregations that developed nearshore and around coastal islands in the spring and summer months (Thomas 1968). Fishery landings reached historically low levels in the early 1980s due largely to sustained levels of overfishing (Vojkovich and Reed 1983). Although white seabass landings have risen considerably since 1997, fishery management decisions remain compromised by insufficient information on white seabass spawning behavior, periodicity, and locations (CDFG 2002).

After two decades of low relative abundance of white seabass, the Ocean Resources Enhancement and Hatchery Program (OREHP) was initiated as part of a management effort to restore stocks by hatchery rearing and release of juveniles. As an extension of OREHP, a net-pen was built in Catalina Harbor in 1997 and is currently used to raise juvenile white seabass and hold adult broodstock. The large size, seminatural conditions, and relatively free-field acoustic properties of this enclosure provided a unique opportunity to observe white seabass spawning behavior and to record the sounds that they produce.

Numerous fish species have developed effective sound production and detection mechanisms (Hawkins and Myrberg 1983; Gilmore 2003), thus taking advantage of the properties of underwater sound propagation (Albers 1965; Urick 1983). Many species of the family Sciaenidae produce pulsed sounds, often referred to as "drumming," by contracting specialized sonic musculature to resonate low-frequency sound off the adjacent gas bladder (Tower 1908; Tavolga 1964; Gilmore 2003). Sonic musculature generally is present in mature male sciaenids but not in females (Smith

* Corresponding author: scott@pier.org
[1] Present address: Pfleger Institute of Environmental Research, 315 North Clementine Street, Oceanside, California 92054 USA.

Received March 29, 2004; accepted March 8, 2006
Published online April 3, 2008

1905; Tavolga 1964); however, the characteristics and functions of white seabass sounds have not previously been described. Although sound production has been associated with fish reproduction (Tower 1908; Mok and Gilmore 1983; Connaughton and Taylor 1995), the sounds produced during actual spawning have rarely been recorded because spawning events are not commonly observed (Lobel 1992). It has been hypothesized that fish sounds communicate reproductive readiness (Fish and Cummings 1972; Mok and Gilmore 1983; Connaughton and Taylor 1996), assist in developing spawning aggregations (Connaughton and Taylor 1994; Gilmore 2003), and synchronize the release of gametes during broadcast spawning (Lobel 1992; Hawkins and Amorim 2000; Lobel 2002).

The purpose of this study was to describe white seabass courtship and spawning behavior and to determine the acoustic characteristics of sounds associated with courtship and spawning. This information will add to the current understanding of fish reproduction and associated acoustic behavior while providing the first detailed description of sounds produced by a Pacific member of the family Sciaenidae.

Methods

This study was conducted between March and July of 2001–2003 at an aquaculture net-pen facility moored in Catalina Harbor, Santa Catalina Island. The system consisted of four 9×9-m pens with 1.3-cm-mesh nylon containment nets suspended to a depth of 6.5 m (526-m^3 volume). Individual pens were enclosed within a 10-cm-mesh nylon predator net. Water depth at the site averaged 17.0 m over a relatively flat bottom.

Forty-one adult white seabass were captured by hook and line from the nearshore waters of Santa Catalina Island between March and June 2000, and an additional 21 fish were collected in May 2001. Fish were transported to the net-pen in a 225-L transport tank supplied with a continuous flow of seawater onboard a 5-m skiff. Once fish became acclimated to the net-pen, they were measured, weighed, sexed, and tagged with passive integrated transponders. Forty-seven females and fifteen males ranging in size from 83 to 126 cm total length and from 4.9 to 19.5 kg in weight were held in a containment net throughout the study period.

White seabass spawning activity was frequently monitored from the elevated deck of a live-aboard boat that was side-tied to the net-pen containing the adult fish. Spawning was verified by routinely sampling for freshly spawned eggs within the containment net. The buoyant fertilized eggs were readily skimmed from the surface of the water with a 500-μm dip net. For approximately 10 h/week, visual observations and video recordings (Sony Corporation, Tokyo, Japan; Model DCR-PC110) of courtship and spawning behavior were taken while acoustically monitoring fish sounds with headphones. Three-minute sound recordings were taken during the hours surrounding peak spawning activity, totaling approximately 100 min/week.

Sounds were received through an omnidirectional hydrophone (International Transducer Corporation, Santa Barbara, California; Model 6050-C) with an essentially flat frequency response between 50 Hz and 35 kHz. The hydrophone was powered by a custom 24-V power supply and amplifier (constructed by F. Aubrey, Hubbs–SeaWorld Research Institute). Sound intensity was displayed at a pascal or decibel scale but not as absolute sound pressure level, because the entire hydrophone system had not recently been calibrated. Sounds were recorded with a portable digital audiotape recorder (Sony Corporation; Model PCM-M1 DAT) set to a constant level at a sampling rate of 44.1 kHz. The hydrophone was suspended at a depth of 3 m in the center of the net-pen.

Using SpectraPlus software, 102 sound recordings were digitally transferred to a computer for spectral analysis. Recorded signals were sampled at a rate of 11,025 Hz in 16-bit format. A 4,096-point fast Fourier transformation (FFT) was applied through a Hanning smoothing window and displayed on a logarithmic scale. Acoustic characteristics, including sound duration, interpulse interval, pulse repetition rate, and peak and harmonic frequencies (Hz), were measured for selected single and multiple pulse trains, drumrolls, thuds, and booms. Thirty sounds of each variety with high signal-to-noise ratios were selected from independent recordings. Sounds of each variety were analyzed from different recordings to maximize contributions from multiple individuals. Once a sound was highlighted, its sonogram, waveform, and power spectrum displays were examined to determine the acoustic characteristics. Sound duration was measured from the beginning to the end of each sound on the sonogram display. Interpulse interval was measured from the sound waveform as the duration from the peak of one pulse to the peak of the subsequent pulse. Pulse repetition rate was then calculated as the number of pulses per second, and the number of pulses were counted for each sound. Power spectra curves were generated by selecting a single FFT window from the waveform at the region of peak sound intensity to reveal the peak and harmonic frequencies.

Results

Courtship Behavior

During courtship, the entire group of white seabass typically circled tightly near the surface. Individual fish were regularly observed finning, flashing, splashing, shuddering, and yawning. Finning behavior entailed fish swimming slowly with their caudal fin partially above the surface of the water, while yawning behavior involved an expansion and rapid contraction of the buccal cavity. The gravid female routinely separated from the circling school and was followed closely by courting males.

Gravid females were identifiable by several physical and behavioral characteristics exhibited 1–3 h before actual spawning. Distinct dark bars developed across the female's dorsal region, along with a single dark band along the dorsal ridge (Figure 1). The female typically moved in a head-down posture with pectoral fins flattened against a distended abdomen. Multiple courting males closely pursued and often spiraled around the female or aggressively nudged against the abdominal region (Figure 1a). No agonistic or territorial behavior was observed between males during courtship or spawning other than competition for prime spawning position (vent to vent). Pseudospawning behavior, when fish briefly assembled into a tight spawning pack without releasing gametes, was commonly observed prior to actual spawning events.

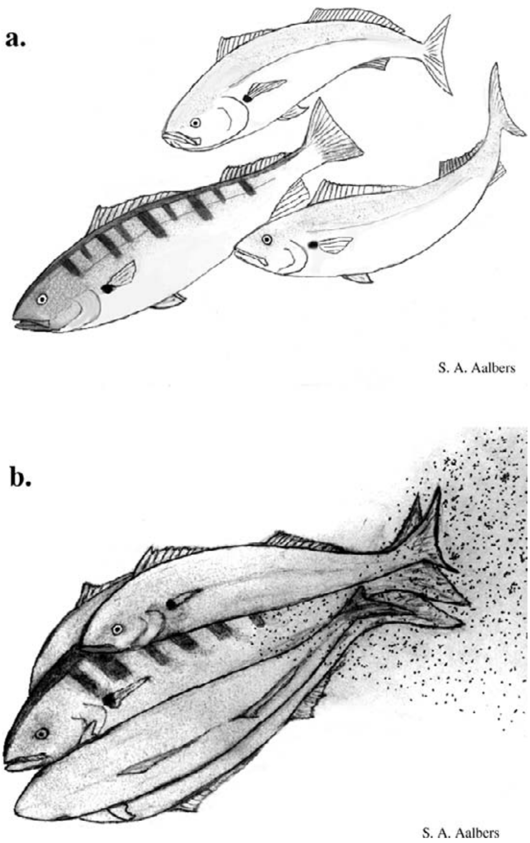

FIGURE 1.—Author illustrations of **(a)** two courting white seabass males shadowing and nudging a darkly barred gravid female and **(b)** a spawning pack of four males and a barred female simultaneously releasing gametes during a broadcast spawning event.

Spawning Behavior

We directly observed 46 spawning events, of which 13 were videotaped. The number of males observed per spawning sequence ranged from one to nine; more commonly, between two and five males participated. The shadowing pack of males tightly pursued the gravid female and initiated lateral contact before encompassing the female to match vents at the inception of spawning (Figure 1b). The spawning female and pack of spawning males remained in tight contact for 5–45 s and shuddered in unison during the simultaneous release of a large, visible cloud of ova and spermatozoa into the water. The spawning female was occasionally elevated partially above the surface of the water by the pack of males, resulting in splashing at the surface that often was audible on sound recordings.

Courtship Sounds

The most common sounds detected during courtship were single and multiple pulse trains (Figure 2a). Pulse trains aurally resembled purring and were produced singly (Figure 3a) or in multiples of two, three (Figure 3b), four, five, or six trains. Total durations averaged 473 ms for a single train, 697 ms for a two-train event, 930 ms for a three-train event, 1,097 ms for four trains, 1,363 ms for five trains, and 1,450 ms for six trains. Multiple pulse trains averaged 6.0, 2.5, 2.0, 1.4, 1.1, and 1.0 pulses/train for trains 1–6, respectively (Figure 3b). The spectral characteristics of single and multiple pulse trains were similar; fundamental frequencies were typically around 32 Hz, and distinct harmonic bands occurred every 26–34 Hz (Figure 4). Peak intensity typically occurred on the second, third, or fourth harmonic band between 56 and 124 Hz.

Spawning Sounds

Sound recordings during 65 spawning events revealed that white seabass produce a distinct procession of sounds during the actual release of gametes, collectively termed a chant. Chants consisted of two distinct types of sound, called drumrolls and thuds (Figure 2b). Drumrolls spectrally resembled pulse trains by having similar peak and harmonic frequencies (Figure 4c) and comparable pulse repetition rates (Table 1). However, drumrolls were relatively compressed in duration and reduced in number of pulses (Figure 3c). Thuds had a narrow frequency range of 40–300 Hz without harmonic structure (Figure 4d).

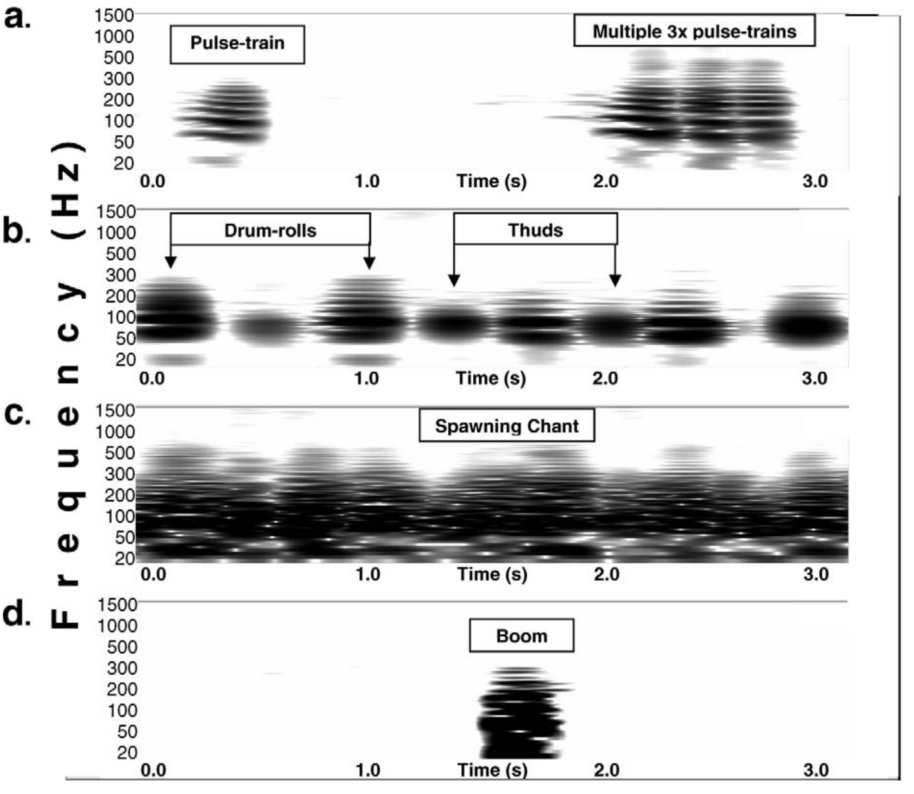

FIGURE 2.—Three-second sonograms displaying **(a)** white seabass courtship sounds, including single and multiple (3×) pulse trains; **(b)** drumroll and thud sounds produced in rapid succession at the beginning of a spawning event; **(c)** a spawning chant of continuous, overlapping drumroll and thud sounds; and **(d)** a hydrodynamic boom. Sounds were recorded from fish held in a net-pen in Catalina Harbor, California.

Thuds were short in duration, and their waveforms consisted of two or three complete cycles (Figure 3d).

Individual drumroll and thud sounds were typically identifiable at the initiation of chants (Figure 2b) but progressed into overlapping sounds that aurally resembled a galloping horse. The overlap made individual sounds indistinguishable from one another on sonogram (Figure 2c) and waveform (Figure 3e) displays. Power spectrum displays of spawning chants (Figure 4e) represent a combination of the spectral characteristics from overlapping sounds. Spawning chants were easily identifiable on sonograms (Figure 5b) when compared with other typical courtship sound patterns (Figure 5 a, c). Short-duration drumrolls (230–360 ms) and thuds (200–310 ms) collectively resulted in chants ranging from 7 to 55 s in duration (mean ±

TABLE 1.—Physical characteristics (mean and SD) of white seabass courtship and spawning sounds recorded from fish held in a net-pen in Catalina Harbor, California.

Sound	Number analyzed	Sound duration (ms)	Peak frequency (Hz)	Harmonic interval (Hz)	Interpulse interval (ms)	Pulse repetition rate (pulses/s)	Total number of pulses
Pulse train	30	473.2 (63.7)	72.6 (10.7)	29.5 (2.4)	33.9 (2.9)	29.7 (2.6)	6.0 (1.7)
Multiple (3×) pulse train	30	930.4 (106.1)	81.1 (18.5)	30.2 (2.6)	33.7 (2.7)	29.9 (2.4)	10.7 (1.6)
Drumroll	30	294.5 (31.3)	77.4 (16.8)	30.1 (4.4)	35.3 (5.4)	29.0 (4.4)	2.6 (0.8)
Thud	30	248.6 (26.0)	69.7 (7.3)	na	na	na	na
Boom	30	361.5 (51.3)	62.8 (22.4)	na	na	na	na

na = not applicable.

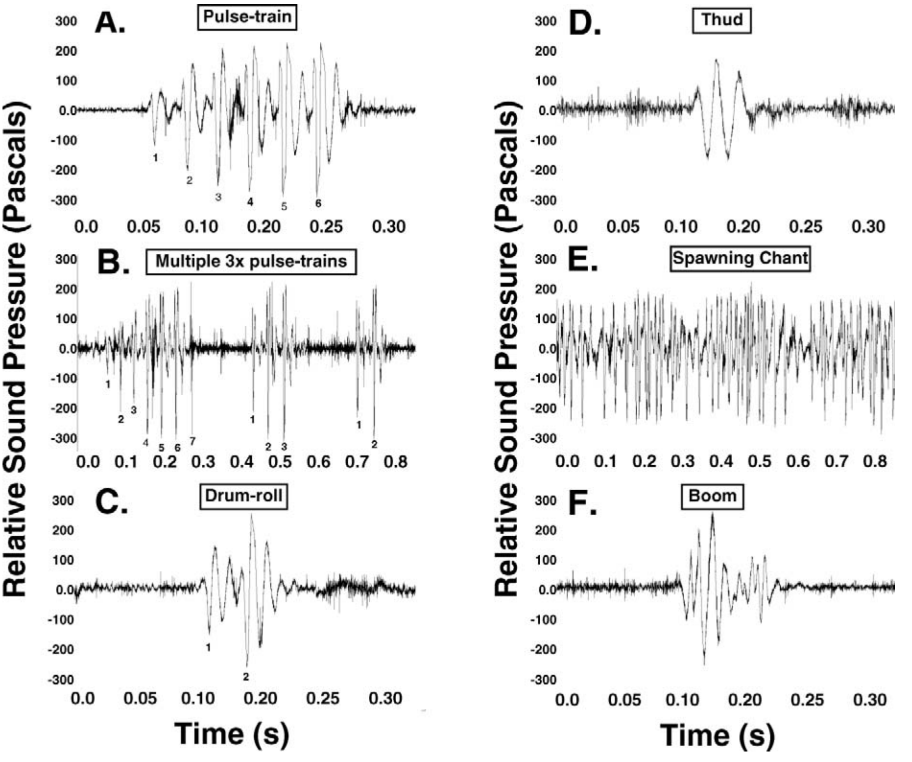

FIGURE 3.—Waveforms of sounds recorded from white seabass held in a net-pen in Catalina Harbor, California: **(a)** courtship sound with a single pulse train (pulses are numbered); **(b)** courtship sound with multiple (3×) pulse trains (pulses within each train are numbered); **(c)** drumroll (pulses are numbered); **(d)** thud; **(e)** spawning chant; and **(f)** hydrodynamic boom. Each pulse consists of three cycles. A 300-ms time scale is used in all panels except (b) and (e), which have an 800-ms scale.

SD = 21.7 ± 10.7 s; $n = 28$). Freshly spawned eggs were consistently abundant in dip-net samples after chants in excess of 7 s, yet eggs were not found in samples after abbreviated chants (1–5 s) occurred. Abbreviated chants terminated abruptly and were commonly recorded during pseudospawning behavior.

Hydrodynamic Sounds

White seabass sporadically produced short-duration sounds that aurally resembled a boom (Figures 2d, 3f). Booms occurred during accelerated swimming bursts or with a rapid expansion and contraction of the buccal cavity during yawning behavior. Boom sounds lacked harmonics and were very low in frequency, ranging from 13 to 450 Hz; the peak intensity of booms was near 60 Hz (Figure 4f; Table 1).

Discussion

The net-pen enclosure presented a seminatural setting in which to reliably observe white seabass behaviors and document the sounds associated with certain behaviors, including gamete release. The acoustical properties of the fish sounds were faithfully preserved because of the virtually free-field acoustic environment of the enclosure. There was no indication of the reverberation, cancellation, or augmentation expected of close-boundary processes (Cummings et al. 1975).

Courtship and Spawning Behavior

Although courtship and spawning behavior could have been altered by confinement, we observed similar courtship behaviors (circling and finning) in natural spawning aggregations around Santa Catalina Island on three occasions. Additionally, similar courtship behavior was documented in an underwater video taken by an expert freediver in June 1990 (T. Maas, Blue Water Freedivers, personal communication). The video depicted a pack of six male white seabass closely pursuing, spiraling, and aggressively nudging a darkly barred gravid female in a kelp bed off Santa Barbara Island. Within the net-pen, we typically observed spawning packs consisting of two to five males around each female, despite a sex ratio of approximately three

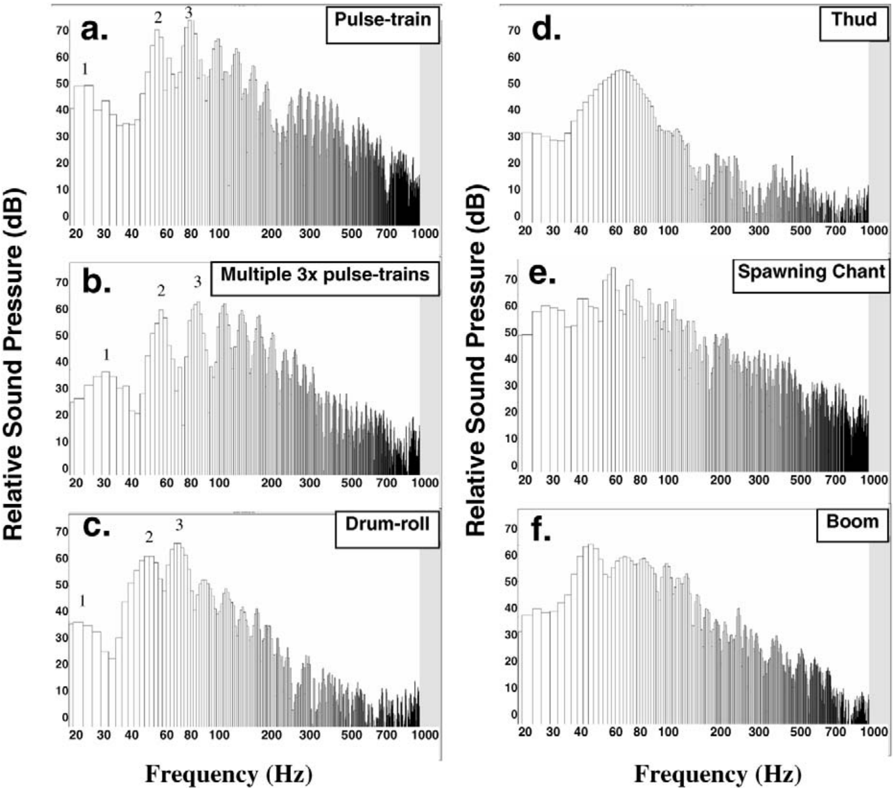

FIGURE 4.—Power spectrum displays (to 1 kHz) for sounds recorded from white seabass held in a net-pen in Catalina Harbor, California: **(a)** courtship sound with a single pulse train; **(b)** courtship sound with multiple (3×) pulse trains; **(c)** drumroll; **(d)** thud; **(e)** spawning chant; and **(f)** hydrodynamic boom. In panels (a)–(c), numeric labels on pulsed sounds indicate (1) fundamental frequency, (2) second harmonic frequency, and (3) peak frequency.

females : one male. Guest and Lasswell (1978) reported group spawning of three male red drum *Sciaenops ocellatus* with a single female within a tank.

Courting male red drum and weakfish *Cynoscion regalis* were observed repeatedly nudging the urogenital region of gravid females (Guest and Lasswell 1978; Connaughton and Taylor 1996), a behavior we observed during male white seabass courtship. Color changes were evident in male red drum (Guest and Lasswell 1978), whereas in white seabass only the gravid females exhibited a temporary banded coloration during courtship and spawning. Juvenile white seabass express a banded coloration that typically diminishes as fish mature. Dark bands were also exhibited by adult white seabass when they actively pursued and fed on live mackerel within the net-pen. Changes in coloration by courting and spawning sergeant majors *Abudefduf saxatilis* were experimentally duplicated by injecting males and females with small concentrations of adrenalin chloride, the pharmaceutical counterpart of epinephrine (Cummings 1968). The hormone injections suggested that shifts in skin pigmentation were influenced by excitation of the adrenal glands.

Sound Production

White seabass produced five basic sound types (Table 1): single and multiple pulse trains during courtship (Figure 2a), drumrolls and thuds during spawning (Figure 2b), and booms during burst swimming and yawning (Figure 2d). The regular pulse repetition rates and harmonic intervals of white seabass single (Figures 3a, 4a) and multiple (Figures 3b, 4b) pulse trains were consistent with sonic muscle contractions and the resonant response of the gas bladder (Sprague et al. 2000). The rate of sonic muscle contractions determines the interpulse interval, pulse repetition rate, and fundamental frequency of sounds (Tavolga 1964; Gilmore 2003). The physical characteristics of white seabass pulsed sounds were similar to the dual-pulse and staccato sounds described for male spotted seatrout *C. nebulosus* (family Sciaenidae;

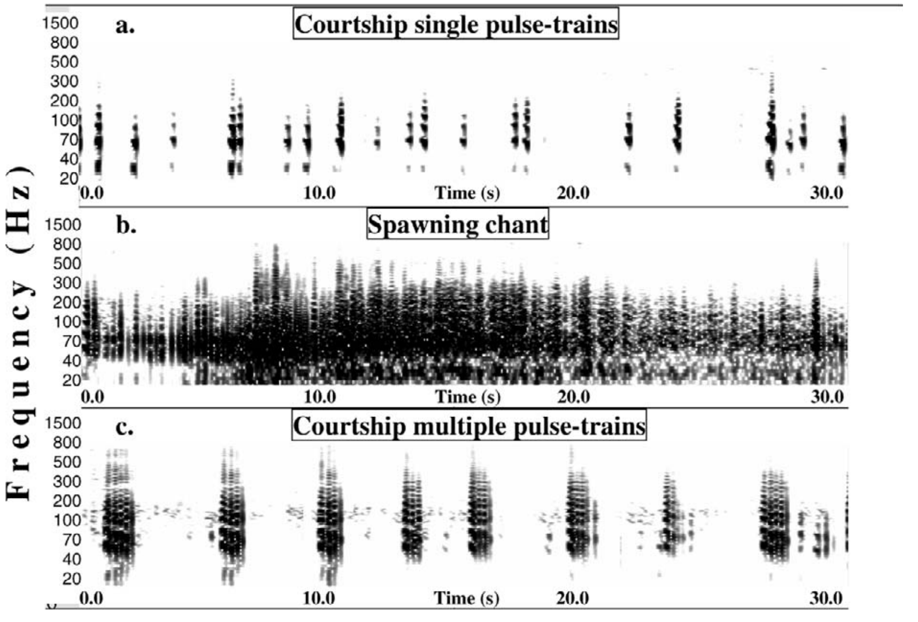

FIGURE 5.—Thirty-second sonograms of sounds produced by white seabass held in a net-pen in Catalina Harbor, California: **(a)** single pulse trains emitted during courtship; **(b)** spawning chant made during release of gametes; and **(c)** multiple pulse trains emitted during courtship.

Gilmore 2003), suggesting similar mechanisms. As in spotted seatrout, we too found sonic musculature that was present only in males upon dissection of 59 male and 48 female white seabass.

The peak and harmonic frequencies of drumrolls were similar to those of single and multiple pulse trains, indicating that they too are probably generated through sonic muscle contractions; however, harmonics were less pronounced in drumrolls (Figure 4c). The short duration and reduced number of pulses in drumrolls resembled the second or third train of multiple pulse trains. Thud sounds were short in duration and low in frequency, and they lacked harmonics. The characteristics of thud sounds indicated that they are generated by a mechanism independent from sonic musculature contractions or perhaps by a suboptimal contraction of the sonic muscle. Although we could not verify the mechanism used to produce thud sounds, it is possible that the succession of thuds is generated by rapid abdominal muscle contractions acting on the gas bladder as fish shudder to expel ova or spermatozoa. Lobel (1992) suggested that the spawning sounds of the butter hamlet *Hypoplectrus unicolor* may be a by-product of the rapid contraction of abdominal muscles during egg extrusion.

Spawning chants were likely generated by the production of drumroll and thud sounds from multiple individuals simultaneously emitting these sounds in rapid succession during a spawning event. The collective sounds produced during the release of gametes resulted in a characteristic galloping sound that was aurally distinguishable and generated identifiable sonogram (Figure 5b) and waveform (Figure 3e) displays. These signals provide an aural and sonographic index for reliably detecting spawning events.

Boom sounds 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). The spectral characteristics of booms were consistent with hydrodynamic pressures generated by rapid movement through the water (Tavolga 1964). Booms were detected in association with rapid swimming bursts and yawning behavior, indicating that the sounds were generated during burst swimming or by the rapid expansion of the buccal cavity. The margate *Haemulon album* generated very low-frequency sounds during swimming bursts and rapid expansions of the buccal cavity during feeding (Cummings et al. 1966). Very low-frequency sounds of short duration were also detected during coughing and yawning behaviors in captive yellowfin tuna *Thunnus albacares* and bluefin tuna *T. thynnus* (Allen and Demer 2003).

Distinctive physical appearances, behaviors, and sound production during courtship and spawning demonstrate that visual, tactile, and acoustic signals evidently are important in the reproductive success of white seabass. Single and multiple pulse trains may function to enhance male courtship displays or to elicit and maintain spawning aggregations. Courtship sounds, including abbreviated chants during pseudospawning, may function to communicate reproductive readiness during the period just before spawning. Mann and Lobel (1998) determined that the domino damselfish *Dascyllus albisella* also produced sounds very similar to spawning sounds during pseudospawning behavior. The production of distinct chants during white seabass spawning may function to enhance the synchronous release of ova and spermatozoa during broadcast spawning to maximize external fertilization rates, as suggested by Lobel (2002) for other fish species.

The production of identifiable sounds during actual spawning has been documented for several fish species, including butter hamlets (Lobel 1992), spotted boxfish *Ostracion meleagris* (Lobel 1996), and European freshwater goby *Padogobius martensii* (Lugli et al. 1995), yet such studies are rare. Pulsed sounds have been described during the courtship periods of red drum (Guest and Lasswell 1978) and weakfish (Connaughton and Taylor 1996) and in association with freshly collected sciaenid eggs in the field (Mok and Gilmore 1983; Luczkovich et al. 1999). However, here we provide the first report of identifiable sounds during the actual release of gametes within the family Sciaenidae. Given the importance of sound to this large family, it seems unlikely that white seabass are the only sciaenids to produce such characteristic spawning sounds. We have demonstrated that valuable information on fish reproduction and associated sound production can be obtained within a net-pen system and that passive hydroacoustic techniques can be used to determine the periodicity and possibly the locations of white seabass spawning activity.

Acknowledgments

This research was made possible through support from Hubbs–SeaWorld Research Institute, Catalina Seabass Fund, and California State University–Fullerton. The Catalina Marine Science Center (University of Southern California) and Hubbs–SeaWorld Research Institute provided facilities and technical support. Two Harbor Enterprises assisted with supplies and services. We thank A. E. Bowles, K. A. Dickson, and M. H. Horn for reviewing the manuscript, P. E. Gardiner, K. C. Lafferty, G. M. Stutzer, and E. Forsman for assistance with the project, and T. Maas and B. Erisman for providing underwater video. Special thanks go to K. A. Dickson for guidance and support and to W. C. Cummings for his personal commitment, technical guidance, and editorial comments. The manuscript considerably profited from comments of three unidentified reviewers.

References

Albers, V. M. 1965. Underwater acoustics II handbook. Pennsylvania State University Press, University Park.

Allen, S., and D. A. Demer. 2003. Detection and characterization of yellowfin and bluefin tuna using passive-acoustical techniques. Fisheries Research 63:393–403.

CDFG (California Department of Fish and Game). 2002. White seabass fishery management plan (WSFMP). California Department of Fish and Game, Sacramento.

Connaughton, M., and M. H. Taylor. 1994. Seasonal cycles in the sonic muscles of the weakfish, *Cynoscion regalis*. U.S. National Marine Fisheries Service Fishery Bulletin 92:697–703.

Connaughton, M. A., and M. H. Taylor. 1995. Seasonal and daily cycles in sound production associated with spawning in the weakfish, *Cynoscion regalis*. Environmental Biology of Fishes 42:233–240.

Connaughton, M. A., and M. H. Taylor. 1996. Drumming, courtship, and spawning behavior in captive weakfish *Cynoscion regalis*. Copeia 1996:195–199.

Cummings, W. C. 1968. Reproductive habits of the sergeant major, *Abudefduf saxatilis* (Pisces, Pomacentridae), with comparative notes on four other damselfishes in the Bahama Islands. Doctoral dissertation. University of Miami, Florida.

Cummings, W. C., B. D. Brahy, and J. Y. Spires. 1966. Sound production, schooling, and feeding habits of the margate, *Haemulon album* Cuvier, off North Bimini, Bahamas. Bulletin of Marine Science 16:626–640.

Cummings, W. C., J. M. Holzmann, and P. O. Thompson. 1975. Underwater sound pressure minima in bioacoustic test tanks. Final report. Naval Undersea Center, Technical Report NUC-TP-450, San Diego, California.

Fish, J. F., and W. C. Cummings. 1972. A 50-dB increase in sustained ambient noise from fish *Cynoscion xanthulus*. Journal of the Acoustical Society of America 52:1262–1270.

Gilmore, R. G., Jr. 2003. Sound production and communication in the spotted seatrout. Pages 177–195 *in* S. A. Bortone, editor. Biology of the spotted seatrout. CRC Press, Boca Raton, Florida.

Guest, W. C., and J. L. Lasswell. 1978. Notes on courtship behavior and sound production of red drum. Copeia 1978:337–338.

Hawkins, A. D., and M. C. Amorim. 2000. Spawning sounds of the male haddock, *Melanogrammus aeglefinus*. Environmental Biology of Fishes 59:29–41.

Hawkins, A. D., and A. A. Myrberg, Jr. 1983. Hearing and sound communication under water. Pages 348–381 *in* B. Lewis, editor. Bioacoustics: a comparative approach. Academic Press, London.

Lobel, P. S. 1992. Sounds produced by spawning fishes. Environmental Biology of Fishes 33:351–358.

Lobel, P. S. 1996. Spawning sound of the trunkfish, *Ostracion* *meleagris* (Ostraciidae). Biological Bulletin 191:308–309.

Lobel, P. S. 2002. Diversity of fish spawning sounds and the application of passive acoustic monitoring. Bioacoustics 12:287–288.

Luczkovich, J. J., M. W. Sprague, S. E. Johnson, and R. C. Pullinger. 1999. Delimiting spawning areas of weakfish, *Cynoscion regalis* (family Sciaenidae), in Pamlico Sound, North Carolina, using passive hydroacoustic surveys. Bioacoustics 10:143–160.

Lugli, M., G. Pavan, P. Torricelli, and L. Bobbio. 1995. Spawning vocalizations in male freshwater gobiids (Pisces, Gobiidae). Environmental Biology of Fishes 43:219–231.

Mann, D. A., and P. S. Lobel. 1998. Acoustic behavior of the damselfish *Dascyllus albisella*: behavioral and geographic variation. Environmental Biology of Fishes 51:421–428.

Mok, H., and R. G. Gilmore. 1983. Analysis of sound production in estuarine aggregations of *Pogonias cromis*, *Bairdiella chrysoura*, and *Cynoscion nebulosus* (Sciaenidae). Bulletin of the Institute of Zoology, Academia Sinica 22(2):157–186.

Moser, H. G., D. A. Ambrose, M. S. Busby, J. L. Butler, E. M. Sandknop, B. Y. Sumida, and E. G. Stevens. 1983. Description of the early stages of white seabass, *Atractoscion nobilis*, with notes on distribution. California Cooperative Oceanic Fisheries Investigations Reports 24:182–193.

Smith, H. M. 1905. The drumming of the drum-fishes. Science 22:376–378.

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 of the Elisha Mitchell Scientific Society 116:124–145.

Tavolga, W. N. 1964. Sonic characteristics and mechanisms in marine fishes. Pages 195–209 *in* W. N. Tavolga, editor. Marine bioacoustics. Pergamon Press, New York.

Thomas, J. C. 1968. Management of the white seabass *Cynoscion nobilis* in California waters. California Department of Fish and Game, Fish Bulletin 142.

Tower, R. W. 1908. The production of sound in the drumfishes, the sea-robin and the toadfish. Annals of the New York Academy of Sciences 18:149–180.

Urick, R. J. 1983. Principles of underwater sound, 3rd edition. Peninsula Publishing, Los Altos, California.

Vojkovich, M., and R. Reed. 1983. White seabass *Atractoscion nobilis* in California–Mexican waters: status of the fishery. California Cooperative Oceanic Fisheries Investigations Reports 24:79–83.