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The utility of a long-term acoustic recording system for detecting white seabass *Atractoscion nobilis* spawning sounds

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This study reports the use of a long-term acoustic recording system (LARS) to remotely monitor white seabass *Atractoscion nobilis* spawning sounds at three sites along the southern California coastline, adjacent to Camp Pendleton. On the basis of previous studies of *A. nobilis* sound production relative to periods of known spawning activity, LARS were set to continuously record ambient sounds for a 2 h period around sunset from April to June 2009. Acoustic analyses identified *A. nobilis* courtship sounds on 89, 28 and 45% of the days at the three locations, respectively. From 474 h of acoustic data, spawning-related sounds (chants) were detected on 19 occasions in 2009 with an additional 11 spawning chants recorded during a 2007 validation period. Most spawning chants occurred within 30 min of sunset during the months of May and June at a mean ± s.d. surface temperature of 18·2 ± 1·2° C. Consecutive daily spawning activity was not apparent at any sites in 2009. *Atractoscion nobilis* spawning chants were recorded at all three sites, suggesting that shallow rocky reefs which support kelp forests provide suitable *A. nobilis* spawning habitat. Results confirm the utility of passive acoustic recorders for identifying *A. nobilis* spawning periods and locations.
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Key words: fish reproduction; reproductive activity; Sciaenidae; sound production

INTRODUCTION

Spatial and temporal information on fish spawning activity is pertinent to effective nearshore fishery management strategies (Mok & Gilmore, 1983; Semmens *et al*., 2010). Traditional methods for determining the spawning locations and reproductive readiness of marine fish populations typically entail the terminal sampling of mature individuals to assess the gonado-somatic index (I_G) and oocyte maturation (DeMartini & Fountain, 1981; Lowerre-Barbieri *et al*., 1996; Murua *et al*., 2003). Fish courtship and spawning activity can be documented through direct observation (Adreani *et al*., 2004), although divers are limited by water clarity and nocturnal spawning. Spawning seasons and areas have also been evaluated with comprehensive ichthyoplankton surveys (Parrish *et al*., 1981; Gruber *et al*., 1982); however, these methods are often costly, labour intensive and spatially variable (Carreon-Martinez *et al*., 2010). Because numerous fish species produce sounds

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that have been associated with reproduction (Mok & Gilmore, 1983; Lobel, 1992; Gilmore, 2003), passive acoustic recording systems can be utilized to non-invasively identify fish spawning activity and locations (Luczkovich *et al*., 1999, 2008; Mann *et al*., 2009).

A variety of bioacoustic techniques have been developed to monitor and interpret the sounds generated by marine species (Mellinger *et al*., 2007). Recent advancements in autonomous acoustic recording systems and signal recognition software now offer the ability to remotely monitor multiple sites over extended time periods at a low cost (Wiggins, 2003; Lammers *et al*., 2008; Mann *et al*., 2009). To date, most of the applications for autonomous acoustic recorders have focused primarily on the study of marine mammals (Wiggins *et al*., 2005; Mellinger *et al*., 2007; Van Parijs *et al*., 2009), although similar tools have also been employed to monitor sound-producing fishes (McCauley & Cato 2000; Van Parijs *et al*., 2009; Mann *et al*., 2010). Long-term acoustic recording systems (LARS) have been utilized to evaluate the spawning periods and sites of several commercially valuable fishes along the Atlantic Ocean and Gulf coasts (Locascio & Mann, 2008; Mann *et al*., 2009; Mann *et al*., 2010), but this application remains underutilized in the Pacific Ocean.

The white seabass *Atractoscion nobilis* (Ayres 1860) is a Pacific member of the family Sciaenidae that is well known for its capacity to produce low-frequency sound (Fish, 1948). Recent work has identified the distinct series of drum-roll and thud sounds that male *A. nobilis* produce exclusively during broadcast spawning events (Aalbers & Drawbridge, 2008). Collectively referred to as spawning chants, this rapid succession of discernible sounds during the release of gametes can readily be differentiated from other courtship sounds. The characterization of identifiable sound-production patterns surrounding periods of known *A. nobilis* spawning activity provides a solid framework for applied field investigations (Aalbers, 2008).

Fishery-related data suggest that *A. nobilis* aggregate to spawn along the coast and inshore islands of California and Baja California during the spring and summer months, although specific information on the locations and conditions that attract spawning aggregations are unavailable (Thomas, 1968; California Department of Fish and Game, 2002). *Atractoscion nobilis* spawning aggregations were traditionally targeted by commercial and recreational fisheries, with the majority of landings made from April to September (Skogsberg, 1939; Thomas, 1968; Allen *et al*., 2007). California landings have fluctuated dramatically over the past century, declining sharply on at least two occasions following periods of apparent overexploitation (Skogsberg, 1939; Vojkovich & Reed, 1983). Since 1997, *A. nobilis* landings and catch per unit effort (CPUE) values have increased following a series of important fishery regulations, the most significant of which went into effect in 1994 when coastal gillnets were restricted within 4·83 km (3 miles) of the California coastline (Allen *et al*., 2007). Additionally, recreational harvest is limited to one fish (<71 cm total length, L_T) angler^{-1} day^{-1} and commercial harvest is prohibited during a portion of the spawning season. Regardless of the safeguards in place to protect spawning aggregations under the current fishery management plan for *A. nobilis*, future decisions remain compromised by insufficient information on key reproductive characteristics such as geographic spawning areas, spawning frequency and larval recruitment indices (California Department of Fish and Game, 2002).

The primary objectives of this work were to (1) validate the utility of a LARS in the detection of wild *A. nobilis* sounds, (2) establish an index of occurrence at three

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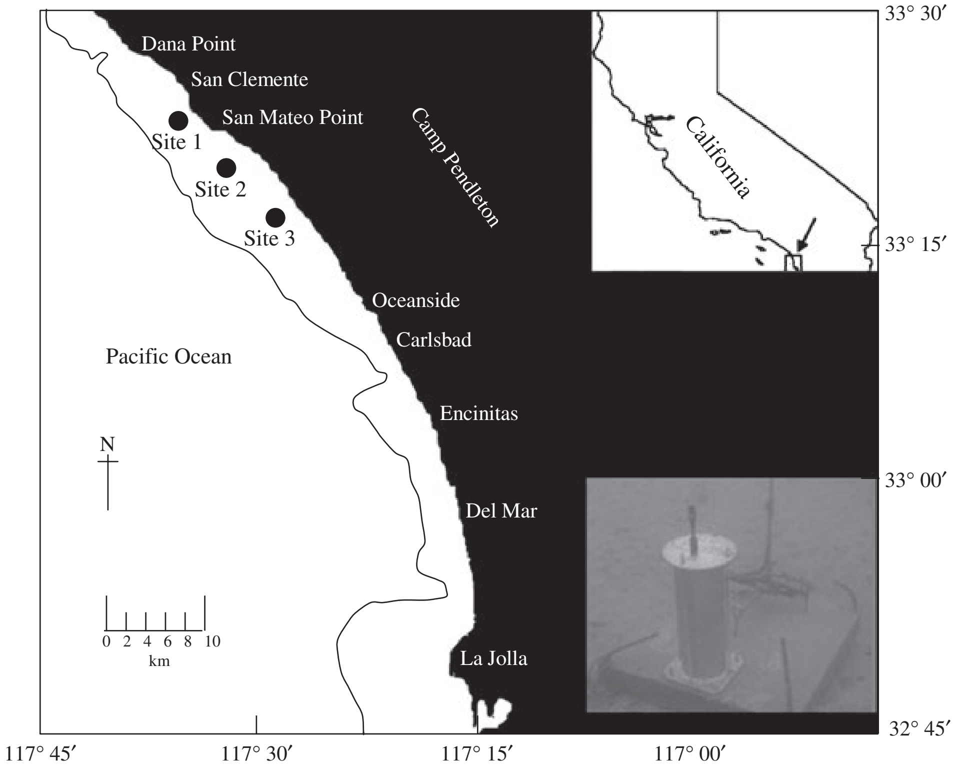

FIG. 1. Site map inset of the southern California coastline and image of a moored long-term acoustic recording system. Bathymetry line represents 100-m depth contour along the edge of the continental shelf.

southern California sites based on the presence of courtship sounds and (3) spectrally isolate and characterize wild *A. nobilis* spawning sounds.

MATERIALS AND METHODS

RESEARCH LOCATION

Long-term acoustic recorders (Loggerhead Instruments; www.loggerheadinstruments.com) were securely affixed to 75 kg concrete moorings at three locations (site 1, 33° 23′ N; 117° 37′ W; site 2, 33° 20′ N; 117° 34′ W; site 3, 33° 17′ N; 117° 29′ W) between Oceanside and San Mateo Point, California (Fig. 1). Sites were selected based on the frequent detection of *A. nobilis* sounds during an initial passive acoustic survey conducted from March to June 2007, using techniques similar to those described by Mok & Gilmore (1983). All sites were in depths of 15–18 m, proximal to giant kelp *Macrocystis pyrifera* forests along low-relief rocky reef surrounded by soft sediment.

Site co-ordinates were marked on the vessel GPS and subsurface floats were spliced to polypropylene mooring lines to assist in relocating LARS. Duplicate TidBit v2 temperature loggers (Onset Computer Corporation; www.onsetcomp.com) were affixed to the mooring line at each site to record hourly water temperatures both near the surface (<3 m) and 1 m above the seafloor.

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LONG-TERM ACOUSTIC RECORDINGS

LARS were serviced by divers every 14–21 days to replace batteries and to download acoustic data. Sounds were received through an HTI 96 min hydrophone (bandwidth: 0·002–37 kHz); sensitivity: −164 dB re 1 μPa; High-Tech Inc; www.hightechincusa.com) connected to a Dell Axim X50 Pocket PC with an 8 GB compact flash card contained in a sealed aluminum housing. Loggerhead v1.48 software was programmed to record daily audio files continuously at a constant level with a sampling rate of 8820 Hz for 120 min beginning 1 h prior to sunset. This recording schedule was based on periods of peak *A. nobilis* spawning and sound production (Aalbers, 2008). Consecutive daily audio recordings were collected at all sites from 4 April to 22 June 2009 ($n = 231$). Additional audio files from site 3 were analysed from 18 to 23 June 2007, when gravid females were collected in conjunction with recorded spawning chants to validate the acoustic techniques employed in this study.

ACOUSTIC ANALYSES

A custom 30 band graphic equalization (EQ) filter was developed using Adobe Audition 3.0 software (Adobe Systems Incorporated; www.adobe.com) to enhance the signal-to-noise ratio within the fundamental and resonant frequency bands of *A. nobilis* sounds (Aalbers & Drawbridge, 2008). The EQ filtration amplified signals up to 16 dB within the 50–200 Hz bandwidth and reduced ambient noise within frequency bands exceeding 250 Hz. Filtered time series data were displayed on a 240 s scale to evaluate the presence or absence of *A. nobilis* sounds on all 2 h recordings. Daily recordings were evaluated for presence or absence, rate and type of *A. nobilis* sounds using a ranking system modified from Connaughton & Taylor (1995). Recordings were classified as absent when *A. nobilis* sounds were not visible in sonogram or waveform displays (240 s scale) over the 2 h recording period. Otherwise, the maximum sound production rate for each recording was ranked with a value of 1 when <5 sounds were detected min^{-1}, 2 with 6 to 15 sounds min^{-1} and 3 with >15 sounds min^{-1}. Because individual males commonly repeated courtship sounds (*i.e.* pulse trains and multiple pulse trains) at 4 s intervals, maximum score values represented periods when multiple individuals were producing sound. The intensity of *A. nobilis* signals were also ranked as 1, 2 or 3 based on the maximum sound pressure level received over the 120 min recording. Rate and relative intensity rankings were summarized over the entire study period for each site.

Waveform and sonogram displays that visually resembled spawning chants were verified by the analyst while listening to clips through amplified subwoofers (Logitech Z-2300 THX; www.logitech.com) and stereo headphones (Sony MDR-XB500; www.sony.com). Spawning chants were defined as a rapid succession of short-duration drum-roll and thud sounds with a cumulative duration >5 s (Aalbers & Drawbridge, 2008). Identifiable spawning chants were spectrally analysed to determine the dominant frequency, duration and number of individual calls using SpectraPlus v2.32 software (Pioneer Hill; www.spectraplus.com). Sonograms were viewed in the post-processing mode on a 120 s time-frequency display with a 50–250 Hz logarithmic scale. Acoustic data were transformed with a 4096 point fast fourier transform (FFT) using a Hanning window to reduce spectral spreading.

VALIDATION

Adult *A. nobilis* were opportunistically collected on hook and line or on speargun in 2007 to verify that *A. nobilis* in spawning condition were present when spawning chants were acoustically detected on autonomous recorders. The I_G was calculated for all sampled *A. nobilis* to determine the relationship between *A. nobilis* wet mass and gonad mass. Because male *A. nobilis* display continuous reproductive readiness and have the capacity to contribute to numerous spawns throughout the spawning season (Gruenthal & Drawbridge, 2012), the assessment of mature female ovaries was more appropriate for validating the likelihood of spawning activity at study sites. Only mature females ($n = 5$) collected from 18 to 23 June 2007 were selected for histological analysis because sampling during this 6 day period coincided with the detection of acoustic spawning chants ($n = 11$) at site 3. Ovary sub-samples were placed into labelled cassettes and preserved in 10% neutral buffered formalin for histological examination under a dissecting microscope (Olympus

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Bx60; www.olympusamerica.com) at ×10 magnification. Reproductive stages were determined using the criteria described by Brown-Peterson *et al.* (1988). Catch composition data from a small-mesh gillnet survey conducted at site 3 during the validation period were used to verify the presence of other sound-producing fish species (Hubbs-SeaWorld Research Institute; www.hswri.org, unpubl. data).

RESULTS

Of the 231 acoustic recordings analysed over an 84 day period in 2009, *A. nobilis* sounds were detected at sites 1, 2 and 3 on 89, 28 and 45% of the days, respectively. When present, sound production rate was highest at site 1, with 84% of recordings scoring a maximum rate value, compared with 35% at site 2 and 32% at site 3. *Atractoscion nobilis* presence was determined by the detection of single and multiple pulse trains (courtship sounds) that were commonly repeated at 4 s intervals (Fig. 2).

A total of 19 spawning chants (Figs 3 and 4) were identified in 2009 with an additional 11 spawning chants documented at site 3 during the validation period (18 to

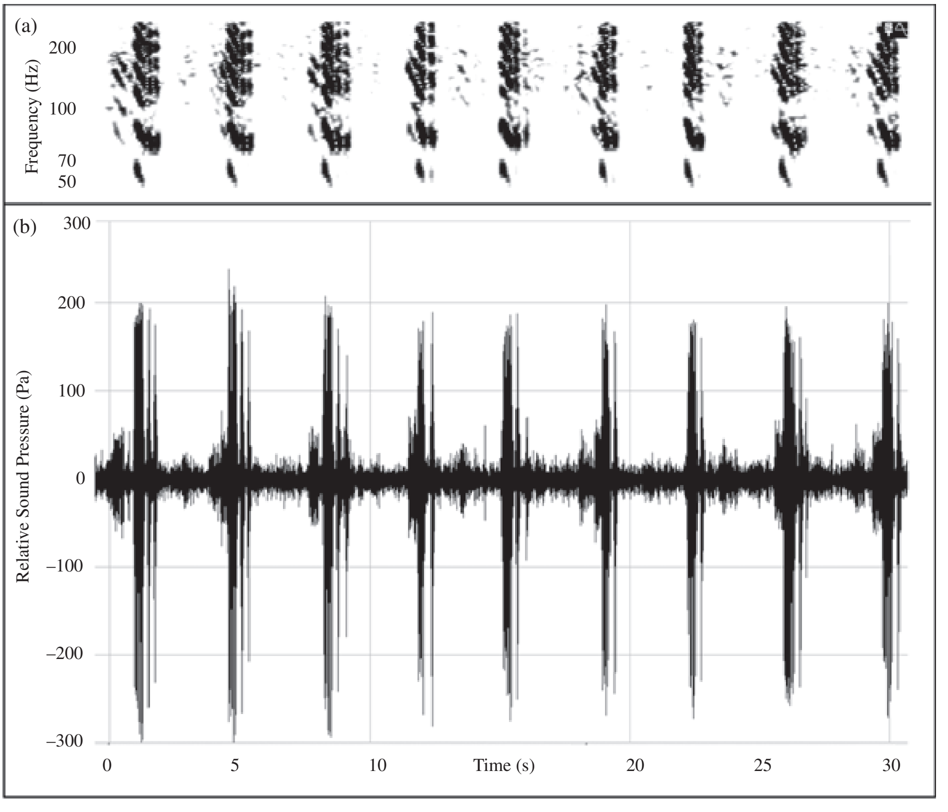

FIG. 2. (a) Thirty s sonogram and (b) waveform displays of courtship sounds (multiple pulse trains) produced repetitively at *c*. 4 s intervals by an individual male *Atractoscion nobilis*. Sounds were received on 26 April 2009 with a long-term acoustic recording system (LARS; site 1) near San Mateo Point, California. A 30 band low-pass graphic equalization (EQ) filter was applied to reduce ambient noise at frequencies >250 Hz.

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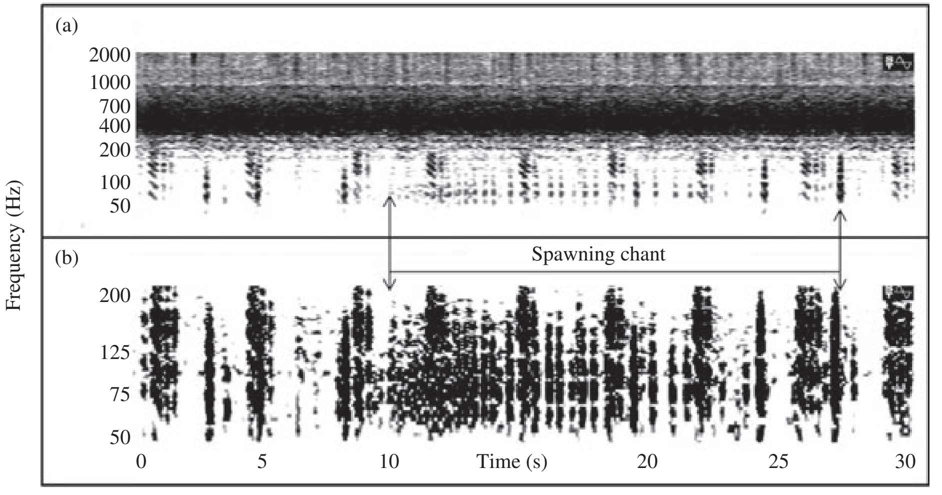

Fig. 3. Sonograms of *Atractoscion nobilis* spawning chant (from 10 to 27 s on a 30 s time scale) recorded at site 1 near San Mateo Point, California, on 1 May 2009. Spectral displays from (a) raw audio recording on a frequency (Hz) scale of 50–2300 and (b) after rendering a 30 band graphic equalization (EQ) filter to increase the signal-to-noise ratio on a frequency (Hz) scale of 50–250 Hz. Note the consistent high sound pressure level in the 400–700 Hz bandwidth from chorusing fishes in (a).

23 June 2007). In 2009, 12 spawning chants were detected at site 1 on 10 separate dates and seven spawning chants occurred successively on 19 June at site 2, while no spawning chants were detected at site 3. Although spawning chants were recorded on consecutive days during the 2007 validation period at site 3, consecutive daily spawns were not acoustically detected at any sites in 2009. The dominant frequency of spawning sounds ranged from 62 to 109 Hz (mean = 90 Hz; $n = 30$). Spawning chant duration ranged from 5 to 51 s and consisted of 13–126 individual sounds.

Spawning chants were recorded between 24 April and 25 June 2009 with 90% of the spawning activity observed in May and June. Ninety-five per cent of the documented spawning chants occurred within a 30 min period, either preceding or following sunset. There was no evidence of lunar or tidal spawning periodicity. Spawning sounds were recorded at surface temperatures ranging from 15·4 to 19·9° C and bottom temperatures from 12·1 to 16·8° C (Fig. 5).

Histological examination of gonad preparations from all female *A. nobilis* (107–142 cm L_T; $n = 5$) collected from site 3 during the 2007 validation period revealed mature, ripe and running ripe ovaries (572–2106 g) containing oocytes in the yolk globular, yolk granular and hydration stages (Fig. 6).

DISCUSSION

This study verified the utility of long-term acoustic recorders to remotely detect and characterize *A. nobilis* courtship and spawning sounds along the coast of southern California. Findings from this work confirm that passive acoustic techniques can be used to non-invasively identify *A. nobilis* spawning areas and may be used to complement traditional reproductive sampling methods.

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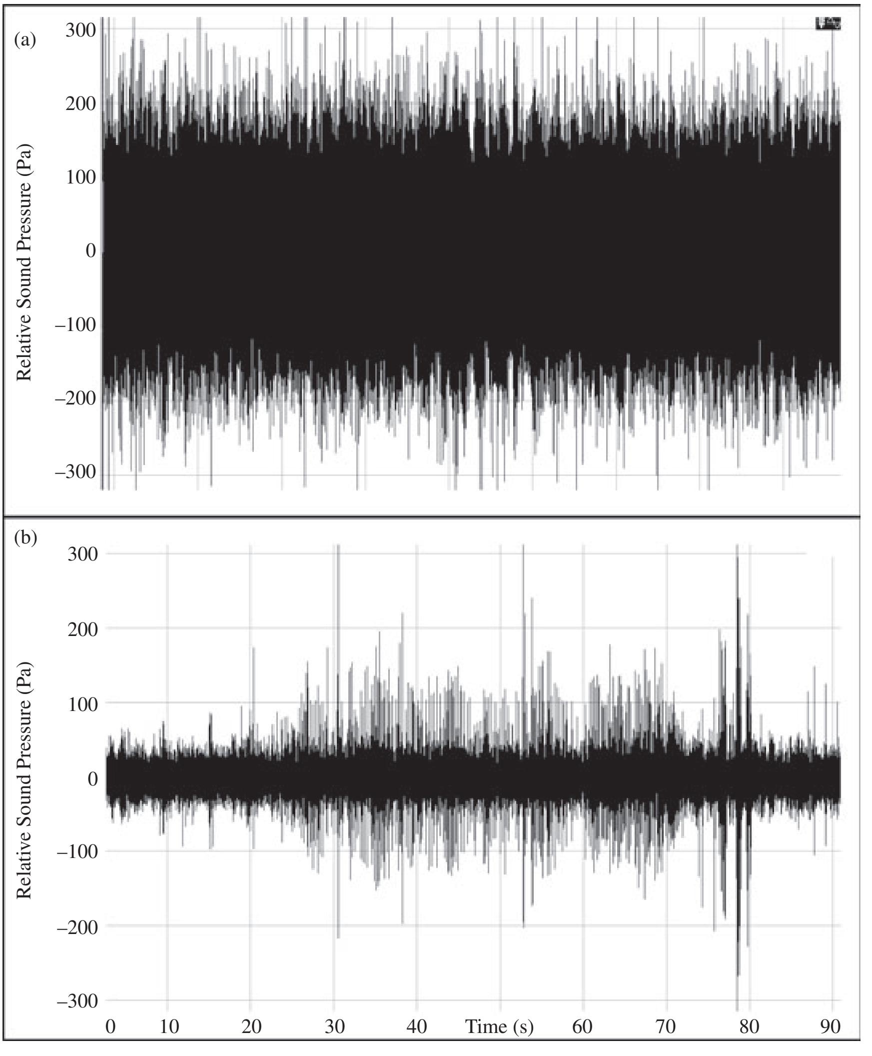

FIG. 4. Waveforms of *Atractoscion nobilis* spawning chant (from 22 to 80 s on a 90 s time scale) recorded at site 1 near San Mateo Point, California, on 28 May 2009. Time-series data from (a) raw audio recording and (b) after rendering a 30 band graphic equalization (EQ) filter to increase the signal-to-noise ratio at frequencies <250 Hz. Note that *A. nobilis* spawning chant is masked behind high level of ambient noise in (a).

The acoustic characteristics (*i.e.* frequency, duration and interpulse interval) of courtship and spawning sounds recorded in this study were consistent with the signals identified surrounding verified spawning events for captive *A. nobilis* (Aalbers & Drawbridge, 2008). Spawning chant durations ranged from 5 to 58 s on LARS recordings, with dominant frequency ranging from 62 to 109 Hz (Fig. 3). Despite differences in recording equipment and techniques, spawning chants recorded in captive *A. nobilis* ranged from 7 to 55 s in duration with dominant frequency ranging from 59 to 116 Hz. Variability in the dominant frequency of spawning chants documented in both wild and captive fishes may reflect differences in fish size or water temperatures,

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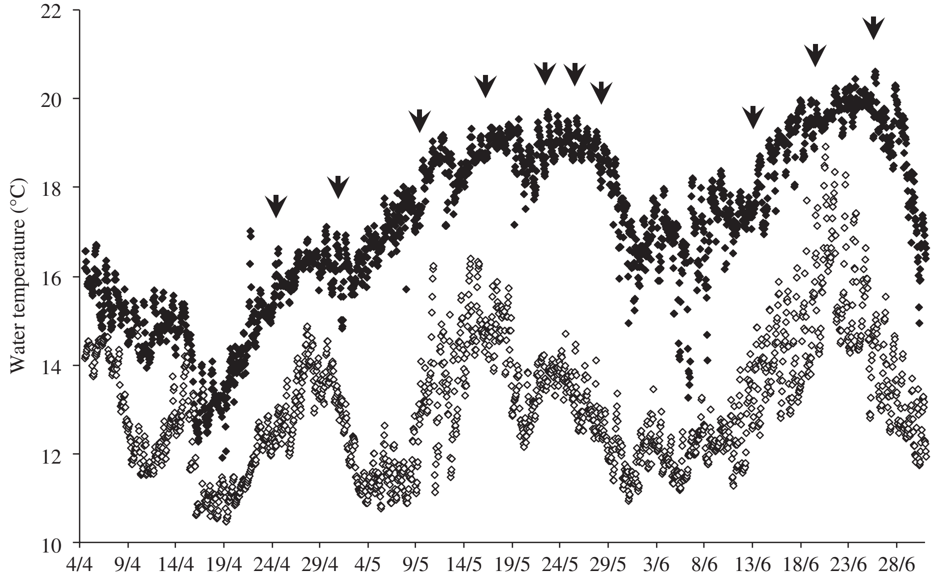

FIG. 5. Surface (◆) and bottom temperature (◇) profiles logged hourly at site 1 near San Mateo Point, California, from 4 April to 30 June 2009. ⮟, instances when one or more *Atractoscion nobilis* spawning chants were detected on long-term acoustic recordings.

as decreases in the dominant frequency of weakfish *Cynoscion regalis* (Bloch & Schneider 1801) sounds have been correlated with reduced ambient temperatures and increased fish size (Connaughton *et al.*, 2002).

Although seasonal shifts in water temperature may have influenced sound production rate, frequency and sound pressure level (Connaughton *et al.*, 2002; Mann & Grothues, 2009), water temperature records were similar for the three proximal sites in 2009. It is possible that the higher frequency of occurrence and increased detection of spawning chants at site 1 could have been influenced by subtle differences in habitat structure or oceanic conditions (*i.e.* surface currents, productivity and kelp canopy density). Seasonal increases in water temperature appeared to influence the occurrence of spawning chants (Fig. 5); however, additional longer-term data analyses are required to substantiate these findings. Similar to observations of captive *A. nobilis*, fish presence or spawning activity was not found to be influenced by lunar or tidal cycles in this study (Aalbers, 2008).

Atractoscion nobilis spawning chants were primarily detected within a 30 min period either preceding or following sunset during the months of May and June at surface temperatures ranging from 15·4 to 19·9° C (Fig. 5); results were consistent with spawning periods and conditions for captive fish (Aalbers, 2008). On average, spawning chants were detected much less frequently on remote acoustic recordings than during studies of captive-spawning *A. nobilis* (Aalbers, 2008), a discrepancy that may be explained by the transient nature of spawning aggregations and movements to areas outside of the LARS detection range. The detection of spawning chants at all three sites over the course of the study suggests that interfaces between sand and shallow rocky reef which support kelp forests are suitable habitat for spawning. These findings support previous fishery-related data (Thomas, 1968) as well as field

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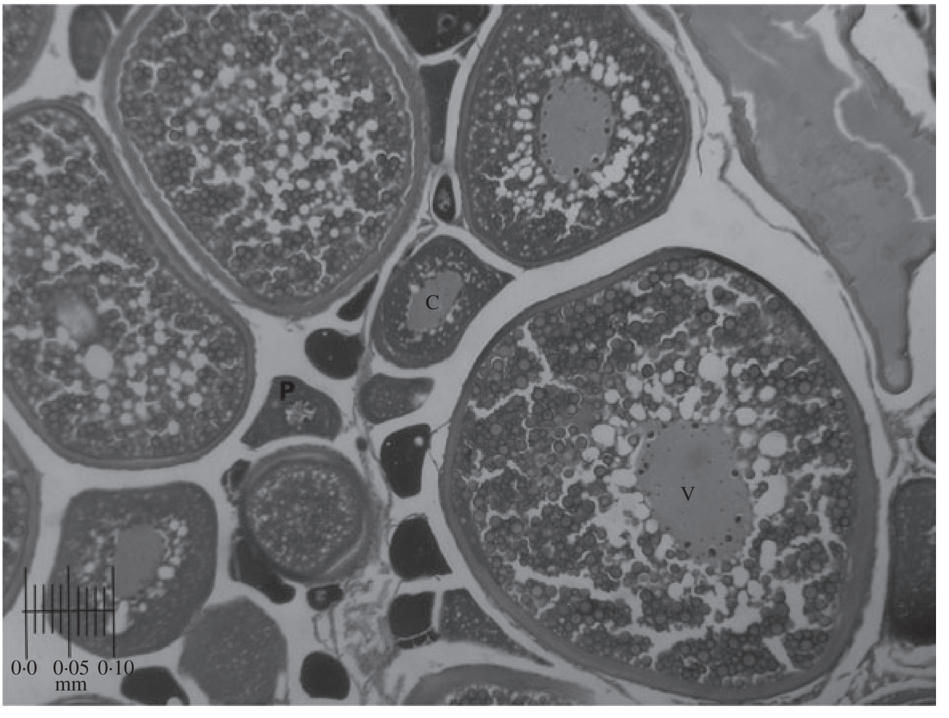

FIG. 6. Histological section of ovarian tissue sampled from a gravid *Atractoscion nobilis* collected at site 3 on 20 June 2007, exhibiting oocytes at various stages of development: vitellogenic oocyte (V), cortical alveoli oocyte (C) and primary oocyte (P). 0·1 mm scale bar at ×10 magnification.

observations of courtship behaviour within southern California kelp forests (Aalbers & Drawbridge, 2008).

AMBIENT SOUNDS

Despite high levels of ambient noise, it was possible to reliably distinguish *A. nobilis* courtship and spawning sounds from other biological and anthropogenic sounds (*i.e.* vessel traffic) on filtered sonogram and waveform displays (Figs 3 and 4). Because information on sound-producing fishes of the Pacific Ocean is limited and acoustic properties have not been characterized for most species, it was not possible to positively identify all biological sound sources. The occurrence of nine sound-producing fish species from three families [Sciaenidae; yellowfin croaker *Umbrina roncador* Jordan & Gilbert 1882, white croaker *Genyonemus lineatus* (Ayres 1855), queenfish *Seriphus politus* Ayres 1860, spotfin croaker *Roncador stearnsii* (Steindachner 1876), black croaker *Cheilotrema saturnum* (Girard 1858), *A. nobilis*: Haemulidae; sargo *Anisotremus davidsoni* (Steindachner 1876), salema *Xenistius californiensis* (Steindachner 1876): Batrachoididae; plainfin midshipman *Porichthys notatus* Girard 1854], however, was verified at site 3 from concurrent gillnet collections in June 2007 (Hubbs-SeaWorld Research Institute, unpubl. data).

It was apparent that fish choruses from other sciaenid species and *P. notatus* peaked after dusk in May and June (Fish & Cummings, 1972; Mok & Gilmore,

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1983; Locascio & Mann, 2008) resulting in reduced signal-to-noise ratios and a reduced capacity for aural detection of *A. nobilis* sounds on raw audio files. Because the dominant frequency of *A. nobilis* sounds (<250 Hz) was lower than the acoustic energy generated by chorusing sciaenids (400–700 Hz) (Fish, 1948; Fish & Cummings, 1972), rectification of raw audio files using a custom EQ filter considerably improved signal-to-noise ratios within the bandwidth of 50–250 Hz (Figs 3 and 4). Resonant energy from *P. notatus* chorusing, however, was not completely reduced because their fundamental frequency ranged from 90 to 150 Hz depending on the water temperature (Brantley & Bass, 1994).

MANAGEMENT

Information on the environmental conditions and habitats that support spawning aggregations is pertinent to the sustainable management of coastal fisheries, while spatial and temporal data can assist in planning networks of marine protected areas (Holt, 2008; Luczkovich *et al*., 2008). Because terminal biological sampling does not align well with the goals of most marine reserve networks, non-invasive bioacoustic techniques may be a tool to monitor the effectiveness of protected areas as sources of larvae for surrounding areas (Luczkovich *et al*., 2008). Although conventional gonad sampling is necessary to assess certain aspects of reproductive potential (*i.e.* size at maturity, fecundity and sex ratio), passive acoustic monitoring can complement traditional methods to evaluate spawning parameters (*i.e.* spawning areas, frequency and periodicity) of sound-producing fishes.

FUTURE WORK

While future interannual analyses may better elucidate the environmental factors responsible for the formation and site fidelity of *A. nobilis* spawning aggregations, this initial study provides direct evidence that passive acoustic techniques can be employed to determine spawning frequency and periodicity in the wild. Further, the 30 spawning chants identified in this study provide a source of input signals (*i.e.* training sets) that may be used to establish appropriate detection thresholds and optimize parameters towards the development of automated detection (Munger *et al*., 2005). As the last broad characterization of Pacific Ocean sonic fishes was conducted over 60 years ago (Fish, 1948), considerable work is still necessary to identify the acoustic properties and patterns of other sound-producing fishes encountered within the Californian coastal waters.

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References

Aalbers, S. A. (2008). Seasonal, diel, and lunar spawning periodicities and associated sound production in the white seabass *Atractoscion nobilis*. *Fishery Bulletin* **106,** 143–151.

Aalbers, S. A. & Drawbridge, M. A. (2008). Spawning behavior and associated sound production of the white seabass *Atractoscion nobilis*. *Transactions of the American Fisheries Society* **137,** 542–550. doi: 10.1577/T04-058.1

Adreani, M. S., Erisman, B. E. & Warner, R. R. (2004). Courtship and spawning behavior in the California sheephead *Semicossyphus pulcher*. *Environmental Biology of Fishes* **71,** 13–19.

Allen, L. G., Pondella, D. J. & Shane, M. A. (2007). Fisheries independent assessment of a returning fishery: abundance of juvenile white seabass *Atractoscion nobilis* in the shallow nearshore waters of the Southern California Bight, 1995–2005. *Fisheries Research* **88,** 24–32. doi: 10.1016/j.fishres.2007.07.012

Brantley, R. K. & Bass, A. H. (1994). Alternative male spawning tactics and acoustic signals in the plainfin midshipman fish *Porichthys notatus* Girard. *Ethology* **96,** 213–232.

Brown-Peterson, N., Thomas, P. & Arnold, C. R. (1988). Reproductive biology of the spotted seatrout, *Cynoscion nebulosus*, in south Texas. *Fishery Bulletin* **86,** 373–387.

Carreon-Martinez, L. B., Holt, S. A., Nunez, B. S., Faulk, C. K. & Holt, J. G. (2010). The use of polymerase chain reaction for the identification of sciaenid eggs. *Marine Biology* **157,** 1889–1895. doi: 10.1007/s00227-010-1441-5

Connaughton, M. A. & Taylor, M. H. (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., Fine, M. L. & Taylor, M. H. (2002). Weakfish sonic muscle: influence of size, temperature and season. *Journal of Experimental Biology* **205,** 2183–2188.

DeMartini, E. E. & Fountain, R. K. (1981). Ovarian cycling frequency and batch fecundity in the queenfish *Seriphus politus*: attributes representative of serial spawning fishes. *Fishery Bulletin* **79,** 547–560.

Fish, J. F. & Cummings, W. C. (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. In *Biology of the Spotted Seatrout* (Bortone, S., ed.), pp. 177–195. Boca Raton, FL: CRC Press.

Gruber, D., Ahlstrom, E. H. & Mullin, M. M. (1982). Distribution of ichthyoplankton in the southern California bight. *California Cooperative Oceanic Fisheries Investigations* **23,** 172–179.

Gruenthal, K. M. & Drawbridge, M. A. (2012). Toward responsible stock enhancement: broadcast spawning dynamics and adaptive genetic management in white seabass aquaculture. *Evolutionary Applications* **5,** 405–417. doi: 10.1111/j.1752-4571.2011.00234.x

Holt, S. A. (2008). Distribution of red drum spawning sites identified by a towed hydrophone array. *Transactions of the American Fisheries Society* **137,** 551–561. doi: 10.1577/T03-209.1

Lammers, M. O., Brainard, R. E., Au, W. L., Mooney, T. A. & Wong, K. B. (2008). An ecological acoustic recorder (EAR) for long-term monitoring of biological and anthropogenic sounds on coral reefs and other marine habitats. *Journal of the Acoustical Society of America* **123,** 1720–1728. doi: 10.1121/1.2836780

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

Locascio, J. V. & Mann, D. A. (2008). Diel periodicity of fish sound production in Charlotte Harbor, Florida. *Transactions of the American Fisheries Society* **137,** 606–615. doi: 10.1577/T06-069.1

Lowerre-Barbieri, S. K., Chittenden, M. E. & Barbieri, L. R. (1996). The multiple spawning pattern of weakfish, *Cynoscion regalis*, in the Chesapeake Bay and Middle Atlantic Bight. *Canadian Journal of Fisheries and Aquatic Sciences* **55,** 2244–2254.

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

Luczkovich, J. J., Pullinger, C. R., Johnson, S. E. & Sprague, M. W. (2008). Identifying sciaenid critical spawning habitats by the use of passive acoustics. *Transactions of the American Fisheries Society* **137,** 576–605. doi: 10.1577/T05-290.1

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Mann, D. A. & Grothues, T. M. (2009). Short-term upwelling events modulate fish sound production at a mid-Atlantic Ocean observatory. *Marine Ecology Progress Series* **375,** 65–71. doi: 10.3354/meps07720

Mann, D. A., Locascio, J. V., Coleman, F. C. & Koenig, C. C. (2009). Goliath grouper *Epinephelus itajara* sound production and movement patterns on aggregation sites. *Endangered Species Research* **7,** 229–236. doi: 10.3354/esr00109

Mann, D. A., Locascio, J. V., Scharer, M., Nemeth, M. & Appeldoorn, R. (2010). Sound production by red hind *Epinephelus guttatus* in spatially segregated spawning aggregations. *Aquatic Biology* **10,** 149–154. doi: 10.3354/ab00272

McCauley, R. D. & Cato, D. H. (2000). Patterns of fish calling in a nearshore environment in the Great Barrier Reef. *Philosophical Transactions of the Royal Society B* **355,** 1289–1293. doi: 10.1098/rstb.2000.0686

Mellinger, D. K., Stafford, K. M., Moore, S. E., Dziak, R. P. & Matsumoto, H. (2007). An overview of fixed passive acoustic observation methods for cetaceans. *Oceanography* **20,** 36–45.

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

Munger, L. M., Mellinger, D. K., Wiggins, S. M., Moore, S. E. & Hildebrand, J. A. (2005). Performance of spectrogram cross-correlation in detecting right whale calls in long-term recordings from the Bering Sea. *Canadian Acoustics* **33,** 25–34.

Murua, H., Kraus, G., Saborido-Rey, F., Witthames, P. R., Thorsen, A. & Junquera, S. (2003). Procedures to estimate fecundity of marine fish species in relation to their reproductive strategy. *Journal of Northwest Atlantic Fishery Science* **33,** 33–54.

Parrish, R. H., Nelson, C. S. & Bakun, A. (1981). Transport mechanisms and reproductive success of fishes in the California Current. *Biological Oceanography* **1,** 175–203.

Semmens, J. M., Buxton, C. D., Forbes, E. & Phelan, M. J. (2010). Spatial and temporal use of spawning aggregation sites by the tropical sciaenid *Protonibea diacanthus*. *Marine Ecology Progress Series* **403,** 193–203. doi: 10.3354/meps08469

Skogsberg, T. (1939). The fishes of the family Sciaenidae (croakers) of California. *California Department of Fish and Game Fishery Bulletin* **54,** 1–62.

Thomas, J. C. (1968). Management of the white seabass *Cynoscion nobilis* in California waters. *California Fish and Game* **142,** 1–33.

Van Parijs, S. M., Clark, C. W., Sousa-Lima, R. S., Parks, S. E., Rankin, S., Risch, D. & Opzeeland, I. C. V. (2009). Management and research applications of real-time and archival passive acoustic sensors over varying temporal and spatial scales. *Marine Ecology Progress Series* **395,** 21–36. doi: 10.3354/meps08123

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

Wiggins, S. (2003). Autonomous acoustic recording packages (ARPs) for long-term monitoring of whale sounds. *Marine Technological Society Journal* **37,** 13–22.

Wiggins, S. M., Oleson, E. M., McDonald, M. A. & Hildebrand, J. A. (2005). Blue Whale (*Balaenoptera musculus*) diel call patterns offshore of Southern California. *Aquatic Mammals* **31,** 161–168. doi: 10.1578/AM.31.2.2005.161

Electronic References

California Department of Fish and Game (2002). White seabass fishery management plan (WSFMP). *Final Report* Available at http://nrm.dfg.ca.gov/FileHandler.ashx?DocumentID=34195&inline=true/

Fish, M. P. (1948). Sonic fishes of the Pacific. *Pacific Ocean Biological Project Technical Report* **2,** 1–144. Available at https://darchive.mblwhoilibrary.org/bitstream/handle/1912/2767/WHOI-48-36.pdf?sequence=1/

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