

**Abstract**—Spawning periodicities of white seabass (*Atractoscion nobilis*) were evaluated by observing spawning behavior, by collecting eggs, and monitoring recognizable sounds produced during the release of gametes. A total of 297 spawning events were documented from 15 male and 47 female white seabass contained within the seminatural confines of a 526-m<sup>3</sup> net pen located in Catalina Harbor, Santa Catalina Island, California. Consistent spawning occurred from March through July 2001–03, and peaked in May at a photoperiod of 14 hours. Most spawning occurred within the 2-hour period following sunset or from 19:00–20:00 hours Pacific Standard Time. White seabass spawned at every phase of the lunar cycle; but an increase in successive spawning events followed the new moon. Most spawning occurred in water temperatures from 15 to 18°C, and there was no apparent correlation with tidal cycles. Seasonal and diel spawning periods were directly correlated with increases in the rate, intensity, and variety of white seabass sounds; this correlation may indicate that sounds function to enhance reproductive success. These findings can be extended to further develop seasonal fishery regulations and to better comprehend the role of sound in the reproduction of sound-producing fishes.

## Seasonal, diel, and lunar spawning periodicities and associated sound production of white seabass (*Atractoscion nobilis*)

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The white seabass (*Atractoscion nobilis*), also known as white weakfish (Eschmeyer et al., 1983), is an oviparous group spawner; multiple males fertilize the eggs of a gravid female as gametes are broadcast into the water column (Aalbers and Drawbridge, in press). As the largest member of the family Sciaenidae (croakers and drums) that inhabits California coastal waters (Miller and Lea, 1972), white seabass produce relatively large eggs, averaging 1.27 mm in diameter (Moser et al., 1983). Fertilized eggs are buoyant and drift with the ocean surface currents for two days before hatching into planktonic larvae that disperse for approximately 30 days and settle out nearshore at a size of 7–10 mm (Moser et al., 1983; Allen and Franklin, 1992).

A previous study, in which the gonads of commercially caught white seabass were examined, indicated that spawning occurs from April through August and peaks in May and June (Skogsberg, 1925). The majority of white seabass have traditionally been landed in the late spring and early summer, when spawning aggregations develop nearshore and around coastal islands (Skogsberg, 1939; Thomas, 1968). Following a sharp decline in California landings, the commercial harvest of white seabass was restricted from March 15 through June 15 to protect spawning

stocks, while recreational bag limits were reduced from three to one fish during this three-month period. Although current restrictions offer white seabass spawning aggregations some refuge, a better understanding of spawning periods will allow managers to further develop seasonal fishery regulations.

Reproduction has been coupled with sound production in other species of Sciaenidae, including the red drum (*Sciaenops ocellata*) (Guest and Lasswell, 1978), spotted seatrout (*Cynoscion nebulosus*) (Mok and Gilmore, 1983), weakfish (*Cynoscion regalis*) (Connaughton and Taylor, 1995), and orangemouth corvina (*Cynoscion xanthulus*) (Fish and Cummings, 1972). Typical of most sciaenids, male white seabass possess sonic musculature that resonates pulsed sounds from the adjacent gas bladder (Tavolga, 1964). Although the sonic musculature and gas bladder structures vary considerably among the 270 sciaenid species (Chao, 1986; Ramcharitar et al., 2006), the sonic structures that Smith (1905) and Tower (1908) described a century ago in male weakfish closely resemble those of white seabass. The importance of sound to this diverse family has been well documented during periods of reproductive activity (Ramcharitar et al., 2006); however, recognizable sounds during the actual release of gametes

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have only been described in the white seabass (Aalbers and Drawbridge, in press).

Acoustically monitoring the sounds produced by spawning fish can reveal the periodicity and critical habitat of spawning aggregations and help managers in the development of fishery regulations and in the better placement of marine protected areas (Luczkovich et al., 1999). However, patterns of spawning-related sound production must be established in order to yield meaningful results for such application. The objective of this investigation was to determine the spawning periodicities and associated sound production patterns of white seabass under seminatural environmental conditions. This study presents a comprehensive assessment of sciaenid sound production as it relates to known spawning activity and establishes the foundation from which passive acoustic surveys can be conducted.

## Materials and methods

### Sampling locations and procedures

Research was conducted from an aquaculture platform consisting of four 9×9×6.5-m net pens moored in Catalina Harbor, Santa Catalina Island, CA. Forty-one adult white seabass were transported live to an individual net pen (526 m<sup>3</sup>) from March through June 2000. An additional 21 fish, collected in May 2001, were excluded from the 2001 spawning data while being acclimated in a separate net pen. In October 2001, all fish were measured to the nearest mm, weighed to the nearest 10 g, examined to determine sex, tagged with a passive integrated transponder (PIT; Avid, Greeley, CO), and combined into a single net pen. Forty-seven female and 15 male fish ranged in initial size from 83 to 126 cm total length (TL) and 4.9 to 19.5 kg in weight. Fish were only manipulated when remeasured in February 2003 and no mortality occurred during the study. Captive white seabass were fed variable rations of freshly caught squid (*Loligo opalescens*), chub mackerel (*Scomber japonicus*), and jack mackerel (*Trachurus symmetricus*) as they became available locally.

### Documentation of spawning

Fish spawning periodicity was assessed from 2001 to 2003 by direct observation from an elevated deck, by sampling the net pen for freshly spawned eggs with a 500- $\mu$ m-mesh dip net, and by acoustically monitoring fish sounds. Successive spawning events were difficult to differentiate from egg sampling alone; therefore multiple spawning events were documented only if visually observed or acoustically detected and accompanied by increased egg abundance in dip-net samples in comparison to previous samples. Gravid females and courting males were occasionally scanned for individual identification with a PIT (passive integrated transponder) reader when fish approached the surface.

### Analyses of spawning data

Date and time of day, photoperiod, lunar phase, and tidal cycle were noted upon detection of a spawning event. Data were grouped by month, hour, and phase of the synodic month to determine seasonal, diel, and lunar spawning periodicities. Hourly spawning periodicity was analyzed in relation to sunset and to the 24-h clock after correcting to Pacific Standard Time (PST), without adjusting for daylight savings time. Water temperature was recorded to the nearest 0.15°C every hour at a depth of 3 m with an Optic Stowaway temperature logger (Onset Computer Corp., Pocasset, MA) suspended from the net pen. Continuous temperature data for the 2002 spawning season were obtained from a temperature logger at an adjacent net-pen site (300 m away) within Catalina Harbor. Additional temperature and salinity measurements were made upon detection of eggs with a YSI 85 instrument (YSI Inc., Yellow Springs, OH).

### Acoustic equipment

Sounds were received with an omnidirectional hydrophone (International Transducer Corporation 6050-C, Santa Barbara, CA) 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 with an incorporated reference tone (Frank Aubrey, Hubbs-SeaWorld Research Institute, San Diego, CA). Sounds were recorded with a PCM-M1 digital audio tape recorder (Sony Corp., Tokyo, Japan) set to a constant gain.

### Audio recordings

Three-minute audio recordings were made at regular intervals with the hydrophone suspended at a depth of 3 m in the center of the net pen. Evening sound recordings, taken on 17 sampling dates from March through July 2003, were focused around periods of spawning activity, and individual recordings were made every 30 minutes from 1 hour before to 3 hours after sunset. Additional recordings were made every hour for 24 hours, once a month, on randomly selected dates from April 2003 through March 2004 to document seasonal and diel sound patterns. No recordings occurred in February 2004 because of extreme weather conditions.

### Acoustic analyses

Sound recordings ( $n=404$ ) were digitally transferred to a PC hard drive for spectral analysis (SpectraPlus, vers. 2.32.04, Pioneer Hill, Campbell, CA). Based on spectral characteristics, the following categories of white seabass sounds were noted: single pulse-trains, multiple pulse-trains, drum-rolls, thuds, abbreviated chants, spawning chants, or hydrodynamic booms as described in Aalbers and Drawbridge (in press). Sound production rates for each sound type were determined from each recording.

The most intense sounds, as recorded, of each type were analyzed against a 1-kHz reference tone on each 3-min recording. Sound intensities were scaled with values consistent to one another, but not as absolute sound pressure level (dB re  $1\mu\text{Pa}$ ) because the entire hydrophone system had not been calibrated recently. The terms “level” and “intensity” are used synonymously to convey the relative data presented here.

### Statistical analyses

A one-way analysis of variance (ANOVA) was used to examine whether diel spawning times were consistent throughout the spawning season both in relation to sunset and the 24-h clock. The numbers of spawning events observed at each phase of the lunar cycle were analyzed against expected occurrences by using a chi-square test. Sound rates from 24-h recordings during the spawning season (March–July) were compared to those when there was no spawning (August–January) using a two-sample *t*-test. Two-sample *t*-tests were also used to compare the rates and relative levels of sounds from evening recordings made on days that spawning did and did not occur.

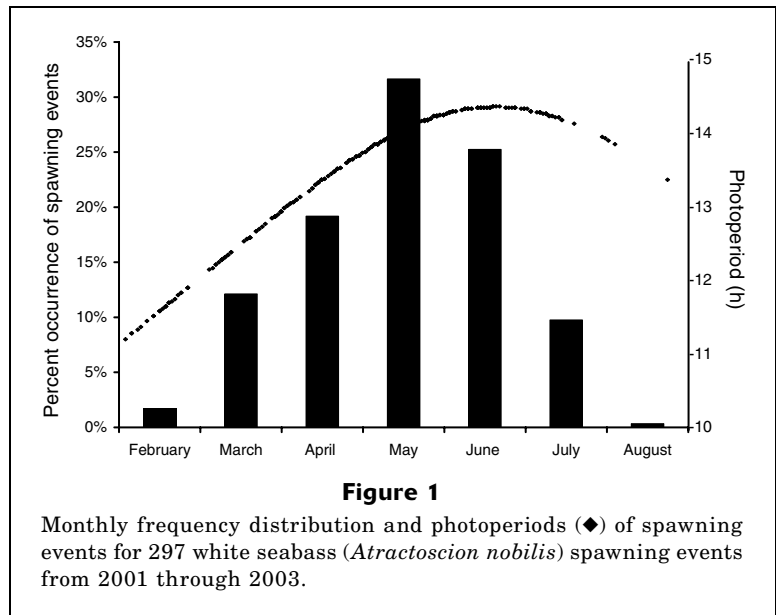
## Results

### Seasonal spawning

Over the three-year study, 297 spawning events were documented; 53, 146, and 98 events were recognized in 2001, 2002, and 2003, respectively. The longest spawning season extended between 22 February and 15 August 2002, whereas the other spawning seasons ranged from 17 March to 27 June 2001 and from 3 March until 16 July 2003. Of the documented spawning events, 76% occurred from April through June, and 98% from March through July over the three-year period. Spawning peaked in May as photoperiod increased to 14 hours (Fig. 1).

### Diel spawning

Spawning occurred from two hours before sunset until 4.5 hours after sunset. Sixty-five percent of spawning activity occurred over the two-hour period following sunset and 91% occurred within the four-hour period spanning from one hour before sunset to 3 hours after sunset (Fig. 2A). A significant shift in the diel spawning periodicity in relation to sunset as the spawning season progressed occurred in all three years (ANOVA,  $F=8.78$ ,  $df=4$ ,  $P>0.001$ ). For instance, in March 2002 the average spawning time was between two and three hours after sunset; however, by July 2002 the average spawning event occurred within the first hour after



sunset. The inverse seasonal trend was observed when spawning times were analyzed in relation to sunrise. No equivalent seasonal shift in the time of spawning occurred when events were analyzed in relation to the 24-hour clock (ANOVA,  $F=2.41$ ,  $df=4$ ,  $P=0.06$ ). Spawning peaked between 19:00 and 20:00 h PST in all three seasons and was not confirmed before 17:30 or after 22:00 h (Fig. 2B).

### Lunar spawning

Spawning occurred at every phase of the lunar cycle, but not uniformly (Fig. 3,  $\chi^2=49.57$ ,  $df=29$ ,  $P=0.01$ ). The greatest amount of spawning occurred from the new moon until four days after the new moon; 63% of documented mass spawning events (dates with at least four successive spawning events) took place during this five-day period.

Successive spawning events were common and as many as eight events occurred in a single night, presumably from different females. The time between successive spawning on 21 sampling dates ranged from 1 to 98 minutes (mean=31 min,  $n=66$ ). A female individual was identified with the PIT reader before spawning on 12 June 2002 and again on 16 June 2002.

### Environmental factors

Ambient water temperatures ranged seasonally from 11.3° to 21.7°C over the study period. Spawning occurred between 12.5° and 20.8°C, and bimodal peaks in the percent occurrence of spawning were apparent at 15° and 18°C. Seventy-six percent of spawning occurred in water temperatures from 15° to 18°C. Salinity at the study site ranged from 34.2° to 34.8 ppt. Spawning occurred throughout the range of tidal cycles with no apparent tendency towards ebb or flow. The ratio of

spawning that occurred around high tide was equivalent to the ratio of high tides that occurred within the fundamental diel spawning period (1 hour before to 3 hours after sunset).

### Sound production

The sound production rate of white seabass peaked in May, averaged 29.2 sounds/min, and reached a minimum average of 1.5 sounds/min (primarily hydrodynamic

booms) in December (Fig. 4). Sound production rates were significantly greater on 24-h recordings made during the spawning season (mean=12.7 sounds/min) than during months without spawning (mean=4.5 sounds/min) ( $t=4.88$ ,  $df=118$ ,  $P>0.001$ ). Within the spawning season, there was a significant increase in the rate of sound production on spawning than on non-spawning days ( $t=9.23$ ,  $df=203$ ,  $P>0.001$ ), and peak rates occurred during spawning events (Fig. 5). Similarly, a significant increase in sound intensity was observed for sounds recorded on spawning days than on nonspawning days ( $t=1.89$ ,  $df=438$ ,  $P=0.030$ ).

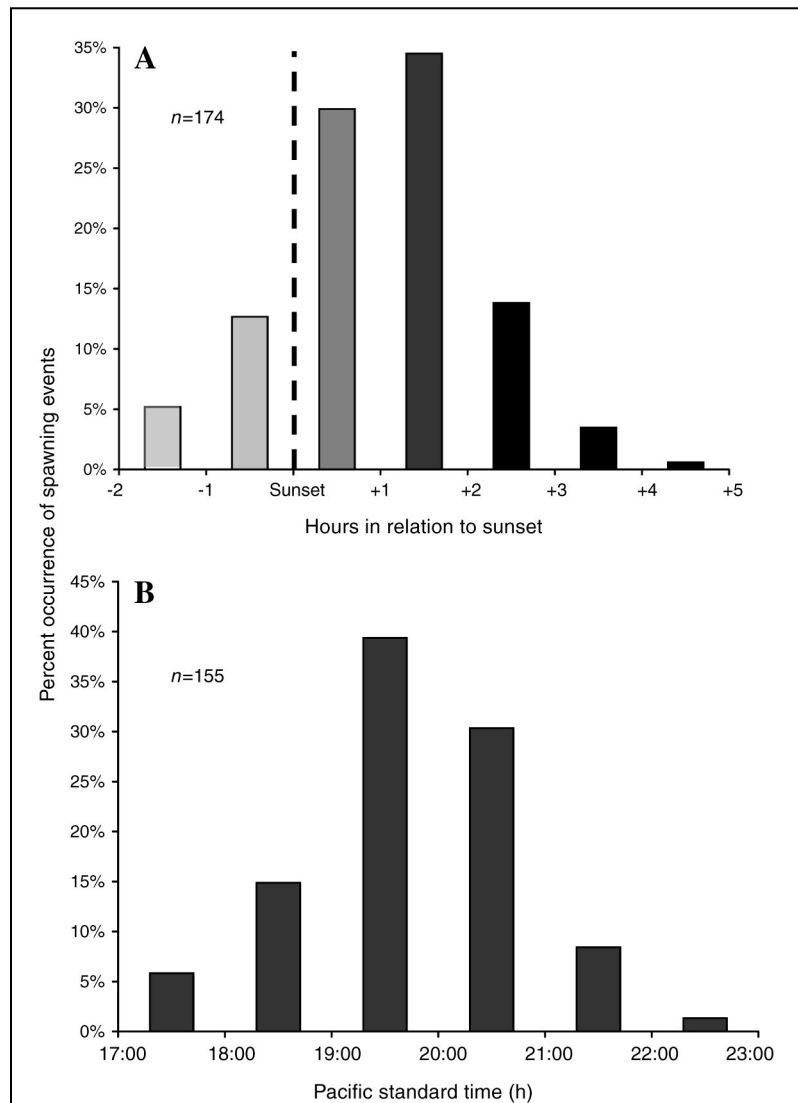
The basic sound types that have been identified for the white seabass are single pulse-trains, multiple pulse-trains, drum-rolls, thuds, and hydrodynamic booms (Fig. 6). A rapid succession of overlapping drum-roll and thud sounds resulted in recognizable spawning chants during the release of gametes. All sound types occurred on days of spawning; however, only hydrodynamic booms along with single and multiple pulse-trains of reduced rate and intensity occurred on days with no spawning (Fig. 7, A and B).

Single pulse-trains increased in rate and intensity on audio recordings that corresponded with spawning. The rate and intensity of pulse-trains remained high between successive spawning events and throughout the 1-h period after spawning.

Multiple pulse-trains occurred as a series of two to six pulse-trains, typically in a rhythmic pattern every 4–6 seconds. Weak multiple pulse-trains were detected throughout the day during the spawning season, but sound intensity greatly increased during the 90-min period after spawning events (Fig. 7B). Post-spawning multiple pulse-trains were of higher intensity than any other type of white seabass sounds.

Drum-rolls and thuds increased in rate and intensity during the initiation of spawning behavior and were not detected outside of the 4-h period surrounding spawning. Drum-rolls and thuds occurred in repetitive trains and were categorized as abbreviated chants or spawning chants when overlapping sounds became audibly indistinguishable.

Abbreviated chants consisted of rapid sequences of drum-rolls and thuds that terminated abruptly after 3–5 sec of spawning behavior and there was no release of gametes. Abbreviated chants were shorter in duration and lower in intensity than spawning chants and were



**Figure 2**

The percent occurrence of white seabass (*Atractoscion nobilis*) spawning events illustrating diel spawning periodicities (A) in relation to sunset and (B) according to Pacific Standard Time for 2001–03. Sample sizes correspond to the number of spawning events that could be assigned to an hourly interval. (A) Dashed line depicts the time of sunset and shading represents diminishing light levels throughout the evening. There is no shading in (B) because of seasonal changes in the time of civil twilight.

most commonly detected within 30 minutes before a spawning or in between successive spawning events.

Spawning chants were detected only during the release of gametes and consisted of an elongate series of intense, overlapping drum-roll and thud sounds at an average rate of 7 sounds/sec that continued for up to 55 seconds. The intensity of spawning chants was second only to multiple pulse-trains recorded after spawning.

Hydrodynamic booms were caused by sudden pressure waves generated underwater by rapid body movement and occurred throughout the day and night over the entire year. Their average rate and intensity remained relatively constant throughout the day and throughout the year, but increased considerably during feeding or in the presence of a predator around the net pens.

## Discussion

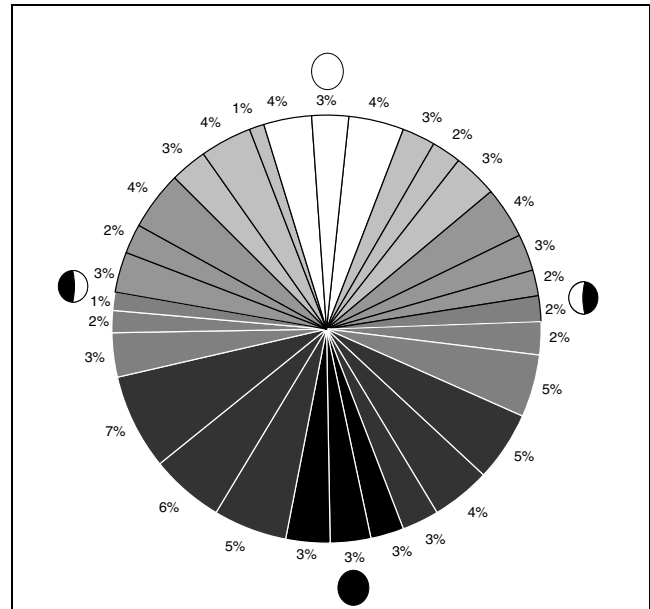
### Seasonal spawning

White seabass maintain a protracted 5-month spawning season from March through July, and 98% of spawning events are documented during this period. Allen and Franklin (1992) identified a peak in the catch per unit of effort of newly settled young-of-the-year white seabass off Southern California in July 1988 and June 1989, supporting the seasonal spawning data presented here. A March–July spawning season is a month earlier than the previously estimated April–August spawning season for white seabass (Skogsberg, 1939). Annual California Cooperative Oceanic Fisheries Investigation (CalCOFI) surveys revealed that white seabass larvae were most abundant off central Baja California from May through August and abundance peaked in July (Moser et al., 1983), which is later than the May peak in spawning described here. Latitudinal differences in photoperiod and water temperature throughout the southern extent of the population range may explain this discrepancy.

One-third of white seabass spawning activity occurred outside the current March 15–June 15 restricted commercial fishing period and time of reduced catch allowable under recreational bag limits. Under present regulations, spawning aggregations off California are exposed to heightened recreational and commercial fishing effort for approximately 60 days each season. Delaying the opening of commercial fishing season in addition to maintaining a one-fish recreational bag limit throughout the spawning season would considerably benefit white seabass spawning stocks.

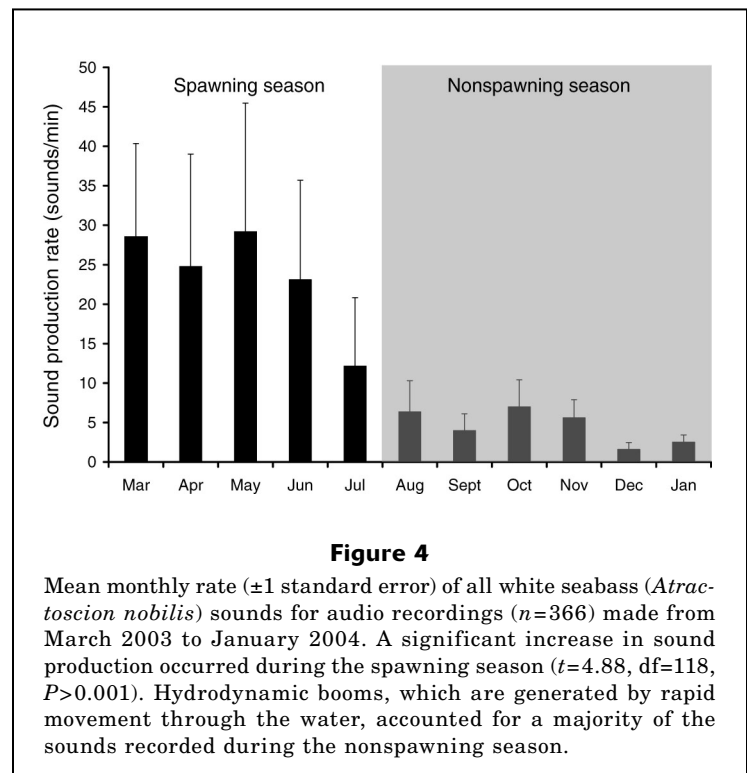
### Diel spawning

A dusk and nighttime spawning period, as documented here for white seabass is common in other temperate sciaenids (Holt et al., 1985;



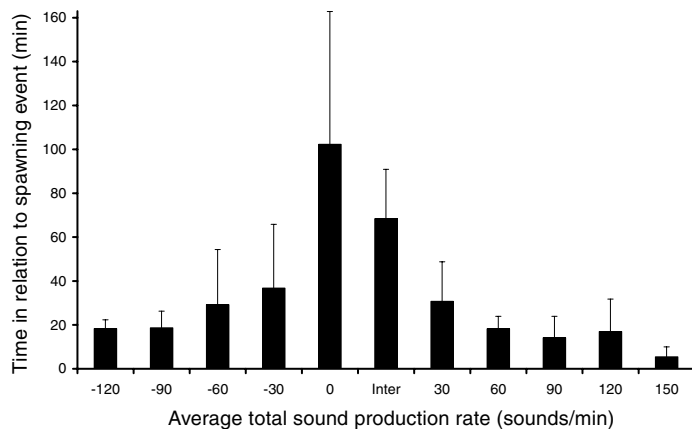
**Figure 3**

Lunar spawning periodicity of white seabass (*Atractoscion nobilis*) for 297 spawning events documented from 2001 through 2003. Values correspond to the % occurrence of spawning events on each day of a synodic month. Increased shading represents the lunar cycle as it moves from full (light) to new (dark). Spawning activity was not uniform over the lunar cycle ( $\chi^2=49.57$ ,  $df=29$ ,  $P=0.01$ ).



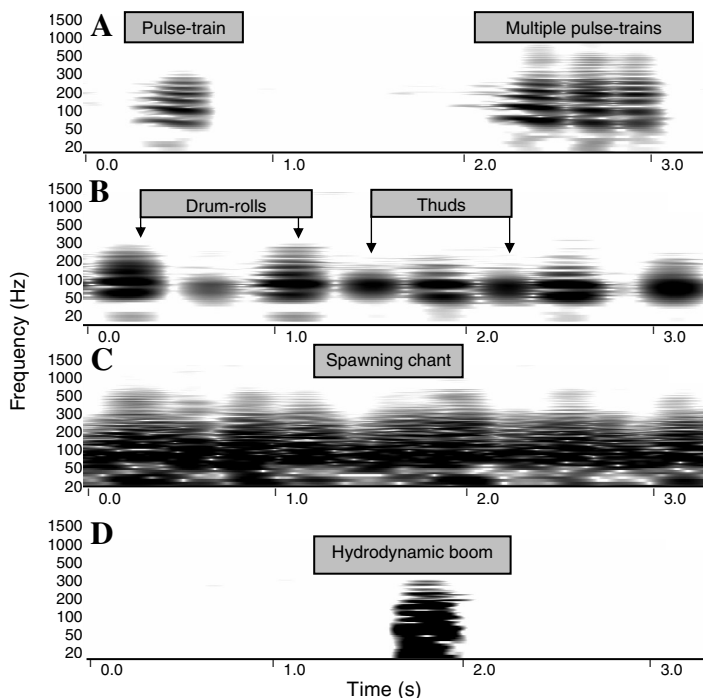
**Figure 4**

Mean monthly rate ( $\pm 1$  standard error) of all white seabass (*Atractoscion nobilis*) sounds for audio recordings ( $n=366$ ) made from March 2003 to January 2004. A significant increase in sound production occurred during the spawning season ( $t=4.88$ ,  $df=118$ ,  $P>0.001$ ). Hydrodynamic booms, which are generated by rapid movement through the water, accounted for a majority of the sounds recorded during the nonspawning season.



**Figure 5**

Mean sound production rate ( $\pm 1$  standard error) of white seabass (*Atractoscion nobilis*) for all combined sound types in relation to the release of gametes during 3-min evening recordings ( $n=102$ ) when spawning was documented from March to July 2003. The term "Inter" refers to the period between successive spawning events. The time between successive spawning was 1 to 98 min (mean=31 min).



**Figure 6**

Three-second sonograms of five basic sound types (A, B, D) generated by white seabass (*Atractoscion nobilis*), in addition to an identifiable spawning chant (C) consisting of overlapping drum-roll and thud sounds generated during the release of gametes. Modified from Aalbers and Drawbridge (in press).

Taylor and Viloso, 1994) and in many fish species worldwide (Johannes, 1978). Spawning during low-light conditions may occur to reduce predation rates on both freshly spawned eggs and spawning adults (Lobel, 1978; Holt et al., 1985). Broadcast spawners may further benefit from synchronizing spawning activity by temporally concentrating reproductive effort and maximizing time allocated for diurnal movements and feeding.

### Lunar spawning

White seabass spawned throughout the lunar cycle; although more individuals may have achieved reproductive readiness following the new moon, because 63% of mass spawning events occurred from the new moon until four days after the new moon. The majority of known lunar spawning periodicities occur around the new or full moon, possibly to reduce egg predation through increased dispersal around larger tidal flows or to ensure that males and females collectively achieve reproductive readiness (Johannes, 1978).

### Environmental conditions

The majority of spawning occurred as water temperature and photoperiod increased during the spring and early summer; these factors appear to be important in stimulating white seabass spawning activity. Most spawning occurred at water temperatures between 15 and 18°C; this range is consistent with that observed under hatchery protocols to artificially induce spawning in broodstock tanks. Although more spawning was documented around high tide, this effect can be attributed to the increased occurrence of evening high tides during summer within the mixed semidiurnal tide regime of southern California (Flick, 2000).

### Experimental variables

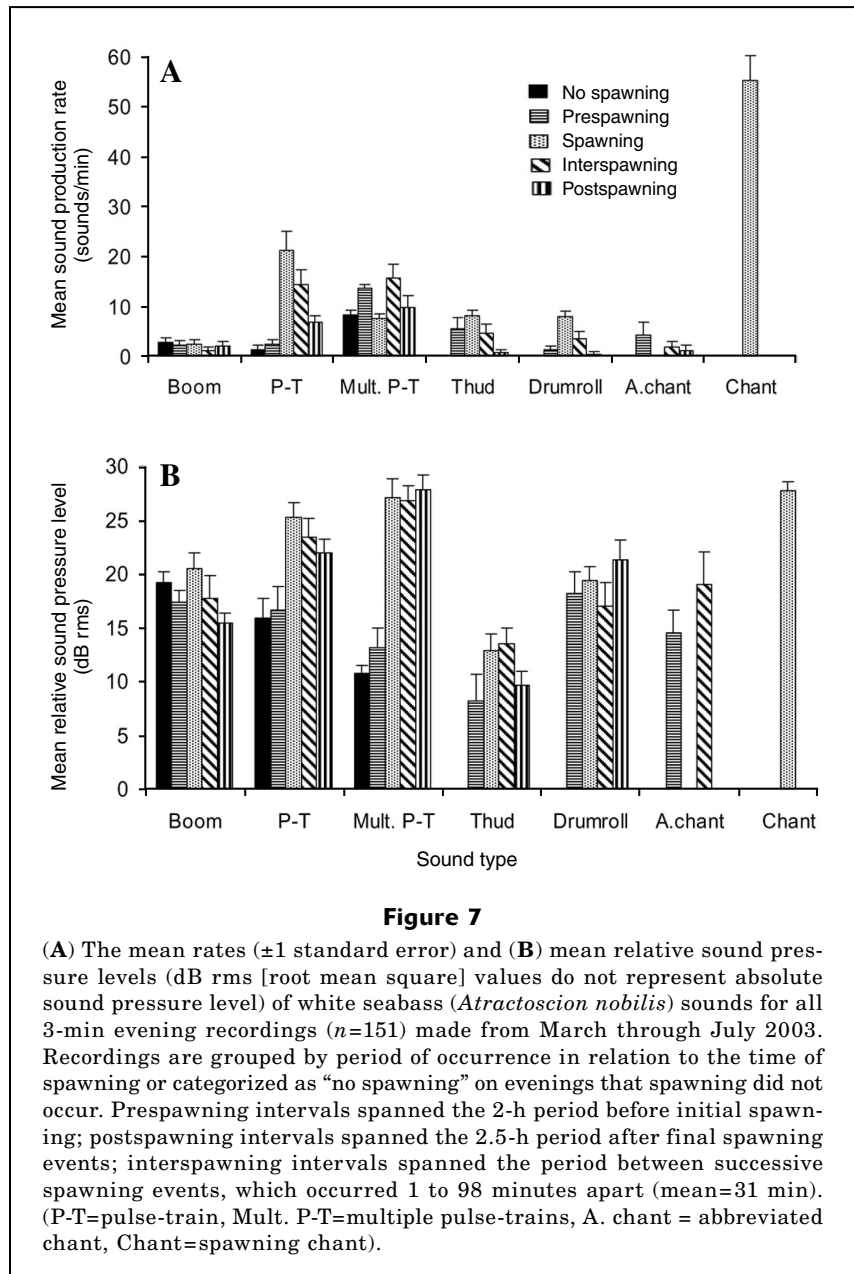
Although variations in the onset and duration of spawning seasons and the number of spawning events per season may represent biological responses to shifting environmental conditions (e.g., temperature changes), differences may be partly attributed to research procedure. The captive population was 34% lower in 2001 because 21 white seabass were not combined with the original 41 fish until after the 2001 spawning season. Additionally, increases in fish size and acclimation time over the 3-year period may have been responsible for the

46% increase in observed spawning activity in 2003 compared to 2001. Improved recognition of fish behaviors and patterns likely enhanced the detection of spawning events in 2002 and 2003. Difficulty in differentiating successive spawning events solely on the presence of eggs considerably reduced the total number of documented events, along with an inability to visually detect spawning after dark. Variations in white seabass feed rations may have influenced interannual spawning activity because condition factor influences fecundity in weakfish (Lowerre-Barbieri et al., 1996), haddock (*Melanogrammus aeglefinus*) (Hislop et al., 1978), and Atlantic cod (*Gadus morhua*) (Kjesbu and Klungsoyr, 1991).

### Spawning frequency

Although data were not extensive enough to accurately determine individual white seabass spawning frequency or fecundity, it was apparent that females are serial spawners. The average number of observed spawning events per female in 2001, 2002, and 2003 was 2.0, 3.1, and 2.1, respectively; however, these values are underestimated because of experimental limitations. The same female spawned on 12 June 2002 between 2010 h and 2040 h and again on 16 June 2002 at 2038 h, indicating a capability for four-day spawning intervals.

The observed shift in the diel spawning periodicity in relation to sunrise and sunset as the spawning season progressed indicates that final oocyte maturation is not triggered solely by light intensity or the time of sunrise and sunset. White seabass exhibited a more consistent 24-h diel spawning pattern throughout the season, indicating that gamete development may occur with a circadian rhythm that could be modified through a combination of environmental cues (Taylor, 1984). Spawning rhythms and gamete development fluctuate synchronously with plasma estradiol-17 $\beta$  levels in female spotted seatrout and with testosterone and 11ketotestosterone concentrations in males (Brown-Peterson, 2003). In addition to regulating seasonal and diel spawning rhythms, increases in the levels of plasma androgens are correlated with seasonal hypertrophy of sonic musculature as male weakfish come into spawning condition (Connaughton and Taylor, 1994; Connaughton et al., 1997).



### Sound patterns

White seabass may experience alterations in reproductive endocrine hormones and physiological features that are similar to those observed in other sciaenids, because peak diel and seasonal spawning rhythms were directly correlated with increases in the rate, intensity, and variety of sound production. Sound production in orangemouth corvina and weakfish also culminates seasonally during peak spawning in May and diminishes in late July as spawning subsides (Fish and Cummings, 1972; Connaughton and Taylor, 1995). Additionally, diel increases in the sounds of weakfish and spotted seatrout have been documented after sunset during hours of

reproductive activity (Connaughton and Taylor, 1995; Gilmore, 2003).

The rate of white seabass sound production increased 20-fold during the release of gametes, establishing the highest rate and second highest intensity for all sounds. Measurable increases in the intensity of white seabass spawning chants and postspawning multiple pulse-trains were consistent with the audible detection of these sounds through the net-pen pipes and the hull of an adjacent boat. A chorus of orange-mouth corvina sounds increased ambient noise within the Salton Sea by 50 dB during the spawning season (Fish and Cummings, 1972). All of the distinct white seabass sound types were present on audio recordings during spawning. In spotted seatrout, four major sound types were reported, all of which occurred during courtship and spawning (Gilmore, 2003).

### Sound function

Direct correlations between spawning activity and sound production substantiate the hypothesis that white seabass sounds function to enhance reproductive success. Weak single and multiple pulse-trains that were audible throughout the spawning season may help white seabass maintain aggregations. Single pulse-trains before spawning may augment courtship behaviors or communicate reproductive readiness. Intense multiple pulse-trains after spawning may serve to attract surrounding females into spawning aggregations. Identifiable spawning chants recorded during actual spawning likely function to enhance reproductive success by synchronizing the release of gametes.

### Conclusion

This study provides a strong correlation between verified white seabass spawning activity and sound production patterns. The noninvasive techniques used in this study can be extended to examine reproductive characteristics of other sound-producing fish species and alleviate difficulties associated with documenting spawning after dark. The essential fisheries information provided on key reproductive characteristics will help fisheries managers in designing strategies to sustain this economically important species and reduce the likelihood of another severe population decline. Baseline findings from this work can be extended to acoustically monitor white seabass spawning aggregations in order to investigate critical spawning habitat and to help determine better placement of marine protected areas throughout California.

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