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Hydrophone identification and characterization of *Cynoscion squamipinnis* (Perciformes: Sciaenidae) spawning sites in the Gulf of Nicoya, Costa Rica

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Abstract: A hydrophone survey of the northern Gulf of Nicoya was conducted to identify spawning sites used by the corvina aguada (*Cynoscion squamapinnis*). Between July 14, and July 17, 1992, thirty-one stations were surveyed during late afternoon and evening hours. Large aggregations of drumming corvina were located as early as 1606 hrs, but were generally restricted to stations characterized by above average depth and moving water. Drumming activity by *C. squamapinnis* peaked between 1655 and 1910 hrs on four evenings and fully subsided by about 2100 hrs. In a stepwise regression model, five variables were selected to predict sound intensity. The overall model was statistically significant ($P < 0.0001$) and explained a high proportion of the variance (R-square = 0.59). The five variables included in the model, in order of decreasing partial R-squares, were tide^2 (0.2103), hour^3 (0.1470), temperature^2 (0.1051), substrate (0.0720), and salinity^2 (0.0562). Local gillnet fishermen are familiar with corvina sound production behavior and some can identify the drumming species. Corvina fishing takes place only during periods known locally as "mareas de corvina" (Corvina tides), which are those that occur immediately after the highest (or lowest) tides of the month, and which gillnet fishermen claim to be the best for fishing. Thus, heaviest fishing concentrates in a period of eight to ten days a month, and we also suspect that fishing during "corvina tides" is focused on natural drumming aggregations. Under present management, the fishery may be reducing natural spawning success and maximizing effort by coinciding temporally with natural spawning aggregations.

Key words: Drumming aggregations, Golfo de Nicoya, habitat, Sciaenidae, sound production.

Drumming by fishes in the family Sciaenidae is primarily associated with spawning behavior (Mok and Gilmore 1983, Saucier *et al.* 1992, Saucier and Baltz 1993). Fishes produce sounds by stridulation (Tavolga 1971), swimbladder vibration (Tower 1908, Burkenroad 1931, Gray and Winn 1961, Fish and Mowbray 1970, Bass 1990), and hydrodynamics (Tavolga 1971). Sound production in fishes has been identified with feeding, fright, schooling, spawning, and territorial behavior (Tavolga 1980). Male fishes in the family Sciaenidae have well developed muscles associated with the swimbladder (Tower 1908, Burkenroad 1931) that are used to produce species-specific, drumming sounds (Mok and Gilmore 1983). The main function of the sound production behavior is to attract females in spawning condition to appropriate spawning sites (Saucier *et al.* 1992, Saucier and Baltz 1993).

Both male and female Atlantic croaker, *Micropogonias undulatus*, and silver perch, *Bairdiella chrysoura*, produce sounds by stridulation of the pharyngeal teeth, while only males produce sounds by muscular vibration of the swimbladder (Burkenroad 1931). During the reproductive season, male spotted seatrout, *Cynoscion nebulosus*, black drum, *Pogonias cromis*, and most other male sciaenids produce drumming sounds (Tower 1908, Burkenroad 1931, Fish and Mowbray 1970, Tavolga 1971). Females generally do not have a well developed drumming apparatus (Tower 1908, Pearson 1929, Hein and Shepard 1979) and only male sciaenids aggregate in suitable spawning habitat and drum to attract females that are ready to spawn (Pearson 1929, Guest and Lasswell 1978). Mok and Gilmore (1983) analyzed temporal and spatial sound production patterns by spotted seatrout, silver perch, and black drum and found that sound production by these species occurred primarily during the spawning season from dusk to midnight.

Hydrophones have been used to locate individuals or schooling aggregations of fishes and to study the behavior of territorial fishes (Mok 1981, Mok and Gilmore 1983, Myrberg and Riggio 1985, Luh and Mok 1986, Saucier *et al.* 1992, Saucier and Baltz 1993). Spawning site selection has been studied for spotted seatrout in the northern Gulf of Mexico and on the southeastern Atlantic coast of the U. S. (Saucier *et al.* 1992, Saucier and Baltz 1993). Typically large numbers of males aggregate in suitable spawning locations in the early afternoon and begin drumming. Females sciaenids are serial spawners (Brown-Peterson 1988, Wieting 1989) that only produce a few batches of eggs during a spawning season that may range from two to six months in duration for a given species (Beckman *et al.* 1990, Fitzhugh *et al.* 1992, Saucier and Baltz 1993). Female spotted seatrout spawn between six and eight times during a six month spawning season (Tucker and Faulkner 1987). Prior to an evening spawn, a female spotted seatrout will begin to hydrate a ripe batch of eggs in the early afternoon (Holt *et al.* 1985, 1988, Brown-Peterson 1988). Spawning begins when males aggregate in suitable spawning sites, usually before sunset and croak or drum to attract females (Pearson 1929). Tabb (1966) described spawning by spotted seatrout as constant milling of the spawning school, with light side-to-side body contact among individual fish. The fertilized eggs are buoyant and float to the surface while the unfertilized eggs gradually sink. Fertilized spotted seatrout eggs hatch in 16 to 20 h at 25°C and larvae emerge at a length of 1.3 to 1.56 mm (Fable *et al.* 1978). Within 20 h of hatching, most sciaenid larvae in the northern Gulf of Mexico are identifiable from the distribution of yellow chromatophore pigment (Holt *et al.* 1988).

On the Pacific coast of Costa Rica, there are 46 species in the family Sciaenidae, including six species of *Cynoscion* (Lopez and Bussing 1982, Bartels *et al.* 1983). Four species of the genus *Cynoscion* occur commonly in the northern Gulf of Nicoya, Costa Rica, and support important artisanal fisheries (Madrigal 1985). In order of commercial importance, the species are *C. squamipinnis, C. albus, C. phoxocephalus,* and *C. stolzmanni*,. In view of their economic importance, their sensitivity to pollution (Szelistowski 1989), potential significant ecosystem water management impacts (UICN 1985), and the rapid development of the coastal zone in the northern Gulf of Nicoya, an understanding of the factors that affect recruitment is needed to permit sustainable management of the estuarine-dependent fisheries. This study focused on the spawning site selection and behavior of the second largest and most abundant species (*Cynoscion squamipinnis*) which has an extended reproductive season with peak activity indicated by a high proportion of females in advanced stages of ovarian development between May and July, however, spawning may continue until October (Campos, in prep).

In an effort to gain insight into spawning site selection and spawning habitat requirements, we asked if an identifiable suite of environmental and temporal variables could be used to characterize spawning aggregation sites used by *C. squamipinnis.* The objectives of this study were to locate and identify drumming aggregations, characterize environmental conditions at male aggregation sites in terms of chemical, physical, and temporal variables, and verify spawning by collecting eggs and rearing them into identifiable larvae. We focused on salinity, dissolved oxygen, current velocity, water temperature, and water depth, but for other fishes without buoyant eggs or soniferous aggregation behavior, other variables such as substrate composition, light intensity, and turbidity might also be important.

MATERIAL AND METHODS

Study area: The Gulf of Nicoya is a large estuary extending 80 km north from the Pacific to mouth of the Rio Tempisque (Voorhis *et al.* 1983). The upper portion of the gulf is shallow (< 20 m) and surrounded by mangrove swamps. The lower portion is deeper and bordered by rocky shores and mangrove forests. During the rainy season, May through November, the estuary in horizontally and vertically stratified. During the dry season, December through April, the stratification breaks down and the system is dominated by winds and tides. Mean spring and neap tides are 2.8 and 1.8 m, respectively. Our survey was concentrated in the upper Gulf (Fig. 1).

Sampling design: We used a stratified search design, planned to include the full range of conditions along depth, substrate, velocity, and salinity gradients that were available to spawning fish. The sampling design was a non-random approach in which we surveyed areas which were accessible at night with a small boat (Fig. 1). Surveys were conducted between 14 July 1992 and 17 July 1992. On July 17 we anchored at Station 31 (Fig. 1) and remained there from 1606 to 2030 hrs.

Hydrophone recording: An InterOcean model 902 hydrophone was used to locate drumming aggregations of fish by monitoring underwater sounds. The hydrophone was lowered one meter below the water's surface and the boat was moved to locate the site of the most intense drumming. Spawning aggregations can be located to within 15 to 20 m by

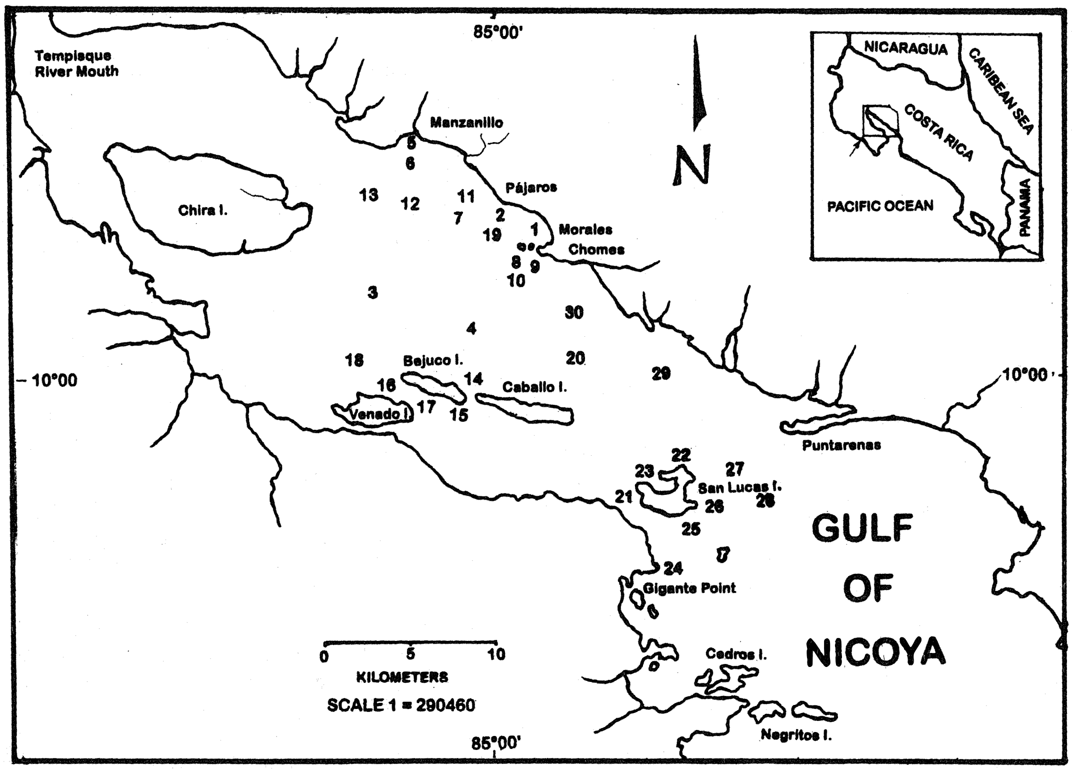

Fig. 1. Sampling sites in the Gulf of Nicoya, Costa Rica, visited between 14 and 17 July 1992.
1- Between Islas Cortezas and Isla Pájaros, 2- 500 m W from station 1, 3- Between la Bocana in Isla de Bejuco and Isla Caballo, 4-Northwest tip of Isla Bejuco, 5-Isla Camarita, 6-Manzanillo, 7-100 m off Isla Pajarita, 8- 300 m off Islas Cortezas, 9-Isla Doña Pepa, 10-Between Islas Cortezas and the Sugar Cane Pier, 11-Same as station 1, 12-Same as station 1, 13-Half way between la Bocana in Isla de Chira and Islas Cortezas, 14-Between Isla Bejuco and Isla Caballo, 15- S.E. tip of Bejuco, 16-Channel between Isla Bejuco and Isla Venado, 17-Off Isla Bejuco, 18-Between Isla Bejuco and Punta Morales, 19- Sugar Cane Pier, 20-Between Punta Morales and Isla San Lucas, 21-S.W.tip of Isla San Lucas, 22-Off Isla San Lucas, 23-Off Isla San Lucas, 24-Punta Gigante, 25-Channel between Isla Ave and Isla Pan de Azúcar, 26-Cirial Point, 27-Channel between Puntarenas and Isla San Lucas, 28- Between Puntarenas and Isla Guayabo, 29-Off Chomes, 30-Off Cocorocas, 31-Same as station 1.

observing the sound intensity (Saucier *et al.* 1992, Saucier and Baltz 1993). Sound intensity in decibels (standard settings were 132 db re 1 m pascal) was used to estimate the source level at the drumming aggregation by adding a one-way spreading loss (*i.e.*, 20 log [depth in meters - 1]) correction to the observed reading. We assumed that attenuation was negligible and that the drumming aggregation was a point source. Based on sound level and overlap of individuals, we also estimated the size of the spawning aggregation on an ordinal scale ranging from 0 to 5 (i.e., 0: no drumming, 1: single drumming individual, 2: two to three drumming individuals, 3: small drumming aggregation, 4: moderate drumming aggregation, 5: large drumming aggregation). When an aggregation was located, a five minute recording was made on a Sony model TCS 450 cassette tape recorder. The recordings were played back in the laboratory and displayed on a Uniscan II frequency analyzer to compare the identity of field samples from different stations. Tentative identifications of recordings *C. squamipinnis* were based on knowledge of spawning season and the assistance of experienced atrisanal gill-net fishermen familiar with sounds produced by several species.

Microhabitat characterization: To characterize environmental conditions at listening locations, including suspected spawning sites, we measured salinity, temperature, dissolved oxygen, current velocity, and depth immediately after each five minute sound recording. Salinity and temperature were measured with a Yellow Springs Instrument (YSI) model 33 SCT meter. Dissolved oxygen (DO) concentrations were measured with a YSI model 57 oxygen meter. A Montedoro-Whitney model PVM-2 flow velocity meter was used to measure surface and mid-water current velocities. Depths were sounded with a lead line to also sample substrates of mud, sand, and rock which were coded 1, 2, and 3, respectively.

Plankton sampling: Three minute plankton tows, using a 0.33 m diameter plankton net with 333 micrometer mesh, were made upcurrent and downcurrent of suspected spawning aggregations to capture recently spawned eggs to verify actual spawning and to identify the spawning species. Following Holt *et al.* (1988), the plankton samples were immediately filtered through 2 mm mesh to remove ctenophores or other potential egg predators. Within three hours, the plankton samples were sorted under a dissecting scope at 10x magnification. Ten to 15 buoyant eggs from each tow were placed in 2 cm of 101 m mesh filtered sea water. Sciaenid eggs hatched 16 to 20 hours after capture and yolk sac larvae were identified as *Cynoscion* sp. approximately 18 h after hatching by comparison with diagrams of anesthetized larvae from Holt *et al.* (1988). The remainder of each plankton sample was preserved in 5% formalin.

Statistical analysis: We used microhabitat and time variables in a stepwise regression model to predict sound source level for *C. squamipinnis*. All independent variables were also available in the model selection process as squared terms to account for nonlinear responses. Time was transformed to hours and available to the model as hour, hour^2, and hour^3. If another species formed a drumming aggregation at a station, the group size and source level variables were set to zero for *C. squamipinnis*. The stepwise procedure selected variables for inclusion or deletion (one to 18 variables including quadratic terms and hour^3) based on a least-squares regression procedure (SAS Institute Inc. 1985) and the maximization of R-square values. We used Mallow's C(p) as our final model selection criterion (Kleinbaum 1987, Neter *et al.* 1989) to reduce the total mean square error and the bias of the regression model. The normality of the dependent variable (source level) was not improved by $\log_{10}(x+1)$ transformation; therefore, the analysis was conducted without transformations. A partial correlation analysis was run on the variables selected by the stepwise procedure to determine their ranking and importance to the model. Bivariate correlation analyses of corvina aggregation size, sound source intensity, water depth, current velocities, dissolved oxygen, temperature, salinity, and hour were used to examine interactions between variables.

RESULTS

Sound characteristics: The sounds produced were similar to the aggregated grunts described for spotted seatrout (Mok and Gilmore 1982). Individual *Cynoscion squamipinnis* aggregated grunts included nine or ten clicks, ranged in duration from 0.325 to 0.368 seconds, and had an inter-click interval of 0.041 seconds. The frequency ranged from near 368 to 736 Hz. We also identified *C. albus* aggregated grunts at one sampling site (Station 9). *C. albus* aggregated grunts were longer in duration (0.98 to 1.11 sec), wider in frequency (216 to 920 Hz), and composed of seven or eight clicks with a 0.16 second inter-click interval.

Temporal pattern: The aggregated grunts produced by *Cynoscion squamapinnis* were observed as early as 1606 hrs, the earliest we attempted to make recordings (Table 1); however, no drumming activity was recorded on another day near the same location until after 1640 hrs. Moderate and large drumming aggre-

TABLE 1

Station data from hydrophone survey of drumming activity in the Gulf of Nicoya, Costa Rica, in July 1992. Drumming fishes are coded 1: Cynoscion squamipinnis, *2:* Cynoscion albus, *3:* Bagre sp., *and 4: unidentified species. Substrates are coded 1: mud, 2: sand, and 3: rock. Tidal stages are coded -1: falling, 0: slack, and +1: rising. Missing data are indicated as empty spaces*

Station	Date	Hour	Sound level dB	Group size	Species	Depth m	Temp °C	Salinity ppt	DO mg/l	Surface velocity cm/s	Mid-water velocity cm/s	Substrate type	Tidal stage
1	14	16:55	135	5	1	22	28.5	31.5	6.1	0.5	0.4	1	-1
2	14	17:30	131	4	1	13.5	28.5	31.0	6.5	—	—	1	-1
3	14	18:25	112	0	0	7	29.0	31.0	5.9	0.6	—	1	-1
4	14	18:46	122	2	1	7	29.0	30.5	5.2	0.6	0.5	1	-1
5	14	19:20	117	2	1	10	29.0	30.0	5.0	0.7	0.4	1	-1
6	14	19:44	122	3	1	8.5	28.5	29.5	5.8	0.9	0.5	1	-1
7	14	20:15	—	1	1	9	28.5	30.0	5.4	0.4	0.2	1	-1
8	14	20:35	129	1	1	19	29.0	30.5	6.3	0.4	0.2	3	-1
9	14	20:46	129	3	2	23	29.0	31.0	6.2	0.2	0.0	3	0
10	14	20:57	—	2	1	12	28.5	31.0	5.0	0.1	0.0	3	0
11	14	21:14	—	2	3	17	29.0	30.2	5.4	0.1	0.0	1	0
12	15	16:46	135	5	1	17	29.0	31.8	6.2	0.1	0.1	1	-1
13	15	17:14	125	2	4	9	28.0	31.5	6.1	0.6	0.6	1	-1
14	15	17:47	117	1	1	7	28.2	31.5	6.4	0.7	0.5	2.9	-1
15	15	17:57	134	5	1	10.5	28.5	31.6	6.5	0.5	0.5	1	-1
16	15	19:10	134	5	1	19	29.0	30.2	6.0	0.7	0.9	1	-1
17	15	20:05	125	3	1	15.5	28.8	30.2	5.7	0.2	0.6	1	-1
18	15	20:32	112	0	0	4	29.5	29.8	5.4	0.2	0.1	1	0
19	15	21:21	125	2	4	16	29.0	30.1	5.4	0.0	0.1	1	0
20	16	16:40	112	0	0	19	27.0	31.5	6.5	0.2	0.1	1	0
21	16	17:25	132	5	1	20.5	28.0	31.2	6.1	0.5	0.4	2	-1
22	16	17:48	127	4	3	20.5	28.0	31.3	5.9	0.7	0.6	1	-1
23	16	18:02	133	4	1	16	28.0	31.2	5.9	0.4	0.2	3	-1
24	16	18:17	125	0	0	6	28.0	31.7	6.0	0.0	0.1	1	-1
25	16	18:34	132	5	1	22	28.0	31.2	6.0	0.2	0.3	1	-1
26	16	19:04	122	0	0	12.5	28.0	31.2	5.6	0.4	0.3	1	-1
27	16	19:15	127	5	3	40	28.0	31.2	6.8	—	—	1.5	-1
28	16	19:37	117	5	3	40	28.0	31.2	6.9	0.5	0.2	1	-1
29	16	20:51	112	1	3	18.5	28.2	30.8	5.5	0.8	0.8	1	-1
30	16	21:28	122	3	4	18	28.8	30.5	5.8	0.4	0.3	1	0
31.1	17	16:06	129	3	1	17	28.8	31.7	6.2	0.3	0.4	1	1
31.2	17	17:00	133	4	1	17	28.9	31.2	6.8	0.2	—	1	1
31.3	17	17:30	133.5	5	1	17	29.0	30.0	6.5	0.0	—	1	0
31.4	17	18:00	134	5	1	17	29.2	30.3	6.7	0.6	—	1	-1
31.5	17	18:30	139	5	1	17	29.0	30.0	6.4	0.4	—	1	-1
31.6	17	19:00	131	5	1	17	29.0	29.9	6.4	0.6	—	1	-1
31.7	17	19:30	131	5	1	17	28.8	30.9	5.7	0.8	—	1	-1
31.8	17	20:00	127	4	1	17	28.8	30.5	5.8	0.8	—	1	-1
31.9	17	20:30	117	2	4	17	28.8	30.3	5.9	0.8	—	1	-1

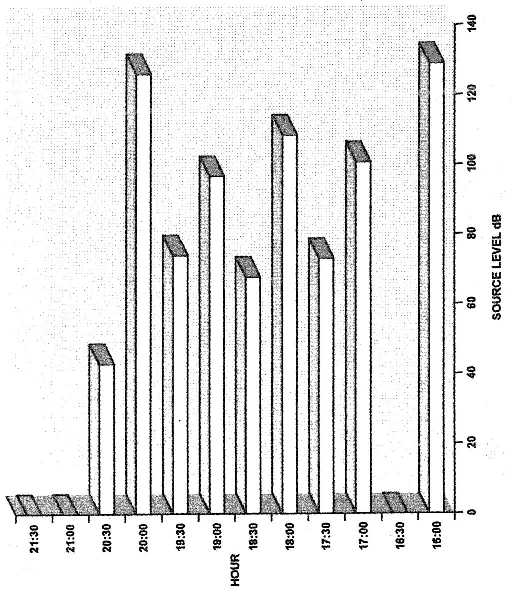

Fig. 2. Temporal pattern of drumming activity, mean source levels **in** decibels, by *Cynoscion squamipinnis* **in** the Gulf of Nicoya on 14 through 17 July 1992.

gations were observed between 1646 and 2000 hrs. Drumming activity by *C. squamapinnis* peaked between 1655 and 1910 hrs on four evenings and fully subsided completely by 2100 hrs (Fig. 2). After *C. squamipinnis* ceased drumming other species were heard, most notably a catfish, identified as *Bagre panamensis*.

Microhabitat characteristics: Twelve of 55 pairwise correlations between nine microhabitat variables and corvina group size and drumming intensity were significant (Table 2). The strongest correlation (r = 0.91) was between group size and drumming intensity. For microhabitat variables, the strongest correlation (r = 0.77) was between surface and midwater velocities, and both velocities were strongly correlated with tidal stage. Salinity was negatively correlated with both temperature and hour and positively correlated with dissolved oxygen concentration. Depth and dissolved oxygen concentration were positively correlated, and hour was correlated positively with temperature and negatively with dissolved oxygen, group size, and drumming intensity.

In univariate comparisons, we were unable to detect significant differences between means in the microhabitat characteristics at large aggregation sites (*i.e.*, coded 5) when compared to all other sampling sites for depth, temperature, dissolved oxygen, water velocity and substrate (Table 1). Nevertheless, the temporal factor, hour, was significantly different (F-value = 5.16, df = 38, and $P < 0.03$). Large drumming aggregations (N = 11) were observed at 1807 hrs ± 55 min (Mean ± SD) and all other observations (N = 28) had a mean of 1916 hrs ± 93 min.

In a stepwise regression model that maximized R-square (Table 3), five variables were selected to predict sound intensity. The overall

TABLE 2

Pearson's bivariate correlation coefficients for microhabitat variables, hour, group size, and sound intesity at sampling locations in the Gulf of Nicoya, Costa Rica, July 1992

	Temperature°C	Surface velocity cm/s	Mid-water velocity cm/s	Depth m	Dissolved oxygen mg/l	Substrate	Tidal stage	Hour	Group size	Intensity
Salinity	-0.58	-0.16	-0.05	0.19	0.36	0.19	0.03	-0.59	-0.04	-0.09
Temperature		-0.04	-0.07	-0.26	-0.21	-0.10	0.20	0.33	0.24	0.28
Surface velocity			0.77	-0.03	-0.04	-0.11	-0.55	0.03	0.08	0.13
Mid-water velocity				-0.05	0.06	-0.29	-0.45	-0.23	0.29	0.32
Depth					0.50	0.05	<-0.01	0.03	0.01	-0.10
Dissolved oxygen						0.01	0.02	-0.54	0.29	0.19
Substrate							0.03	0.15	-0.09	0.10
Tidal stage								-0.02	-0.14	-0.14
Hour									-0.44	-0.41
Group size										0.91

TABLE 3

Stepwise regression model using environmental and temporal variables to predict sound intensity (source level dB) at Cynoscion squamipinnis *drumming sites in the Gulf of Nicoya, Costa Rica, in July 1992*

	DF	SS	MS	F	Prob>F
Regression	5	166918	33384	8.37	0.0001
Error	29	115623	3987		
Total	34	282542			
Variable	Parameter estimate	Standard error	SS	F	Prob>F
Intercept	402.61	673.33	1425.5	0.36	0.55
Salinity^2	-0.99	0.40	24109.9	6.05	0.02
Temperature^2	0.96	0.46	17704.8	4.44	0.04
Substrate	39.05	17.28	20356.3	5.11	0.03
Tide^2	82.07	29.14	316623.7	7.93	<0.01
Hour^2	-0.04	0.01	68696.4	17.23	<0.001

model was statistically significant ($P < 0.0001$) and explained a high proportion of the variance (R-square = 0.59). The five variables included in the model, in order of decreasing partial R-squares, were tide^2 (0.2103), hour^3 (0.1470), temperature^2 (0.1051), substrate (0.0720), and salinity^2 (0.0562).

Egg capture and rearing—Eggs of several species, including one sciaenid identified as *Cynoscion* species, were successfully reared through the yolk-sac stage in filtered water from the sampling sites. Unfortunately, yolk-sac larvae of Costa Rican sciaenids have not been described, so we were unable to identify the species.

DISCUSSION

In this study, *Cynoscion squamapinnis* males aggregated in the deeper portions of the upper gulf and began drumming by early afternoon and continued until about 2000 hrs. Aggregation sites were most easily characterized as locations in the gulf with relatively high salinity (ca 30 ppt) and fast moving water. Nevertheless, other variables such as depth and velocity are probably more important than our study indicated because it was restricted to a narrow range of salinity and temperature variation and falling tides. The mean depth of large drumming aggregations was not significantly greater than the mean of all other depths surveyed; however, we suspect that depth maybe an important factor (Saucier *et al.* 1992, Saucier and Baltz 1993). Tide and hour probably play an important role by restricting spawning to those periods during the month when tidal movement occurs at dusk.

For some estuarine-dependent fishes that spawn in low salinity coastal waters, suitable spawning habitat may be characterized by a combination of environmental and temporal variables (Peebles and Tolley 1988, Baltz 1990, Saucier *et al.* 1992, Saucier and Baltz 1993). The study of spawning site characteristics used by a species allows insights into important ecological factors that influence the success of populations in habitats throughout the species range. For some fishes, reproductive success may be limited by the quantity and quality of suitable spawning habitat. Spawning site selection should place early life history stages in or near habitats that will foster growth and survival (Peebles and Tolley 1988). Nevertheless, the actual spawning sites used by a species may vary both seasonally and annually because of climatic variation and changing hydrological conditions (Childers *et al.* 1990, Saucier and Baltz 1993).

Future research needs to enhance our understanding of the reproductive requirements of important fishes in the Gulf of Nicoya include descriptive studies of fish sound production, larval development, and female spawning frequency. Since many species produce more than one sound (Mok and Gilmore 1983), an analysis of the full repertoire of all *Cynoscion* species and other important fishes is necessary for positive identifications. Descriptive egg and larval studies would be useful to verify actual spawning and to study recruitment phenomena (Holt *et al.* 1985, 1988). Corvina fisheries management would be enhanced by a better understanding of the spawning patterns of females (Tucker and Faulkner 1987, Saucier and Baltz 1993), which is necessary to estimate their age-specific reproductive potentials (Nikolskii 1969, Parrish *et al.* 1986).

The artisanal exploitation of corvina in the Gulf of Nicoya is predominantly a gillnet activity. Although trawling has been banned in the inner Gulf for the past 30 years, in an effort to protect what was supposed to be a natural spawning and nursery area, gill nets rigged with round concrete weights are used to "sweep the bottom" by drifting on the incoming or outgoing tides, thus increasing the efficiency of capture. Such fishing may alter habitat characteristics and make the nominal unit of fishing effort more effective, especially if the gill net passes through a natural drumming aggregation. Local gillnet fishermen are familiar with corvina sound production behavior and some can identify the drumming species. Corvina fishing takes place only during periods known locally as "mareas de corvina" (Corvina tides), which fall immediately after the highest (or lowest) tides of the month, which gill netters claim to be the best for fishing. Thus, heaviest fishing concentrates in a period of eight to ten days a month, and we also suspect that fishing during "corvina tides" is focused on natural drumming aggregations. Under present management, the fishery may be reducing natural spawning success and maximizing effort by focusing on natural spawning aggregations.

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