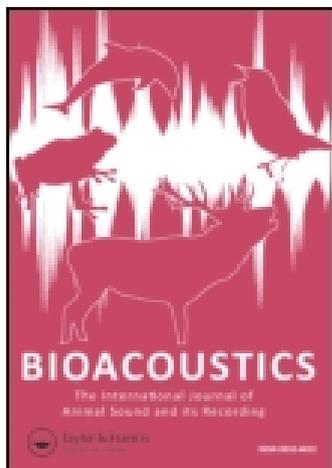


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Bioacoustics: The International Journal of Animal Sound and its Recording

Publication details, including instructions for authors and subscription information:

<http://www.tandfonline.com/loi/tbio20>

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Published online: 13 Apr 2012.

To cite this article: DAVID A. MANN & PHILLIP S. LOBEL (1995) PASSIVE ACOUSTIC DETECTION OF SOUNDS PRODUCED BY THE DAMSELFISH, *DASCYLLUS ALBISELLA* (POMACENTRIDAE), *Bioacoustics: The International Journal of Animal Sound and its Recording*, 6:3, 199-213, DOI: [10.1080/09524622.1995.9753290](https://doi.org/10.1080/09524622.1995.9753290)

To link to this article: <http://dx.doi.org/10.1080/09524622.1995.9753290>

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PASSIVE ACOUSTIC DETECTION OF SOUNDS PRODUCED BY THE DAMSELFISH, *DASCYLLUS ALBISELLA* (POMACENTRIDAE)

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ABSTRACT

We developed and field-tested a passive acoustic detector that collects data on sound production by sonic fish. The detector was deployed to measure the timing of sound production by males of the damselfish *Dascyllus albisella* (Pomacentridae), at Johnston Atoll, Central Pacific Ocean. Sound production rates were higher during the reproductive season (April) than during the non-reproductive season (October). The highest rates of sound production occurred on the day before and day of egg-laying. Sound production rates decreased during brood care, and increased again after hatching. The correlation of sound-production rate with the spawning cycle provided a reliable acoustic signal that was monitored by the detector. This new technology provides a capability for obtaining detailed measurements of reproductive activity over long time periods. Multiple detectors can be used simultaneously to monitor reproduction over large spatial scales.

Key words: passive acoustic detection, sound production, damselfish, *Dascyllus albisella*, dawn chorus.

INTRODUCTION

We invented and tested a new oceanographic instrument that monitors fish reproductive activity using passive acoustic detection of courtship and mating sounds. This detector monitors individuals within a delineated area, and multiple detectors can be used to monitor populations over wide spatial scales. Most importantly, this device provides continuous time-series measurement of reproduction that can be matched to data recorded by physical oceanographic instruments simultaneously.

Quantitative measurement of reproductive cycles is crucial to an understanding of the population biology of fishes. In comparison with

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many other reef fishes that spawn planktonic eggs, reproduction in pomacentrids is more easily studied because they lay demersal eggs. However, measuring reproduction simultaneously at many sites over large spatial scales (e.g. tens to hundreds of kilometers) on a daily basis is not logistically feasible.

Earlier studies on the timing of sound production and reproduction suggest the potential broad applicability of using passive acoustic detection technology with sonic fishes. Johnson (1948) first suggested the diurnal and seasonal occurrences of fish sounds might be useful to study the ecology of fishes. Brawn (1961) found that the level of sound production and reproduction in the cod *Gadus callarias* (Gadidae) varied both seasonally (highest from September to November) and daily, with peaks of sound production after dusk associated with spawning. Lobel (1991) found that the parrotfish *Scarus iserti* (Scaridae) produced a broad-band sound during the spawning rush, and that the hamletfish *Hypoplectrus spp.* (Serranidae) produced specific sounds during courtship and mating. The time and place of spawning of several sciaenids *Pogonias cromis*, *Bairdella chrysoura* and *Cynoscion nebulosus* have been identified using hydrophones and listening for sounds produced by spawning aggregations (Mok and Gilmore 1983, Saucier et al. 1992, Saucier and Baltz 1993).

We tested the ability of the passive acoustic detector to quantify patterns of sound production and reproduction with the pomacentrid *Dascyllus albisella*. Pomacentrids are well-known sound producers (e.g. Myrberg 1972, Spanier 1979, Chen and Mok 1988). Male *D. albisella* are territorial and produce stereotypical sounds associated with courtship and mating, making them ideal for testing this detector (Lobel and Mann 1995). The purpose of this study was to evaluate the feasibility and utility of using sounds to quantify patterns of pomacentrid reproduction.

MATERIALS AND METHODS

Passive acoustic detector

The passive acoustic detector consists of a sonobuoy (an FM-wideband radio transmitter on a surface buoy) connected to a hydrophone (BioAcoustics, Box 549, Woods Hole, MA) anchored in an individual male's territory. Sounds are transmitted from the hydrophone by the radio transmitter to a nearby laboratory where they are received and processed through a bandpass filter (between 200 Hz and 600 Hz) to reduce noise from other sound sources. The dominant energy in the calls produced by *Dascyllus albisella* is in this frequency range (Lobel and Mann 1995). The filtered sounds are then processed by our

custom-built signal detector that recognizes individual sound pulses and measures and stores to computer pulse duration (ms), pulse amplitude and the time of sound production (ms). The acoustic detector is capable of processing input from four separate sources simultaneously, sampling each of them at 1 kHz. This sampling rate would provide adequate detection of pulses greater than 5 msec. Since we are not estimating the signal frequency, there is not a problem with aliasing.

The calls produced by *D. albisella* contained multiple pulses and were reconstructed from the computer data file using the following species-specific criteria, based on the pulse and call characteristics of courtship calls (Lobel and Mann 1995):

1. Accept pulses with duration > 5 msec and < 50 msec.
2. Group pulses into a call if two consecutive pulses are within 30–79 msec of each other. Otherwise begin constructing a new call.
3. Discard 1- and 2-pulse calls.

The resulting data set includes: the time of a call (ms), number of pulses, call duration (ms), and the amplitude of the call. Calling rates were calculated by binning the data into time periods of 10 minutes, 1 hour, and 1 day.

Field study

The acoustic detector was deployed at Johnston Atoll, Central Pacific Ocean, (16° 44.2' N, 169° 31.0' W) in October 1993 and April 1994. Data on sound production activity was collected for one male (Male 2) *D. albisella* in October 1993 when no reproduction took place, and for three males in April 1994, all of which spawned during the study period. In April, two individuals were monitored simultaneously. One hydrophone was located in the territory of Male 2 from April 1–20. The other hydrophone was located in the territory of Male 1 from April 1–15, and was then moved to Male 3 from April 16–28. The input volume was controlled using attenuators on the detector. The acoustic signal was monitored in the laboratory on audio speakers, and LED lights on the detector indicated when a sound was detected on a given channel. The attenuator was adjusted so that the input levels to the channels were equal and *D. albisella* sounds were only detected on one channel at a time, so that the same sound was not detected simultaneously by two different channels. The input level was not changed when the hydrophone was moved from Male 1 to Male 3.

The nesting status of eight males was visually assessed daily from April 1–28, between 0800–1200h. In October surveys were made October 14, 16, 20, 22 and 27. Quantitative measurement of brood sizes was not possible due to their irregular shape, accessibility, and because

they occurred on substrates with varying topography, from flat rocks to highly structured *Acropora spp.* coral. Brood sizes were estimated by comparison to a standard area of approximately 185 cm², and then were assigned to a size category. The approximate ranges of the brood-size categories are: brood size 0 = no eggs, brood size 0.5 = >0–139 cm², brood size 1 = 139–278 cm², brood size 2 = 278–463 cm², brood size 3 = 463–648 cm², brood size 4 = 648–833 cm², brood size 5 = 833–1018 cm². Male territories were mapped by measuring the distance and compass bearing between pairs of sites. The distances between male territories were Male 1–2 = 11.1 m, Male 2–3 = 8.0 m, Male 3–4 = 2.7 m, Male 1–3 = 16.6 m.

Light level (solar irradiance) was recorded using an integrated measurement every 10 minutes with a pyranometer sensor sensitive to 400–1100 nm (i.e. sunlight) (LICOR Inc., Lincoln, Nebraska).

Statistical tests were performed with StatWorks (Cricket Software, Philadelphia, PA). Spearman rank correlations (r_s) were calculated, since log and square root transformations did not yield normally distributed data for call rates in 10-minute bins.

Calibration

For analysis of call detection accuracy, the transmitted signal from the hydrophones was split with one input to the detector and the other input to a tape recorder (SONY Walkman Professional WM-D6C). These sounds were manually analyzed in the laboratory using the signal processing program SIGNAL (Engineering Design, Belmont, MA) and compared to the reconstructed calls recorded by the detector.

RESULTS

Accuracy of the acoustic detector

To measure acoustic detector accuracy, calls recorded on audio tapes were compared with the detected calls (Table 1). The purpose of the accuracy test was to determine: a) if the device correctly detected calls by the single fish that was being monitored, b) if calls of other, more distant *Dascyllus albisella* males were also detected, and c) if sounds from other fishes, such as squirrelfishes (Holocentridae), or other sources were detected and falsely categorized as *D. albisella* sounds.

D. albisella calls recorded on audio tapes were processed on a sound-analysis computer system, identified manually, and categorized based on amplitude as either proximate or background calls. Proximate calls were high amplitude *D. albisella* sounds, which were likely produced near the hydrophone by the resident male. Background calls

TABLE 1

Call detection accuracy. Comparison of the calls manually detected from a tape made of the detector input with the calls detected by the acoustic detector. Only channels 1 and 3 (Ch1 and Ch3) were used during the deployment (channel 2 and channel 4 were not used). False detections show the # sounds detected by the acoustic detector/# sounds manually detected from the tape.

	Hydrophone Input	Ch-3 (Male 2)	Ch-1 (Male 1)	Ch-1 (Male 3)	Ch-1 (Male 3)	Ch-1 (Male 3)
Tape Recording Information	Date	4 April	12 April	17 April	17 April	24 April
	Time of Recording	23:17	19:35	15:30	17:45	08:04
	Minutes Analysed	45	45	45	45	11
Calls Manually Detected on Tape	Proximate	16	120	44	184	189
	Background	0	25	5	20	16
Calls Detected by Acoustic Detector	Calls Detected Ch1	10	72	44	108	169
	Calls Detected Ch3	4	44	0	7	*
	Total # Calls Detected /Proximate Calls Manually Detected	14/16	116/120	44/44	115/184	169/189
	Background Calls Detected on Main Channel	0/0	3/25	0/5	3/20	8/16
	Calls Detected Both Channels	2 **	0	0	2 **	*
False Detections	Hydrophone Bites	0/0	0/3	0/0	5/16	0/0
	Squirrelfish or Unknown	0/25	0/21	0/0	0/0	0/0

*Channel 3 was not operating on 24 April 1994.

**For calls detected by both channels the call detected on channel 3 was louder than the calls detected on channel 1.

had lower amplitudes and different frequency characteristics than proximate calls (Lobel and Mann 1995) and were likely produced by more distant males.

Accuracy tests of the detectors deployed in the territories of Males 1 and 2 indicated that 96% of the calls were correctly detected (130 calls detected/136 calls), with less than 2% false detections of other individuals (3 false detects/151 calls). We could not determine whether the detector in the territory of Male 3 was also detecting calls made by Male 4, since his territory was nearby and not separately monitored. For Male 3, 79% (328 calls detected/417 calls) of the proximate calls were detected, with 2% (11 false detects/458 calls) false detections of other individuals.

Sounds that might be falsely detected were grouped into those that were presumably produced by holocentrids (possibly *Myripristis berndti*), and those produced by other fishes (e.g. scarids and acanthurids) biting the hydrophone (Table 1). Sounds presumably made by holocentrids were produced at night (from 19:30 to 00:00), and none (0/46) of these were detected. 26.3% of the bites on the hydrophone produced false detections (5/19 bites), but they were rare relative to the number of correct call detections (5 hydrophone bites were detected out of a total of 458 *D. albisella* calls detected).

Sounds produced by SCUBA diver bubbles were also falsely detected (57 diver bubble calls detected/97 total calls detected). The acceptable pulse duration range was reduced (from 6–49 msec to 6–25 msec) to try to decrease the number of false detections, but this adjustment also decreased the number of correct call detections, so the range was left unchanged. The time periods when divers were present within 20 m of the hydrophone were recorded on each dive (mean \pm SD = 20.75 \pm 14.3 minutes per day). Divers were in the study area for 21 minutes when the 57 false detections were made. The time periods of diver presence were not removed from the data.

Calling rate and timing of spawning

Reproduction in April was synchronized for the eight males within the study area, such that 72% (16/22) of the spawnings occurred on the same day, 23% (5/22) within one day, and 5% (1/22) within two days. Spawning was cyclic with 72% of the spawnings taking place on April 7, 13, 20 and 26. Brood care lasted four days for broods that were laid and hatched during this study (n = 13 nests of 8 males). There were no overlapping broods. The beginning of spawning was never observed. Spawning was observed as late as 13:00, but was usually completed by 08:00.

The daily calling rates of Males 1 and 3 increased prior to nesting with peaks either the day before or day of spawning, after which they

rapidly decreased and remained low during brood care (Figure 1a and b). After hatching, the calling rate of the males increased again. Thus, sound production regularly increased and decreased with the spawning cycle. The April 6 brood of Male 1 did not develop, and embryos were not present on April 8. Calling at night peaked on the day of egg-laying (Figures 1 and 2).

Male 2 exhibited the same pattern of sound production as Males 1 and 3, although embryos were not found in his territory on the first two laying cycles (Figure 1c). His calling rate decreased on each of these spawning cycles, even though he did not receive eggs. Since these sites were not surveyed until after spawning activity was completed, it is possible that spawning occurred and that the eggs were cannibalized or eaten by predators before the survey was conducted (07:40 on April 7; 11:00 on April 13). Male 2 received eggs on the third spawning cycle (April 20), and the pattern of sound production was the same as the patterns of other males.

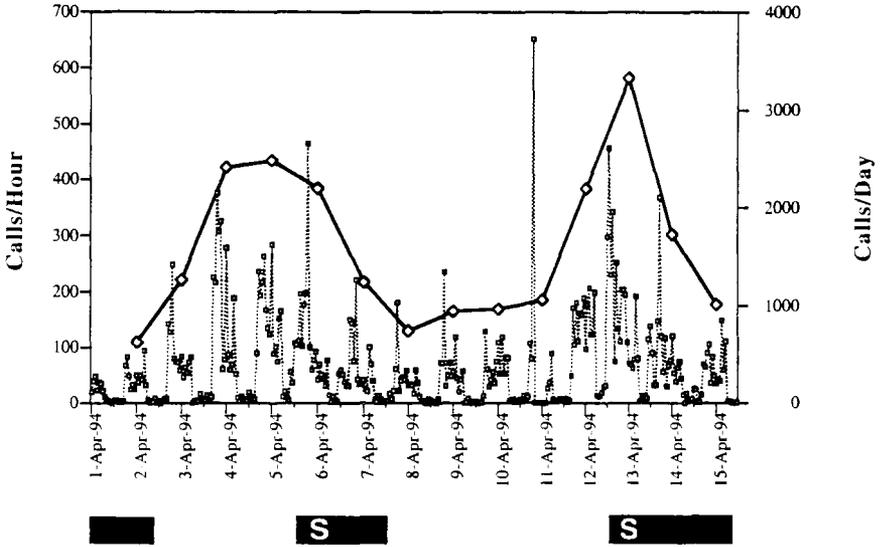
The acoustic detector was deployed during October 1993 in the territory of Male 2 (Figure 1d). We did not observe spawning by Male 2 or any other male in October, although we did see visiting behavior by some females ($n = 3$ observations of visiting behavior). A diel cycle in sound production occurred as in April. The calling rate in October was significantly lower than the calling rate during April (October: mean \pm SD 658 ± 258 , range = 171–1064; April: 1205 ± 631 , range = 499–2648; $p = 0.015$, one-tailed t-test on log-transformed data) (Figure 1c and d).

SCUBA bubble interference during this study was negligible, because divers were present for a short period each day (about 21 minutes) and the estimated number of false detections (about 57 per day) were low compared to the daily calling rates of the fish (daily calling rate range: Male 1 = 623–3327, Male 2 = 499–2648, Male 3 = 1686–7850). The accuracy test for the detector indicated that the data from Male 3 also included calling by another nearby fish, Male 4 (background calls detected on main channel, Table 1). This contention is supported by data for the calling rate of Male 3, which was more than twice as high as Males 1 and 2 (daily calling rate mean \pm SD: Male 1 = 1585 ± 809 , Male 2 = 1205 ± 631 , Male 3 = 4324 ± 2493).

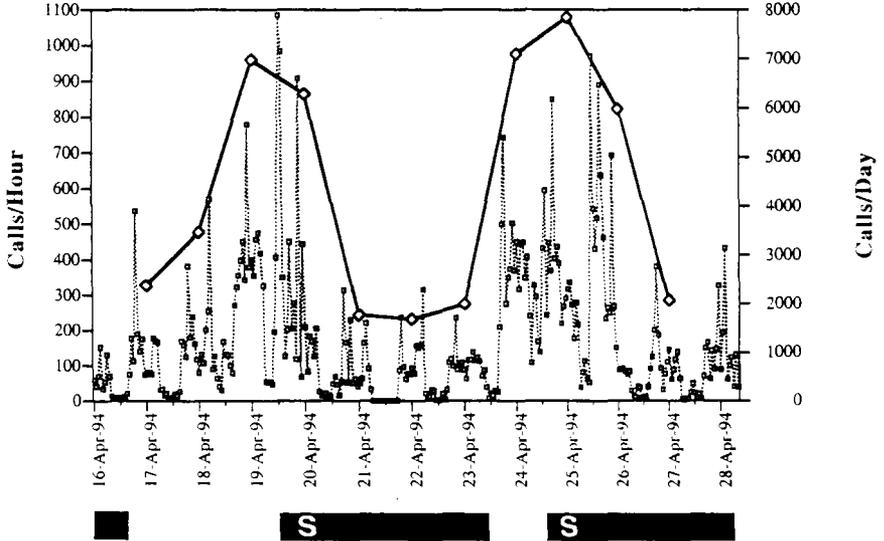
Accuracy of spawning event detection

Two features of sound production were associated with the spawning cycle in *D. albisella*. The highest daily rates of calling occurred on the day before and on the day of spawning, and calling rates between 00:00–06:00 peaked on the day of spawning. To quantify the accuracy of spawning detection, the following paradigm was applied to the detector data. A day was designated as a spawning day if the total calls

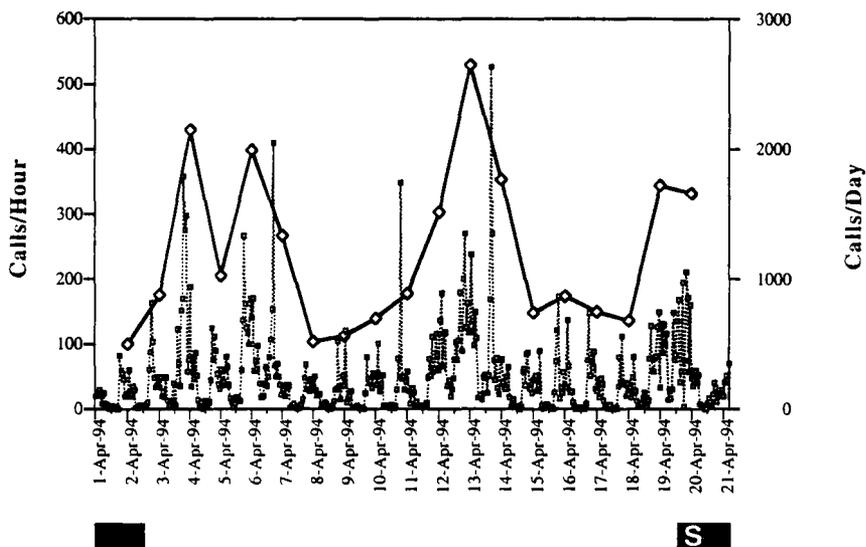
A. Male 1



B. Male 3



C. Male 2



D. Male 2

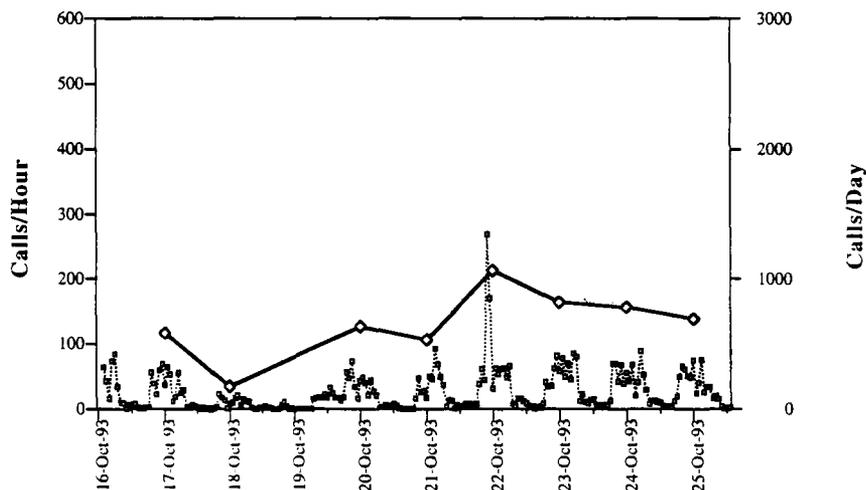


Figure 1. Rate of sound production in calls/hour (squares, dotted line) and calls/day (diamonds, solid line) and occurrence of eggs. Boxes below dates indicate days eggs were present in a male's nest. The day of egg-laying is indicated by an 'S' in the box. Labelled tick marks are at 1200h. Unlabelled tick marks are midnight. Note the difference in scales for A, B and C.

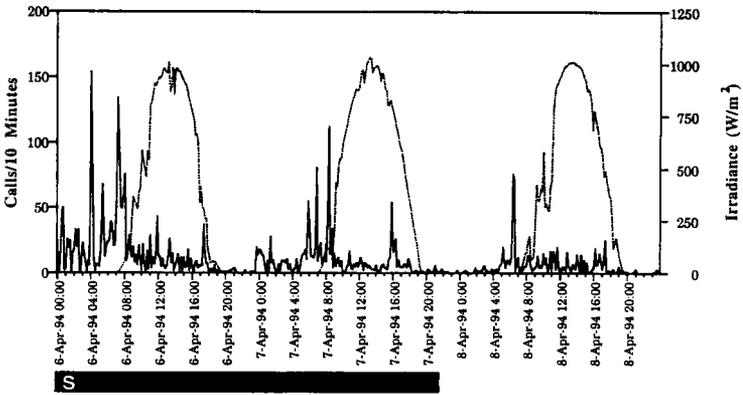
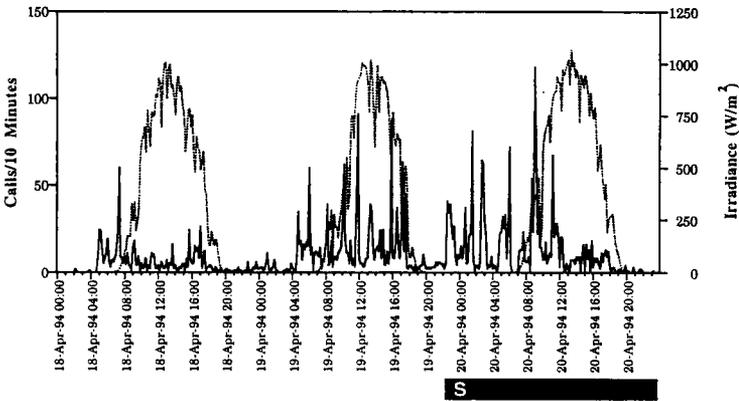
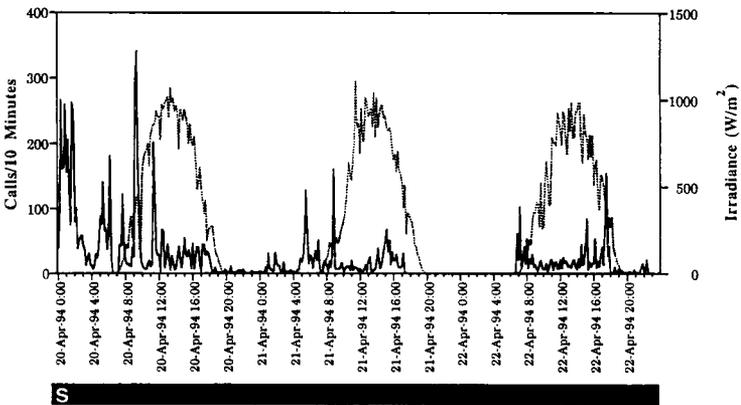
A. Male 1**B. Male 2****C. Male 3**

Figure 2. Rate of sound production in calls/10 minutes (solid line) plotted with irradiance (dotted line) for three individuals. Boxes below dates indicate days eggs were present in a male's nest. The day of spawning is indicated by an 'S' in the box.

per day were at least twice the lowest levels three days before and three days after that date. If two dates satisfying the previous criterion were within two days of each other, then the spawning day was designated as the day with the greatest number of calls from 00:00–06:00.

80% of the spawning events (4/5) were correctly designated; one spawning event was designated a day later than it actually occurred (April 25 spawning of Male 3). 4% (2/49) of the days were misclassified as spawning days, when no eggs were found (April 6 and 13 of Male 2). However, Male 1 received eggs on both those days, and Male 3 received eggs on April 13.

Sound-production rate and brood size

To test the hypothesis that measures of calling rate could be used to estimate brood size, six measures of calling rate (maximum calls/10 minutes, calls/hour and calls/day, both the day before and after spawning) were correlated with brood size ($n = 6$). The highest correlation was for maximum calls/10 minutes the day before spawning ($r_s = 0.754$, $p = 0.084$). When Fish 3 was excluded from the analysis, because it may represent calling by more than one male, the maximum calls/10 minutes was better correlated with brood size ($r_s = 0.949$, $p = 0.051$, $n = 4$).

Patterns of sound production

Most sound production took place during the daytime with lower levels of calling at night-time (Figures 1 and 2). Sound production peaked each day at dawn ($n = 45$ days for 3 males) (Figure 2).

To test the hypothesis that calling rates were consistent over consecutive ten-minute time periods, the calling rate in one ten-minute period was plotted against the calling rate in the following ten-minute period (Male 1 $r_s = 0.170$, $p < 0.001$, Male 2 $r_s = 0.313$, $p < 0.001$). Although these correlations are significantly different from zero, they are low. Most of the calling was less than 50 calls/ten minutes (Male 1 96% (2072/2153), Male 2 98% (2862/2916)). Periods with high rates of calling (> 50 calls/ten minutes) were generally followed by periods with little calling (< 50 calls/ten minutes) (e.g. % time periods with > 50 calls/ten minutes followed by time period with < 50 calls/ten minutes: Male 1 75% $n = 61/81$, Male 2 81% $n = 44/54$).

To test the hypothesis that adjacent males influence each others' calling rates, the calling rates (calls/10 minutes) of Male 1 and Male 2 were compared from April 1–15 ($r_s = -0.208$, $p < 0.001$). The correlation was significantly different from zero, but the correlation was low. Most

calling (95%, $n = 2048/2153$) was less than 50 calls/ten minutes, and high rates of calling (> 50 calls/ten minutes) by one male were associated with low levels of calling by the other male (< 50 calls/ten minutes) for 93% ($n=98/105$) of the data.

Periods with high rates of courtship probably result from female visiting events. One full visiting event in which one female travelled to the nests of three males was recorded on video and analyzed. The number of courtship calls in the time period preceding and during visiting are listed in Table 2. Calling rates of these three males increased 68-fold during female visiting. This was the only full visiting event recorded on video. Many visiting events were observed during the nest surveys, and the calling rates of the males were noted to be qualitatively much higher ($n = 25$ events for 15 males in April 1994).

Since *D. albisella* are diurnal planktivores, one would suspect that they would be inactive at night (between sunset and sunrise). However, sound production was detected at night and was most intense just before spawning. We believe these sounds were calls by *D. albisella* and not from some other source because; a.) analysis of the audio recordings of the detector input showed *D. albisella* made sounds during the night (19:35–00:00) that were detected by the detector (Table 1), b.) divers heard sounds characteristic of *D. albisella* at night, and c.) the most likely potential source of non-*D. albisella* sounds, those produced by holocentrids, were not detected by the acoustic detector during calibration tests. The sound-producing *D. albisella* were not seen during the night dives, so it is unknown whether they perform the signal jump with these sounds.

TABLE 2

Calling rates before and during one visiting event by one female to three males. The duration of the visiting event was 2.18 minutes. The time period before visiting was 13.27 minutes. Calling rate is calls/minute. The individual fish were not the same males monitored with the detector (i.e. Males 1, 2 and 3).

Fish	Before Visiting		During Visiting	
	# Calls	Calling Rate	# Calls	Calling Rate
Fish A	3	0.23	17	7.80
Fish B	0	0	10	4.59
Fish C	0	0	7	3.21
Total	3	0.23	30	15.60

DISCUSSION

Sound production by *Dascyllus albisella* peaked at dawn each day during the reproductive season and varied in intensity with the daily spawning cycle. Crepuscular peaks in sound production are common for sonic fishes. Steinberg et al. (1965) and Myrberg (1972) found dawn and dusk peaks in sound production by *Pomacentrus partitus* (Pomacentridae). Breder (1968) made observations on the timing of sound production of sonic fishes from 1961–1965, with virtually continuous year-round coverage. He found a peak in calling of the sea catfish *Galeichthys felis* (Ariidae) at dusk, and that most boat-whistling of the toadfish *Opsanus beta* (Batrachoididae) occurred at sunset. Winn et al. (1964) and Steinberg et al. (1965) found that sound production by the squirrelfish *Holocentrus rufus* (Holocentridae) peaked at both dawn and dusk, with less during the day, and little at night. In contrast, Salmon (1967) did not find a crepuscular peak in the calling of the squirrelfish *Myripristis berndti* (Holocentridae); most sonic activity occurred between 05:00–19:00h when they were aggregated in caves.

We have demonstrated that the passive acoustic detector accurately detects and records sounds made by *D. albisella*. The pattern of sound production was predictive of the timing of spawning on a daily basis for the fish studied. These results corroborate data from *Dascyllus trimaculatus* and *Dascyllus marginatus*, which also show increased courtship activity on days of spawning (Fricke 1973, Holzberg 1973). The lack of social facilitation of courtship by neighboring males (Males 1 and 2) may be because a male courts most vigorously in response to female visiting, not other male courtship, and a female will not visit two males simultaneously, but is likely to visit several males during visiting.

False detections of spawning were rare. The two false detections of spawning occurred on days when immediately neighboring males received eggs. They did not occur during non-spawning periods. In this sense, the acoustic detector was accurately measuring female reproductive activity. Thus, one acoustic detector could be used to accurately monitor reproduction of a local group of *D. albisella*, even though the individual being monitored might not receive eggs during each identified spawning event.

The maximum calling rate (calls/10 minutes) on the day before spawning was positively correlated with brood size, and took place during female visiting, although the result was not statistically significant at $\alpha = 0.05$. More males need to be sampled to statistically verify this relationship. These results corroborate those of Gronell (1989) who found that the calling rate during female visiting on the day before spawning in *Chrysiptera cyanea* (Pomacentridae) was correlated to male spawning success. Furthermore, signal jumping

rates of *Pomacentrus partitus* were correlated with male reproductive success in two separate studies (Schmale 1981, Knapp and Warner 1991). These studies suggest that passive acoustic detection may be broadly applicable to measuring reproduction in pomacentrids. Co-mingling species may be more difficult to study, such as many of the pomacentrids in the Caribbean, if their courtship sounds are not distinguishable by pulse number or pulse rate. For these situations more complex analyses using sound localization by analyzing differences in time of arrival at multiple hydrophones could be used to obtain data on calling by individuals in groups (Spiesberger and Fristrup 1990).

ACKNOWLEDGMENTS

Acoustic equipment was provided by grants from the NOAA National Undersea Research program (NOAA/NURC-FDU 89-09-NA88A-H-URD 20), the Sea Grant program at W.H.O.I. (NA86-AA-D-SG090 project R/B-97-PD), the U.S. Army Chemical Materiel Destruction Agency (via NOAA Sea Grant NA90-AA-D-SG535 and the Office of Naval Research N00014-91-J1591 and N00014-92-J-1969), the U.S. Army Legacy Resource Management Program (DAMD 17-93-J-3052), the Island Foundation and the Kelley Foundation. Sippican Inc. provided expertise in sonobuoy technology through the kind help of Jim Hannon and others. Jim Bowlin, D. Koehler, and K. Wannop developed the electronics for the passive acoustic detector. G. Sancho, E. Horgan, J. Barimo, D. Ma, A. Economakis, and M. and K. Busquets provided many hours of help both above and below water. G. McCloskey, G.W. Walton, M. Boyce, R. DiRosa and many others at Johnston Atoll provided invaluable logistical support. We thank G. Sancho for providing comments on this paper, and G. Taroncher for German translations. Finally, we thank Art Myrberg, Jr. and an anonymous reviewer for their helpful comments.

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Received April 5, 1995, revised June 5, 1995 and accepted 21 June 1995