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Spawning vocalizations in male freshwater gobiids (Pisces, Gobiidae)

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Synopsis

Males of two freshwater Italian gobies, the common goby, *Padogobius martensii* and the panzarolo goby, *Knipowitschia punctatissima*, emit trains of low-frequency pulses, i.e. 'drumming' sounds, in the presence of a ripe female in the nest. In *P. martensii* the drumming sound is usually followed by a tonal sound (complex sound). Examination of the pulse structure suggests that these sounds are produced by muscles acting on the swimbladder. Both species exhibited high emission rates of spawning sounds, especially before the beginning of oviposition. Moreover, spawning sound production ceased only after the female abandoned the nest, which always occurred at the end of oviposition. This is the first study reporting the production among fishes of distinct sounds during protracted spawning. Unlike sounds produced just before mating by fishes with planktonic or demersal zygotes, the spawning sound production of these gobies does not function to coordinate mating events in the nest. The presence of a two-part vocalization by male *P. martensii* even suggests a functional dichotomy of spawning sounds in this species.

Introduction

Sound production during reproductive activities is a widespread phenomenon among territorial fishes (Fine et al. 1977, Myrberg 1981); nevertheless, sound production during spawning itself has not been reported for any of the taxa investigated (e.g. Myrberg et al. 1965, Stout 1975, Mok 1981, Crawford et al. 1986). Only recently, Lobel (1992) provided the first documentation for the production of unique acoustic signals during mating by *Hypoplectrus unicolor* (Serranidae), a coral-reef fish that reproduces by releasing gametes into the water. In this species sounds are produced just prior to, or simultaneously with, gamete release; hence they probably ensure synchronous gamete release. The apparent general muteness of fishes during actual mating is surprising when one considers that vocalization under such circumstances is well documented for other vertebrate groups (e.g. Smith 1977, Pierce et al. 1989), and among insects (e.g. Alexander 1967, Aiken 1985). Far from simply synchronizing the copulatory act between partners, these signals have been thought to facilitate mating in several ways, including their role as advertising displays. The lack of spawning sounds among fishes is puzzling. One possible reason, already reported by Lobel (1992), is that unlike courtship or aggression, mating events occur sporadically and are concealed. Thus, they probably go unnoticed during field observations. This is a plausible explanation for species that form spawning aggregations and/or produce pelagic eggs, whose reproductive behaviour has seldom been observed in the laboratory (but see Brawn 1961). Nevertheless, this does not explain the absence of spawning sounds in species with demersal eggs, where the production of sounds during pre-spawning activities has been more comprehensively documented, both in the field and in the laboratory (Myrberg 1981).

Among teleosts, gobiids are well known for their ability to produce sounds in the course of reproduction (Tavolga 1958, Kinzer 1961, Kishi 1979, Mok 1981, Takemura 1984, and for the Italian freshwater goby *Padogobius martensii*, see Torricelli & Romani 1986, Torricelli et al. 1986, Torricelli et al. 1990). Each courtship sound in *P. martensii* is a short vocalization lasting a few hundred milliseconds and consists of a train of rapidly repeated pulses (40–220 pulses sec^{-1}) with the repetition rate decreasing throughout the sound emission. Water temperature has a marked and predictable effect on the sound parameters under consideration: the pulse rate and its modulation increases and the sound duration decreases when temperature increases. The number of courtship sounds emitted by the male is primarily affected by his position within the territory, the greater number of sounds being produced when the male is inside the nest. The male continues to vocalize when he is joined in the nest hollow by the female, albeit at a lower rate than when the female is outside. When the female is in the nest the male regularly produces drum-like vocalizations (Lugli unpublished data). Similar vocalizations are also emitted by the other freshwater goby of northern Italy, *Knipowitschia punctatissima* (Canestrini, 1864) (= *Orsinigobius punctatissimus*) when both partners are in the nest (Lugli unpublished data). Interestingly, *K. punctatissima* is mute during courtship. In both species the sound emission is always associated with a slight lifting of the head and opercular covers of the male (Lugli 1990, Lugli unpublished data). Thus, the female remains silent either before, during, and after oviposition.

Specifically, this study analyzes the acoustic behaviour of male *P. martensii* and *K. punctatissima* during pre-spawning and spawning behaviour in the nest. We show that in both *Padogobius martensii* (Günther, 1861) and *K. punctatissima* the emission of these unique vocalizations, which we refer to as 'spawning' sounds, continues throughout the mating period, i.e., from the beginning of oviposition until the female departure from the nest hollow. Thus, the presence of distinct vocal activity during protracted mating is hereby reported for the first time among fishes. A detailed description of the acoustic properties of spawning sounds from the two species is reported and sound producing mechanisms are discussed. Furthermore, field-recorded spawning sounds of male *P. martensii* are compared with laboratory sounds.

Materials and methods

Fish collection and housing

Fishes were collected from the Stirone Stream, north-west of Parma, Emilia-Romagna (*P. martensii*) and in the spring-waters of Valle Re, north-west of Reggio Emilia, Emilia-Romagna (*K. punctatissima*), at the beginning of the reproductive season. A group of 7 adult *P. martensii* (four males and three females; size range 55–82 mm TL) was established in a large tank (160 × 80 × 40 cm) in the laboratory. Two laboratory groups of *K. punctatissima*, each comprising three males and six females (size range 25–45 mm TL), were maintained in 20 and 80 l aquaria. A few adult males of both species were also maintained singly in small tanks (44 × 24 × 26 cm). All tanks had the bottom covered with a 2–3 cm layer of sand. Tanks were also provided with a filter and one (small tanks) or more (community tanks) shelters to serve as hiding-places/nests). Tunnel-shaped PVC shelters were used as nests by male *P. martensii*. Stones and bivalve shells (genus *Unio*) were used as nests by males *K. punctatissima*. Bunches of *Elodea canadensis* were planted in the community tanks of *K. punctatissima* to approximate the naturally heterogeneous environment. All tanks were set on vibration-absorbing material (small rectangles of foam rubber, 2 cm thick) to minimize background vibrations.

Sound recording techniques and signal processing

Laboratory sounds were collected with a small, custom-made hydrophone of high sensitivity (– 146 dB re 1V μPa^{-1}, frequency response flat from 10 Hz to 2 kHz), positioned before the entrance of the nest housing the male. Sounds for spectrographic analysis were recorded on 1/4″ tapes with an open reel recorder operated at 19 cm sec^{-1} and, simultaneously, on the audio track of a video tape recorder used for behavioural observations. The hydrophone was connected to a conditioning amplifier (B&K 2626) with high- and low-pass filters set at 30 Hz and 3 kHz, respectively. Field sounds were collected with the pre-amplified ITC hydrophone type 8073 (sensitivity: – 167 dB re 1V μPa^{-1}), placed before the nest entrance housing the vocalizing male. The hydrophone was connected to a portable DAT recorder.

All field (*P. martensii*) and laboratory (both species) recordings were analysed in real time with a Digital Signal Processing Workstation (Pavan 1992). Selected sounds by both species were stored in digital format and subsequently analysed: sounds emitted by *P. martensii* were analysed in the ranges 0–0.5 kHz and 0–1 kHz, while those emitted by *K. punctatissima* were analysed in the ranges 0–1 kHz and 0–2 kHz. Analysis parameters (i.e. time resolution, bandwidth and dynamic range) were set to obtain the best spectrographic representation of signals in relation to their acoustic structure (Tsao 1984, Beecher 1988).

Data collection and analysis

For both species, laboratory sounds were recorded from pairs engaging in pre-spawning and spawning activities in the nest hollow. This was achieved by observing fish communities, and making recordings when sexual interactions of interest were detected. Recordings from solitary males were obtained after introducing a ripe female into the male's tank. Aquarium filters were stopped and water temperature was measured (range: 16–24° C, for both species) before sound recording was started. Sounds used for analyses were obtained from a total of 15 different pairs of *P. martensii* (see also Table 1), including 2 from the community tank, and from 5 pairs of *K. punctatissima*, including 4 from the 2

Table 1. Characteristics of sounds emitted by males *P. martensii* and *K. punctatissima*. Mean values of the male total length and of the water temperature are also reported. Range values are given in parentheses.

Species	Number of pairs	TL (mm)	Sound type	Number of sounds	Temperature (° C)	Duration (ms)	Number of pulses sound^{-1}	Pulse rate (Hz)
P. martensii	15	74.9 (62–87)	complex	120	21.2 (15.6–23.1)	556.1 (185–1113)	–	–
	15	74.9 (62–87)	tonal (complex sound)	120	21.2 (15.6–23.1)	290.2 (72–695)	46.7 (14–88)	164.5 (112.5–194.4)
	15	74.9 (62–87)	pulse train (complex sound)	120	21.2 (15.6–23.1)	268.4 (57–815)	9.7 (2–25)	35.8 (21.7–54.4)
	15	74.9 (62–87)	pulse train	125	20.4 (15.6–23.1)	429.8 (50–787)	14.4 (2–27)	33.5 (22.5–48.2)
	15	75.1 (62–87)	tonal	83	21.3 (15.7–23.1)	408.7 (114–745)	65.4 (18–156)	162.7 (114–187)
K. punctatissima	5	40.0 (32–54)	pulse train	40	20.2 (16.0–24.0)	715 (450–1040)	21.8 (17–30)	31.8 (24–41)

community tanks. Spawning occurred in 6 to the 15 pairs of *P. martensii*, 1 of which was in the community tank. Three pairs of *K. punctatissima* spawned, 2 in the community tanks. Spectral analyses revealed no obvious differences between the basic acoustic structure of sounds emitted by solitary males and those emitted by community males, nor between sounds produced before oviposition and those emitted after the beginning of oviposition. Hence, all the recordings obtained for one species were pooled regardless of the source (i.e. isolated or community males) and position in the spawning sequence, unless specified otherwise. The following three sound parameters were quantified: duration (ms); number of pulses per sound; mean pulse rate (Hz), calculated dividing the number of pulses by the duration of the sound. In order to measure vocal activity and examine the association between sound and behavioural patterns of the male, behavioural sequences and accompanying sound production were recorded on a VHS videotape-recorder. In total, behavioural observations were made from 7 h of video-recorded spawning interactions by 5 different pairs of *K. punctatissima*, and from 14 h video-recorded spawning interactions by 14 different pairs of *P. martensii*. Emission rates (both species) and proportion of different sound types (*P. martensii*) were calculated for each pair before or just after the beginning of oviposition, when sound production by the male was highest.

In the field (Stirone Stream), sound production by 4 *P. martensii* males was elicited by introducing ripe females into the nest hollow. Water temperature, measured at the time of sound recording, ranged from 20° C to 24° C. Sound pressure levels (dB_{SPL} re 1 μPa) of field recordings were determined using peak-to-peak values taken from the portion of the signal with highest amplitude.

Results

General organization of the sexual behaviour in the nest

The observations from video recordings showed that the organization of sexual behaviour of pairs in the nest was basically similar in the two species, and conformed to the typical gobiid pattern (e.g. Tavolga 1954). The female inverted herself when she was in the nest, thereby adopting the mating posture, with her belly contacting the ceiling of the nest on which she was to lay her eggs. Eggs were extruded one by one onto the spawning surface, and attached to it by means of adhesive filaments. The female remained upside-down until mating was complete and she was ready to leave the nest. Eventually, a single-layered clutch of more or less densely packed eggs covered the central portion of the spawning surface. The male periodically turned upside-down during spawning and inseminated the eggs by crossing the entire spawning surface with wide symmetrical undulations of the body (mating movements), before reverting to the normal position. These mating movements by the male were also noted before the onset of oviposition in both species under study, thereby suggesting that release of sperm actually preceded the beginning of oviposition. Similarly, Tavolga (1954) found that in the goby *Bathygobius soporator* the release of sperm by the male also occurred before oviposition began.

Species-specific differences were also noted in the spawning activity and types of behavioural displays performed by the male. In all 14 spawnings of *P. martensii*, males tended to stay turned upside-down during most of the period of pair interactions in the nest preceding the beginning of oviposition; from this inverted position they repeatedly displayed to the female by means of vigorous sidewise undulations of body and tail (Tail Beating) while swimming around her in close circles (Circling). Some courtship movements were also performed by the male during this period, but they were infrequent. Throughout the spawning period the male continued to perform Tail Beating toward the female mainly from the normal position, albeit with lower frequency than before. Conversely, in all 5 spawnings of *K. punctatissima*, males did not perform Circling or any other obvious motor pattern toward the female and they turned upside-down only for short intervals both before and during oviposition, possibly only for preparing the spawning substrate or for releasing sperm.

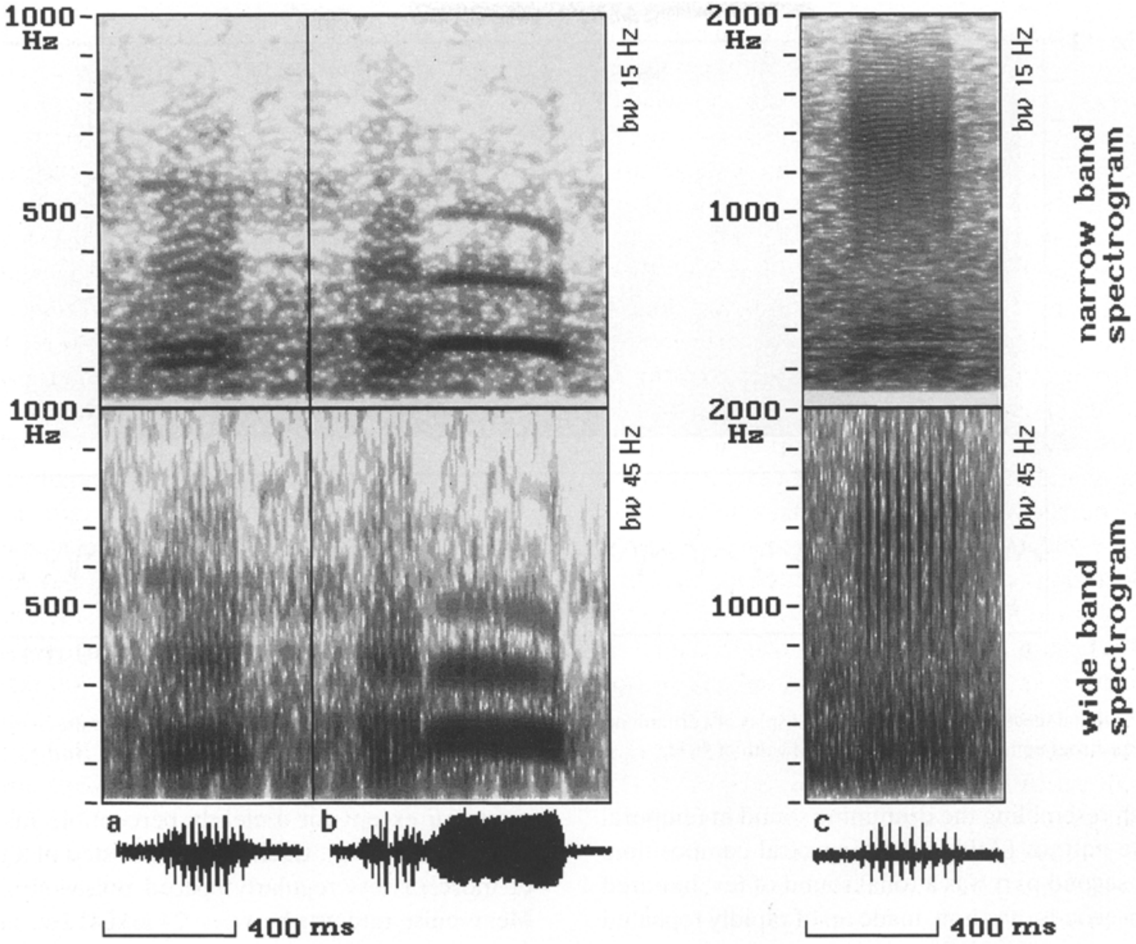

Fig. 1. Digital spectrograms and envelope display of sounds recorded from *P. martensii* (a = drumming sound; b = complex sound) and *K. punctatissima* (c). Spectrograms were computed with 15 Hz (top) and 45 Hz (bottom) bandwidth.

Spectral analysis of sounds

P. martensii. – The male produced two types of sound, namely the 'drumming sound' and the 'complex sound'. The drumming sound (Fig. 1a) was made up of a train of distinct and more-or-less regularly spaced, narrow-band pulses. The mean pulse rate ranged from 22 to 48 Hz; the sound duration varied from 50 to 790 ms (Table 1). Narrow-band spectrographic analysis (bandwidth 15 Hz) resolved the drumming sound into a large number of harmonically related bands. Single pulses were distinguishable both on spectrograms obtained from wide-band analysis (bandwidth 45 Hz), and on the oscillograms (Fig. 2). The frequency spectrum of each pulse typically did not go beyond 700–800 Hz. The highest amplitudes were below 200–300 Hz and peak frequency was around 100 Hz (Fig. 1a, 2). The clearest recordings, obtained either from the field or from the laboratory, showed each pulse as a highly damped, non-linear oscillatory system characterized by both amplitude and frequency decay (Fig. 2). Inspection of waveform plots also showed that, with the exception of a few low-amplitude pulses at the beginning of the sound, the onset of successive pulses occurred before the oscillation of the preceding pulse was over, i.e., for most of the sound duration, the pulse train consisted of a succession of damped, partially overlapping, oscillations.

The complex sound had two distinct parts (Fig. 1b). The first part was a train of discrete pulses very

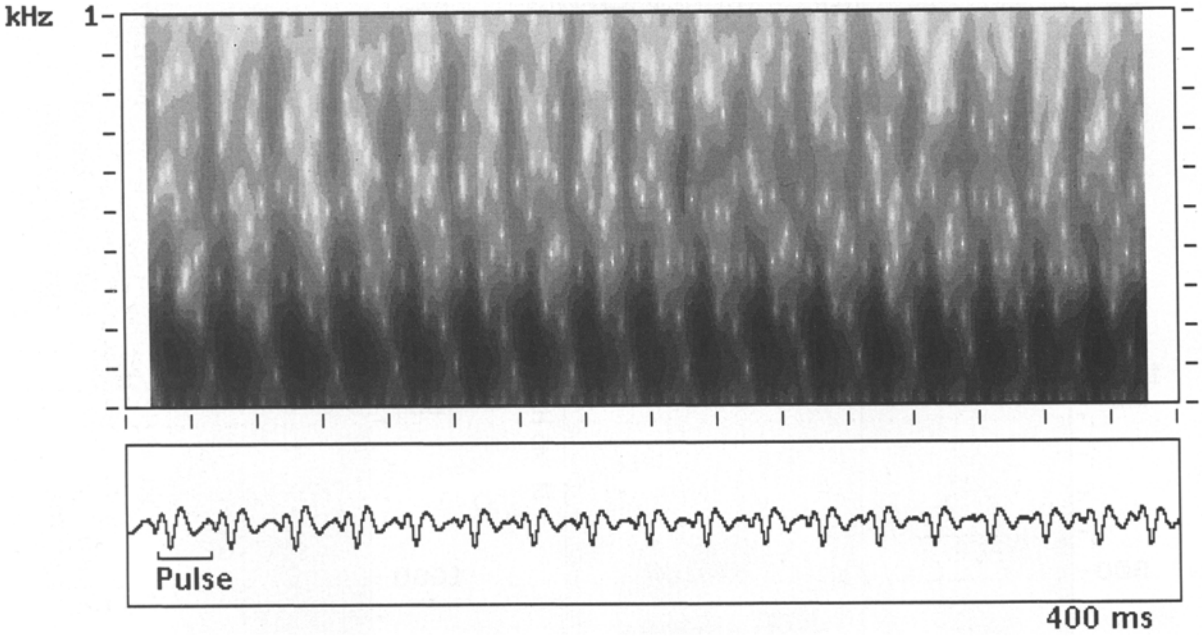

Fig. 2. Digital spectrogram and waveform display of a drumming sound made by a *P. martensii* male. The train of discrete pulses is evident. The spectrogram is computed with a bandwidth of 96 Hz.

much resembling the drumming sound in temporal pulse pattern (Table 1) and spectral composition. The second part was a tonal sound of few hundred milliseconds duration, made up of rapidly repeated pulses which yielded a continuous tone-like waveform (Fig. 3). Most of the energy of the tonal part was present at the fundamental frequency, which was also downward modulated, i.e., there was a decrease in the pulse rate. In all the complex sounds examined, the drumming part always preceded the tonal part, without pause between the two.

In addition to drumming and complex sounds, the male also produced isolated tonal sounds (Table 1). The isolated tonal sound had the same waveform and spectrographic configuration of the courtship sound described by Torricelli & Romani (1986). Therefore the structure of this sound will not be discussed further.

Field measurements of the sound pressure level at 2–10 cm from the emitter ranged from 113 to 123 dB for all types of vocalizations.

K. punctatissima. – Male sounds were drum-like, and audibly resembled the drumming sound of *P. martensii* except for a clearly perceptible rasping character (Fig. 1c). Each sound consisted of a train of more or less regularly spaced pulses (Fig. 4). Mean pulse rate was between 24 and 41 Hz; sound duration was between 450 and 1040 ms (Table 1). On the clearest recordings, the oscillographic trace at the onset of each pulse was an oscillation of irregular shape; the remainder of the pulse waveform was a series of smooth oscillations of decreasing amplitude. Narrow-band spectrograms showed the pulses had a discontinuous frequency spectrum in the range from a few hundred Hz up to 2 kHz. In particular, two well-defined frequency bands were recognizable from the power spectrum of each pulse. A first narrow band had peak amplitude at about 240–270 Hz, corresponding to the main pulse oscillation (Fig. 4). A second, higher-pitched and broader frequency band extended more or less continuously from just below 1 kHz up to 2 kHz or more. This component was time-aligned with the initial irregular part of the pulse waveform.

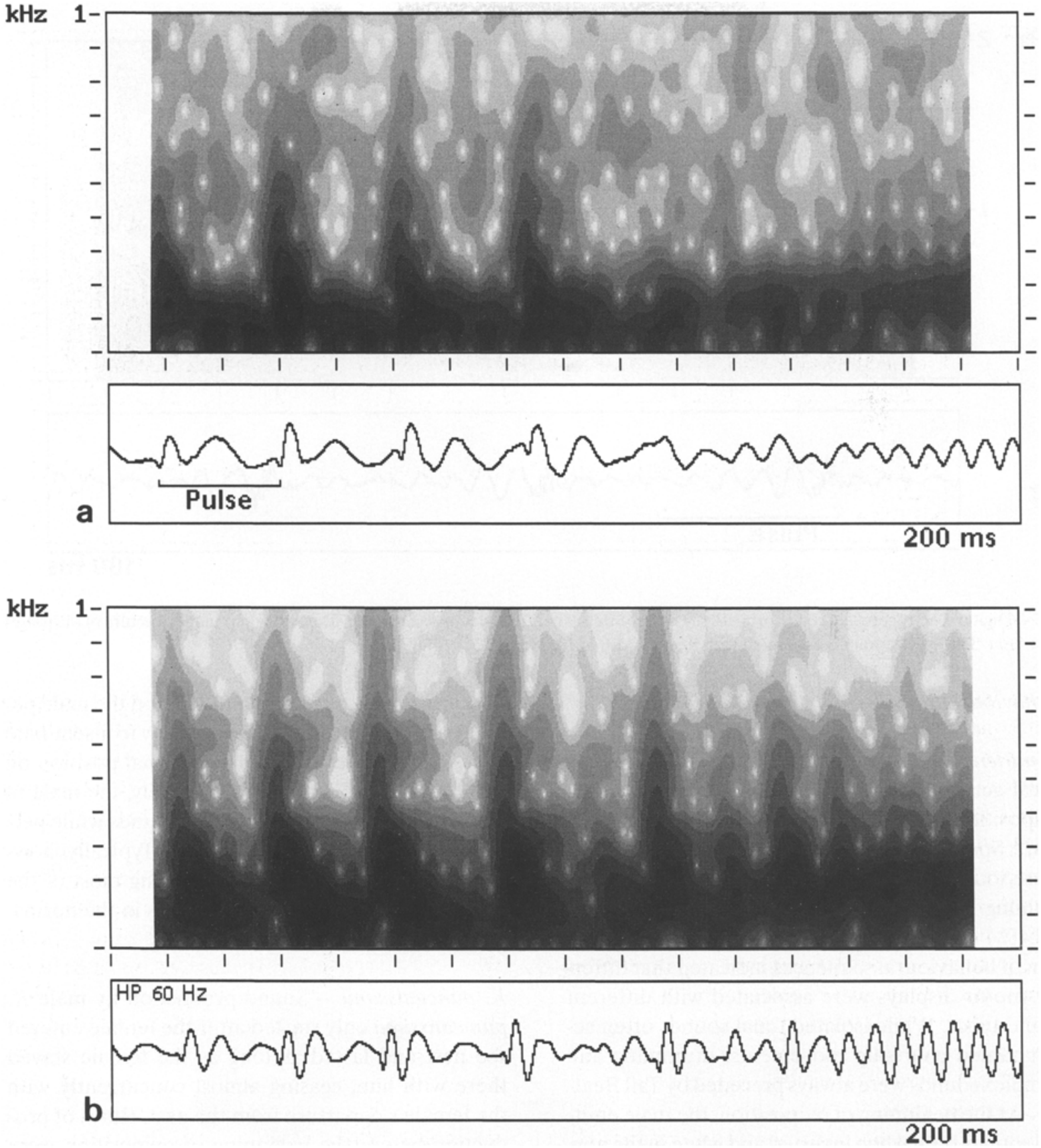

Fig. 3. Digital spectrogram and waveform display of two representative *P. martensii* complex sounds recorded in (a) the field and (b) the laboratory (the signal was high-pass filtered by means of a digital filter to remove frequencies below 60 Hz). In both cases, the portion with discrete pulses and the beginning of the continuous or tonal portion of the complex sound is shown. Both spectrograms are computed with a bandwidth of 96 Hz.

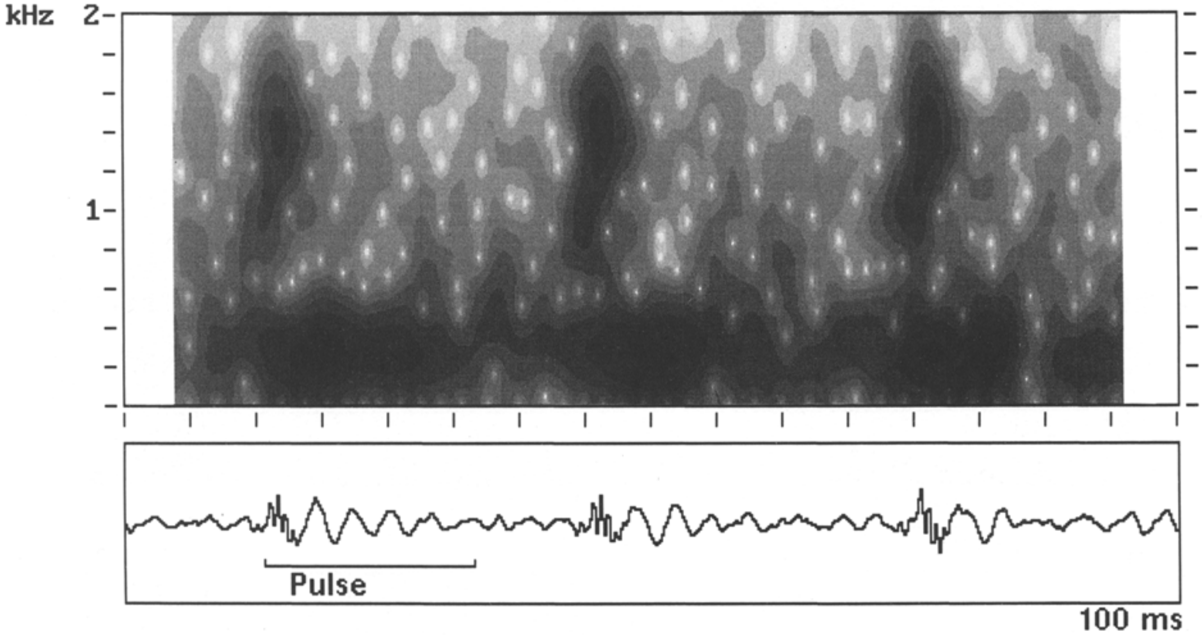

Fig. 4. Digital spectrogram and waveform display of three pulses emitted by *K. punctatissima*. The two-component structure of the pulses is evident. The spectrogram is computed with a bandwidth of 192 Hz.

Behavioural context of male sound production

P. martensii. – All video-recorded pairs showed high vocal activity before and during the beginning of oviposition (Fig. 5), producing 6.7–19.2 sounds min^{-1}. Spectrographic analysis revealed that most of these sounds (66.0%) were complex sounds, the remaining vocalizations being drumming sounds (18.4%) or isolated tonal sounds (15.6%). Inspection of behavioural sequences indicated that different motor displays were associated with different sound types. While isolated tonal sounds often accompanied courtship movements, drumming and complex sounds were always preceded by Tail Beating. At the beginning of oviposition, the male emitted sounds both when inverted and when in the normal position (Fig. 5a).

The male never suspended sound production at the onset of spawning (Fig. 5a, b); nevertheless, sound production decreased markedly as more eggs were laid. Moreover, the acoustic behaviour of the male throughout oviposition was often characterized by the emission of drumming sounds, and of complex sounds with a long-lasting drumming portion. Throughout the spawning period the male periodically turned upside-down mainly to inseminate eggs, but soon reverted to the normal position on each occasion (Fig. 5b). Occasionally, the male in the mating posture emitted a few sounds while performing insemination movements. Typically, however, sound emission occurred during most of the spawning period when the male was in the normal posture.

K. punctatissima. – Sound production by male *K. punctatissima* only started after the female entered the nest and lasted as long as the female stayed there with him, ceasing almost concurrently with the female's departure from the nest. Rates of production before the beginning of oviposition were 2.0–10.7 sounds min^{-1}. In all 4 spawnings examined, sound production continued at lower rates throughout the spawning period. Although it was occasionally infrequent, i.e., less than 1 sound min^{-1}, none of the males entirely ceased sound production as long as they remained in the nest. Distinct interruption of acoustic activity during oviposition was noted only when the male left the nest hollow, usually for

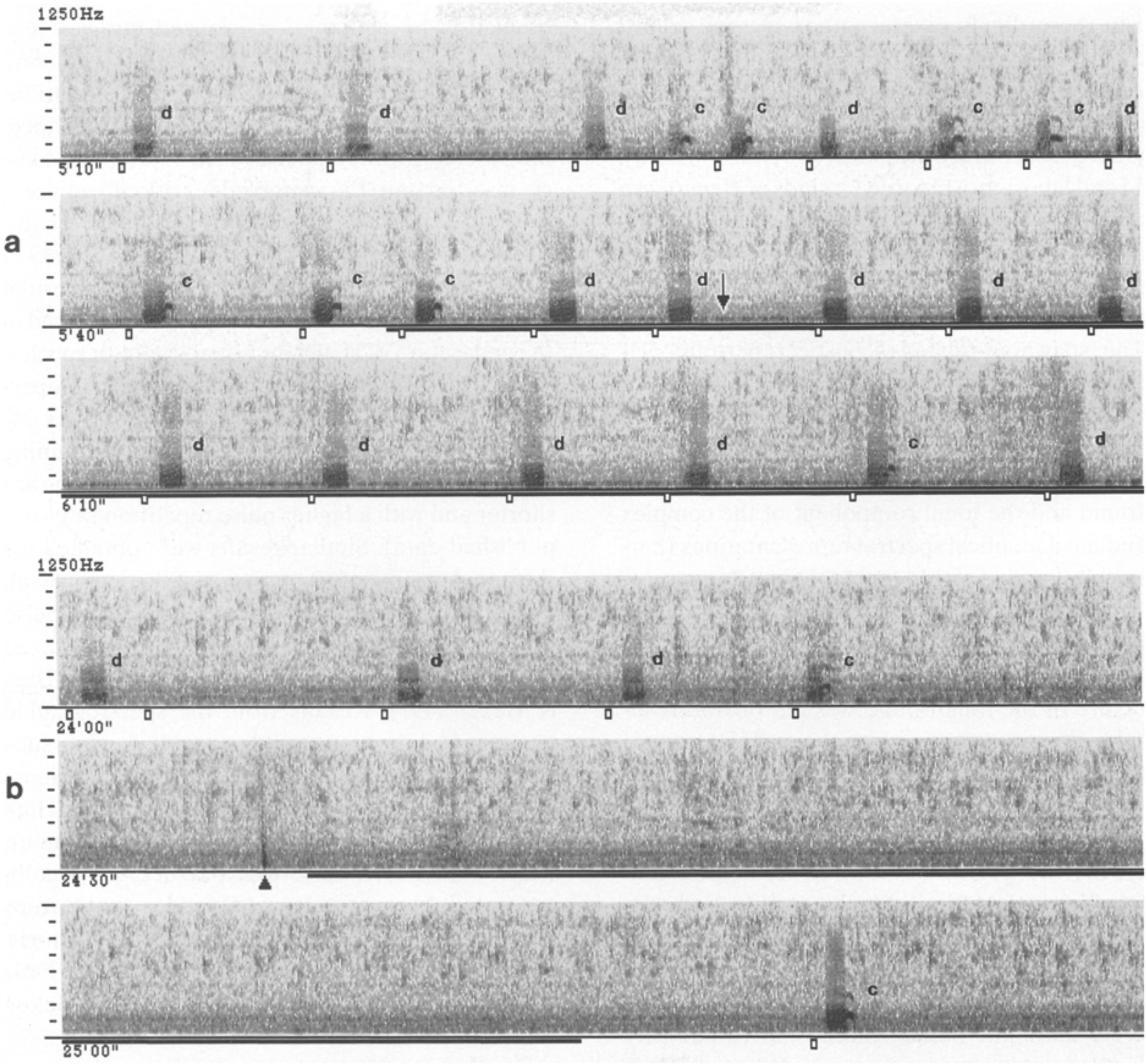

Fig. 5. Two continuous 90 s sound spectrograms showing the vocal activity of male *P. martensii* (c = complex sound, d = drumming sound) at different times during a typical spawn: a – emission of long sequences of drumming sounds occurring after the beginning of oviposition (vertical arrow); b – decreased vocal activity as a consequence of the progression of spawning. The behaviour of the male in each sequence is indicated by symbols below the reference line of each spectrogram: male inverted (continuous line), tail beating (open rectangles), bite (closed triangle). The time value at the beginning of each reference line indicates the time elapsed from the last inversion of the female.

very short periods of time, and while the male was turned upside-down, presumably to inseminate eggs.

Discussion

Spectral features of sounds and mechanism of sound production

The recording of sounds under good acoustic conditions is a prerequisite for a correct interpretation of the sound structure, which is, in turn, relevant to the elucidation of the probable underlying sonic mechanism. Accordingly, several authors warned against the possibility of obtaining good quality sound recording within aquaria commonly used for laboratory investigations (Parvulescu 1966, Hawkins & Myrberg 1983, but see Schneider 1966). In our study, field and laboratory recorded sounds of *P. martensii* had similar waveforms and frequency spectra. Thus, most of the laboratory sounds had been correctly recorded, despite the unfavorable acoustic conditions present in the tanks.

The spawning-related acoustic repertoire was more complex in *P. martensii* than in *K. punctatissima*. Male *P. martensii* could produce tonal sounds separately from drumming sounds, or combine them to form the complex sounds. The isolated tonal sound and the tonal component of the complex sound have identical spectral representations (harmonically banded with most of the sound energy set at the fundamental or tone frequency) and show considerable overlap in their overall duration and pulse repetition rate (see Table 1). Thus, the basic structure of the tonal sound was not obviously altered by its incorporation into the complex sound.

Repertoire aside, spawning sounds of the two species were similar in many characteristics. Each consisted, at least in part, of a train of distinct, regularly repeated, pulses. Acoustic theory suggests that spectral representation of pulse train sounds depends critically on the filter bandwidth employed (Watkins 1966, Michelsen 1983). At narrow-band spectrographic analysis, these sounds resolve into discrete harmonic bands whose relative intensity reflects the pulse power spectrum. When employing a wide-band filter, pulses are individually discriminable and their spectral features apparent. The difference in the spectral patterns of the sound which results from the two conditions of analysis, characterizes the drumming sound of the two species and the drumming portion of the complex sound of *P. martensii*. Other similarities between the sounds of the 2 species emerged at a finer level of examination by integrating the waveform display and power spectra analyses of individual pulses. Specifically, the time course of the pulse wave exhibited a decay in amplitude which is typical of a damped oscillator. It is known that the fish swim bladder may have such properties when driven into oscillation by action of specialized muscles (e.g. Schneider 1966, Demski et al. 1973, Hawkins 1986). Indeed, preliminary morphological investigations confirmed the presence of a simple oval-shaped, thin-walled, swimbladder in both species. No muscle inserted onto the swimbladder or onto adjacent specialized structures, as reported for many extrinsic sonic mechanisms among fishes (e.g. Demski et al. 1973). Nonetheless, the available circumstantial evidence suggests that sonic muscles are involved in the generation of spawning sounds in both species. Since fishes are poikilotherms, the water temperature has a marked influence on muscle activity. Indeed, as temperature increases, the drumming sounds of both *P. martensii* and *K. punctatissima* are shorter and with a higher pulse repetition rate (unpublished data). Similar results were obtained for the tonal sound of *P. martensii* (Torricelli et al. 1990). The temperature dependence of the pulse rate has been reported in cases where specialized muscles are involved in sound production (e.g. Bass & Baker 1991). Results from the spectrographic analysis of spawning sounds provide further supporting evidence for the involvement of sonic muscles in the sound production of the 2 species. Harmonic sounds result from high pulse repetition rate which yields a tone-like wave, and these are usually generated by a muscle-swimbladder mechanism (Tavolga 1964). Each pulse is produced by a single contraction of the sonic muscles (Skoglund 1961, Tavolga 1964, Demski et al. 1973, Bass & Baker 1991).

Finally, both the drumming and the tonal parts of the complex sound of *P. martensii* are shorter and with lower number of pulses then their isolated counterparts (see Table 1). In addition, the drumming and the tonal part of the complex sound never overlap. Therefore, a single sonic mechanism seems responsible for the sound production in *P. martensii*. In particular, males of this species should be able to vary the muscle contraction rate in order to generate either lower rate, discrete pulses (drumming sound) or rapidly repeated pulses yielding a continuous, tone-like wave (tonal sound). Such marked variation of the pulse repetition rate within the same sound is known to occur during the emission of aggressive vocalizations by male *P. martensii* (Lugli 1990).

Sound producing mechanisms among gobiids are still largely unknown. Hydrodynamic sounds were thought to be generated by the marine goby *Bathygobius soporator* during the squirting of jets of water through its opercular openings (Tavolga 1958). Takemura (1984) suspected that sounds made by the freshwater goby, *Odontobutis obscura*, were produced by rubbing the pharyngeal plates together and then amplifying this sound via the swimbladder. The upper pharyngeal plates were moved by a pair of well-defined muscles running dorsally to the Y-shaped swimbladder, each muscle having one insertion point on its associated upper pharyngeal toothed plate and the other on the 4th vertebra. We found similar arrangement of muscles in the two gobies studied here. Thus, a similar mechanism may be responsible for the stridulatory component at the onset of each pulse of all *K. punctatissima* sounds recorded in the laboratory. The production of sounds by pharyngeal stridulation, either with or without reinforcement by swimbladder resonance, is frequent in fishes (Fish 1954). However, the contribution of these muscles to the generation of sound pulses can only be determined through physiological investigations.

Functional aspects of spawning sound production

As stated earlier, the discovery of acoustic signals exclusively emitted just before or during mating is not new for fishes. Sound production during mating has been described by Lobel (1992) and, earlier, Myrberg (1981) found that male damselfishes emit low level 'grunts' just before the beginning of each spawning bout. These authors suggested that the function of these sounds was to assure synchronous mating of partners. Theoretical considerations predict (Krebs & Dawkins 1984) that signalling under such circumstances should occur with minimal cost, and at the lowest level to avoid interference from competitors. Both predictions are supported by recent investigations on vibrational communication during spawning behaviour in the himè salmon (Satou et al. 1991). The type of acoustic signalling we are describing among gobies, however, seems quite different from the aforementioned cases. Sound production accompanied insemination only sporadically in *P. martensii* and never in *K. punctatissima*. Although males of both species were acoustically active throughout the spawning period, the largest number of spawning sounds occurred during pre-spawning interactions and early stages of oviposition. Indeed, the vocal activity of the male *P. martensii* under such circumstances approached levels regarded as typical for the acoustic signal during overt courtship (Torricelli et al. 1986). Such a redundancy in signalling is a common feature of displays that advertise individual quality or resource ownership. For example, the advertisement of male status has been shown to elicit female choice in a variety of animals (e.g. Alcock 1984). In *P. martensii*, ripe females typically visit several male's nests in succession before releasing eggs (Torricelli et al. 1993) and males may compete for the spawning female both before and during oviposition (Bisazza et al. 1989). The impending occurrence of spawning in *P. martensii* is associated with the production of distinct sounds by the male, nevertheless, the female, when ready to spawn, also contributes to spawning by releasing a sexual pheromone (Bisazza et al. 1989, Lugli 1990). Thus, in *P. martensii* the effects of female chemical and male acoustic stimuli combine, and the resulting redundant signalling complex might provide the last opportunity for the female to choose the best male. Clearly, the hypothesis that the sounds made inside the nest may not be for advertizing but rather, for continued male-female synchrony of behaviour, can not be entirely ruled out at present.

As spawning activity among gobiids is protracted over time and occurs within a concealed cavity, selection may have favored correspondingly protracted male acoustical communication in both *P. martensii* and *K. punctatissima*. However, the absence of spawning sounds in some other sonic gobiids that show similar spawning habits and behaviour (Tavolga 1954, Kinzer 1961, Mok 1981) indicates that this is, at best, an incomplete explanation. We will attain better understanding of the role and cause of male sound production throughout spawning once studies have integrated the physiological and behavioural aspects of sound production with greater knowledge of the other characteristics of the species.

To summarize, mating in fishes, like those of other vertebrate groups, may be preceded and accompanied by special acoustic signals. Previous anecdotal reports (Myrberg 1981) and recent findings (Lobel 1992, present study) indicate that this phenomenon is probably commoner than is now appreciated. We agree with Lobel (1992) that acoustic behaviour of fish associated with spawning is an almost unexplored field in which further investigations are extremely desirable.

Acknowledgements

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