J. Mar. Biol. Ass. U.K. (2007), **87**, 5682/1–7 Printed in the United Kingdom

Acoustic signalling during courtship in the painted goby, *Pomatoschistus pictus*

M.C.P. Amorim*[‡] and A.S.M. Neves[†]

*Unidade de Investigação em Eco-Etologia, ISPA, Rua Jardim do Tabaco 34, 1149-041 Lisboa, Portugal. †Unidade de Investigação em Biodiversidade e Desenvolvimento, Universidade Lusófona de Humanidades e Tecnologias, Campo Grande 376, 1749-024 Lisboa, Portugal. ‡Corresponding author, e-mail: amorim@ispa.pt

Gobies emit sounds during different stages of reproduction, including courtship, pre-spawning events (in the nest) and spawning. The breeding sounds of the painted goby *Pomatoschistus pictus* and associated courtship behaviour were recorded in captivity and described for the first time. Males emitted thump-like sounds mainly when displaying alone in the nest and produced drumming sounds outside the nest. Thumps have never been reported for other species of the genus *Pomatoschistus*. Thumps were short (~80 ms) very-low frequency (below 100 Hz) non-pulsed sounds, whereas drums were longer (hundreds of ms) and consisted of low frequency (~300 Hz) pulse trains. Thump characteristics varied significantly among males but also showed high within-male variability. The frequency of thump emissions and courtship behaviour (total number of courtship displays, lead and nest display) were positively correlated with male size but not with male somatic condition. Thump bursts emitted during nest displays were significantly longer than when emitted with other behaviours. These results suggest that larger males courted females more intensively, both with visual and acoustic displays, than smaller ones.

INTRODUCTION

Sound production in teleost fishes is especially conspicuous in the breeding season and is typically related to territorial defence and mating activities (Myrberg & Lugli, 2006). Fish sounds are considered to play an important role during social communication required for successful mating, such as the expulsion of intruders from the territory where spawning will take place (Myrberg, 1997), mate attraction (Lugli et al., 1996) and mate choice (Myrberg et al., 1986). Mating sounds may also stimulate the gonadal development of conspecific females (Marshall, 1972) similarly to bird song, promote synchronous gamete release (Hawkins & Amorim, 2000), and potentially support species recognition (Myrberg et al., 1978; Amorim et al., 2004).

The family Gobiidae is considered a case study for the understanding of acoustic signalling in fish (Bass & McKibben, 2003) because it includes many vocal species (reviewed in: Lugli et al., 1997; Myrberg & Lugli, 2006) and it is one of the few fish taxa where sound playback experiments have been successful (Tavolga, 1958; Lugli, 1997; Lugli et al., 1996, 2004). Playback experiments of male goby courtship sounds have shown that they are effective in female attraction (Tavolga, 1958; Lugli et al., 1996) and facilitate courtship and sound emission in males previously stimulated with female conditioned water (Lugli et al., 2004).

Male gobies typically defend nests that are used as spawning sites and provide parental care during the reproductive season (Miller, 1986). Sounds emitted during breeding behaviour have been described for males of several species of gobies and can be observed during courtship, pre-spawning (in the nest, while females are inspecting prospective nests) or spawning events (Lugli et al., 1997; Myrberg & Lugli, 2006). With few exceptions, goby sound emissions can be grouped into three major sound types: pulsed sounds that consist of pulse trains repeated at a slow rate and that can be amplitude modulated, tonal sounds characterised by faster pulse repetition rates where pulses fuse together resulting in a sinusoidal-like waveform, and complex sounds that are made of a combination of the two (Lugli et al., 1997).

The emission of drumming sounds during pre-spawning and spawning activities has been documented in five species of sand gobies belonging to the genera *Pomatoschistus* and *Knipowitschia* (Lugli et al., 1995; Lugli & Torricelli, 1999; Lindström & Lugli, 2000). Lugli & Torricelli (1999) and Lindström & Lugli (2000) have proposed that these acoustical signals could be used in mate choice since females enter several nests before deciding where to spawn and sounds are only emitted by the male in the nest. Moreover, sand gobies often live in sympatry in coastal zones or in freshwater (Miller, 1986) suggesting that possible inter-specific differences in breeding sounds (e.g. Lugli & Torricelli, 1999) could also potentially be used in species-specific recognition.

Despite the widespread use and the significance of acoustic signals in gobies, a detailed and quantified characterisation of the acoustic repertoire has been carried out for only one species of the genus *Pomatoschistus* (Lindström & Lugli, 2000). The present study describes the breeding sounds of the painted goby *Pomatoschistus pictus* (Miller, 1973) and

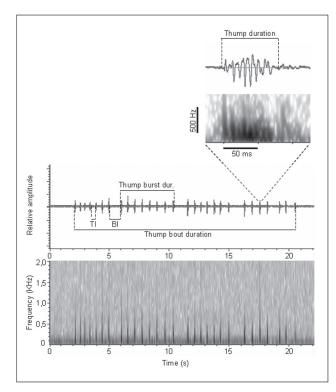


Figure 1. Oscillogram and spectrogram of a thump bout produced by a *Pomatoschistus pictus* male. This thump bout is made up of 5 thump bursts of 7, 8, 7, 4 and 3 thumps (from the left to the right). On top, the detail of the oscillogram and spectrogram of one thump is depicted. Filter bandwidth 124 Hz, FFT size 512 points, time overlap 50.0%, Hamming window. TI – thump interval; BI – burst interval.

associated courtship behaviour for the first time. Sounds are compared among individuals and associated with particular behavioural displays.

MATERIAL AND METHODS

Study species

The painted goby *Pomatoschistus pictus* is an exclusively coastal benthic species that lives on shallow gravel and sand substrate areas (Miller, 1986). It is a short-lived small goby living up to 2 years, attaining a maximum length of 57 mm total length, and reproducing from approximately February to July, depending on the location (Miller, 1986). Like other sand gobies, males build nests under empty valves, such as *Pecten* or *Cardium*, and partially or entirely cover the valves with sediment leaving only one opening (Bouchereau et al., 2003). Females enter the nest attracted by male displays and lay their eggs in a single layer on the ceiling of the nest, and thereafter leave the male to provide parental care (Bouchereau et al., 2003). Nest owners actively defend their nest from intruders both outside and during the reproductive period (personal observation).

Fish collection and maintenance

Fish were caught from shallow water (water depth: 2–9 m) with the help of hand nets during SCUBA diving in Arrábida, Portugal (38°26'N 9°06'W), in December 2005

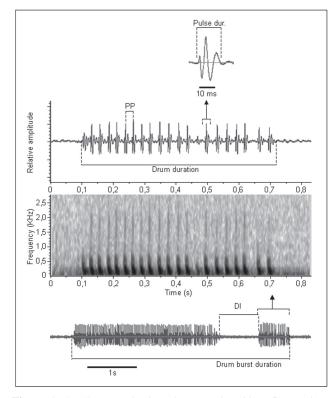


Figure 2. Oscillogram of a drum burst produced by a *Pomatoschistus pictus* male (bottom). The drum burst is made up of two drum sounds with 114 and 21 pulses and 2981 ms and 611 ms duration (from left to right). Above, the oscillogram and spectrogram of the shorter drum is depicted, as well as the detail of one pulse. Filter bandwidth 124 Hz, FFT size 512 points, time overlap 50.0%, Hamming window. DI – drum interval; PP – pulse period.

and February 2006. Males and females were housed in separate aerated stock tanks (11-I) provided with a mixture of artificial and natural seawater, internal power filters, sand substrate and shelters. Fish gender was recognised by examining the external papilla (that is rounded in females and longer and pointed in males) and the existence of nuptial colours (Bouchereau et al., 2003). Ripe females could also be recognised by their swollen bellies. A maximum of eight fish were kept per stock aquarium. Throughout the study, including sound recordings, fish experienced an approximate water temperature of 15–16°C, a natural photoperiod, and were fed daily with shrimps and clams.

Sound Recording

Recording sessions were carried out in May 2006 in two 25-l experimental tanks (similar to the stock tanks) that were divided in three compartments of equal sizes by means of double (one opaque and one transparent) removable partitions. The experimental aquaria were placed on top of a 14 cm thick layer of rock wool that proved to be effective in minimizing the conduction of external noise to the tanks and therefore improved the quality of fish sound recording. Each end compartment was provided with one half flower pot of 4.5 cm in diameter, to be used as a nest, and housed a single male that was left to acclimatise for a minimum of eight days before it was used in trials. All males covered the nest with sand, revealing high breeding motivation (e.g. Lindström & Lugli, 2000; Svensson & Kvarnemo, 2005). The middle compartment housed one ripe female.

Approximately 15 minutes prior to sound recordings aeration was stopped and one opaque partition was removed to allow one subject male to have visual contact with the female, as a courtship pre-stimulus. At the start of the 20 min recording sessions, the transparent partition was also removed allowing the male to interact freely with the female. Once the recording was complete, the male was removed, weighed (fresh weight, W) and measured (standard length, SL), returned to a stock tank and replaced with another male. A total of twenty males with mean \pm SD (range)=29.2 $\pm 3.1~(25~to~37)~mm$ SL and 0.39 $\pm 0.09~(0.28\text{--}0.57)~g$ W, were used and recorded. Sounds were registered with a High Tech 94 SSQ hydrophone (sensitivity -165 dB re 1 V/µPa, frequency response within ±1 dB from 30 Hz to 6 KHz) placed just above the rim of the artificial nest (4 cm above the substrate), and recorded in wav format to a professional digital sound recorder (Marantz PMD670) directly to a 1 GB IBM microdrive storage card (sampling frequency of 16 KHz and 16 bit resolution). Sounds were subsequently analysed with Raven 1.2.1 for Windows (Bioacoustics Research Program, Cornell Laboratory of Ornithology, Ithaca, NY, U.S.A.). Only the sounds that presented a good signal to noise ratio were analysed, which were typically emitted very close to the hydrophone (~ 2 cm). Only males emitted sounds. Sounds could be unequivocally attributed to males because their intensity varied with distance from the hydrophone and were consistently associated with particular displays (see results).

Two sound types were registered during the recording sessions. The most common sound type resembled a thump and was composed by a long sound wave (~80 ms) that did not have a pulsed structure (Figure 1). More rarely, drumming sounds (drums) made up of short (~8 ms) low-frequency repeated pulses were also heard (Figure 2). The acoustic pulse is considered the fundamental unit of the drum sound (Lindström & Lugli, 2000), but thumps could not be divided into clear units. Thumps and drums were emitted in acoustic bouts. Thumps were emitted in sequences of several sounds (thump bursts, Figure 1). Frequently, thump bursts would be further clustered into groups, which we named thump bouts (Figure 1). Similarly, drums were also clustered into drum bursts (i.e. a succession of drum sounds, Figure 2).

To establish an objective criterion to group thump sounds into bursts and bouts, and drum pulses into sounds (drums) and bursts, a log-survivor analysis on time intervals between sounds (in the case of thumps) or pulses (in the case of drums), was performed following Lindström & Lugli (2000). This is a simple graphical method for determining the minimum interval separating successive bouts of events (Martin & Bateson, 1993), by plotting the cumulative frequency of the log-time intervals between events (sounds or pulses in this case) against time intervals. An abrupt switch point represents the objective estimate of the minimum interval that distinguishes separate bouts (Martin & Bateson, 1993). For this purpose, 142 intervals between thumps from the 20 males were used. Thump intervals were measured from the end of one sound to the onset of the subsequent sound. Similarly, for drums, 45 pulse intervals (i.e. pulse periods)

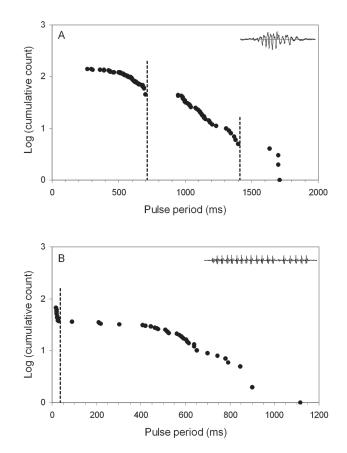


Figure 3. Log survivorship plots of time intervals for thumps (A) and drums (B) produced by Pomatoschistus pictus males. The visual inspection of both plots reveal that intervals of 700ms and of 1400 ms (indicated by dotted vertical lines) are the maximum within thump burst and thump bout intervals, i.e. intervals larger than 700 ms and 1400 ms separate different thump bursts and different thump bouts, respectively. Likewise, intervals of 31 ms (indicated by the dotted vertical line) represent the maximum within-drum pulse period.

concerning sound emissions from the 20 males were used. Pulse period was measured peak to peak between consecutive pulses. The visual inspection of the log-survivor analysis for thumps (Figure 3A) and drums (Figure 3B) confirmed the presence of a hierarchical organization of time intervals both in thump and in drum emissions. Intervals larger than 700 ms separated thump bursts and those larger than 1400 ms separated thump bouts (Figure 3A). Likewise, time intervals of 31 ms represented the minimum pulse period within drums, i.e. pulses with periods larger than this value belonged to different sounds (Figure 3B). These criteria were used during sound analysis.

Thumps were analysed for sound duration (ms) and dominant frequency (Hz, the frequency where the sound has maximum energy). The number of thumps in a burst, the interval between thumps within a burst (ms), the duration of a thump burst (s), the number of bursts in a thump bout, the interval between thump bursts (s), the number of thump bursts per bout, and the duration of a thump bout (s) were also measured. Durations were measured from the onset to the end of a thump, a thump burst or a thump bout, depending on the case. Time intervals (within or between

Table 1. Means, SDs, range, within male coefficient of variation (CV) for thump parameters among 20 painted goby Pomatoschistus pictus
males. Twenty thumps and an average of 11 thump bouts were considered per male. Descriptive statistics is based on male means except for absolute
range values (rangeabs) that concern all data. SL - standard length; CF - condition factor [(weight/SL ^{1.65})*1000]; CV - within male coefficient of
variation [(SD/mean)*100]. H values are the results of Kruskal–Wallis tests comparing thump parameters among males.

Thump parameters	Ν	Mean	SD	Range	Rangeabs	\mathbf{CV}	Н	P value
Thump duration (ms)	400	81.4	3.97	74.7-88.8	50-101	13.4	49.70	< 0.001
Peak frequency (Hz)	400	83.2	9.70	71.3-104.9	37.7-134.6	32.9	41.03	< 0.01
Burst duration (s)	400	4.06	1.32	1.71-6.88	1.40 - 22.35	69.0	84.64	< 0.001
No. of thumps	400	7.3	1.98	3.6-11.7	2-30	64.2	76.65	< 0.001
Thump interval (ms)	400	584.9	23.10	535.3-622.5	265-912	17.8	13.79	NS
Bout duration (s)	200	8.45	3.49	1.16-13.64	0.35-41.83	75.2	54.22	< 0.001
No. of bursts	215	1.96	0.53	1.43-3.33	1-8	59.1	18.53	NS
Burst interval (ms)	171	2.01	1.72	1.05-8.47	0.92 - 24.41	31.7	102.58	< 0.001

bursts) were measured from the end of one thump to the start of the following one. Some of these parameters are depicted in Figure 1.

Drums were analysed for duration (ms), total number of pulses in a drum sound, pulse duration (averaged for 10 pulses, ms), pulse period (average peak to peak interval of 10 consecutive pulses within a drum, ms) and dominant frequency (Hz) (Figure 2). Durations were measured from the onset to the end of a pulse or a drum. Drum and thump temporal features were measured from the oscillograms and dominant frequencies were measured from both the power spectra and the sonogram (filter bandwidth 124 Hz, FFT size 512 points, time overlap 50.0% and a Hamming window).

Behaviour repertoire and recording

Behaviour was observed ad libitum, i.e. with no systematic constraints (Martin & Bateson, 1993), in stock tanks and during preliminary sound recordings (two months) to describe the courtship behavioural patterns of *P. pictus*. Females were not seen to court the males. Six distinct male courtship behavioural categories were described:

- Approach: the male makes a series of jerky jumps towards the female, while undulating his body and fins. The fins are erected (pelvics, pectorals and dorsal fins) and the head is darkened. This behaviour is frequently followed by lead.

- Nudge: the male swims towards the female and nudges her against her flank.

- Lead: the male moves towards and around the female and attempts to lead her back to the nest swimming in front of her fluttering the dorsal and caudal fins.

– Eight display: the male swims rapidly in front of the female in an eight-figure pattern.

- Nest rubbing: the male turns upside down in the nest and rubs his belly against the nest ceiling. In other gobies this behaviour is associated with the preparation of mucus trails that contain active sperm (Svensson & Kvarnermo, 2005) and pheromones that are used in female attraction and synchronization of spawning activities (Locatello et al., 2002).

 Nest display: With the body inside the nest, the male leaves his head out and makes jerky movements raised on the pelvic fins, while making downward thrusts with the head, with rapid opercula movements. This display is frequently emitting sounds. This behaviour is displayed mostly with the male alone in the nest but sometimes also with the female inside.

To associate sound emissions with particular behavioural categories, male behaviour and sound emissions were registered during one of the sound recordings sessions (one session per male) using the Observer (version 4.0 for student). Only thumps were registered during behavioural recordings.

Statistical analysis

Thump acoustic features were compared among males with Kruskal–Wallis tests. Within-male coefficients of variation (CV=SD/mean×100) for thump parameters were calculated to assess the individual stereotypy of acoustic parameters. The Spearman correlation test was used to explore the potential relationship between the number of thump bouts emitted per recording session and thump acoustic parameters with male traits: SL and condition factor [CF=(W/SL^b)*1000; b is the estimated slope from the regression between log(SL) and log(W) from the 20 male group used in the experiments and equalled 1.65].

A χ^2 test was used to test for independence of behaviour and thump production. Adjusted residuals from the χ^2 test were used to assess which behaviours were positively or negatively associated with the emission of thumps. Similar analyses were not carried for drums since very few sounds were registered. Comparisons of thump acoustic parameters that co-occurred with different courtship displays were made with Kruskal–Wallis tests. The number of different courtship behaviours observed per recording session (behaviour frequency) was correlated with the male traits (SL and CF) and with total courtship frequency using Spearman rank correlations.

RESULTS

Acoustic repertoire

During recording sessions all males actively courted the females when they were given free access to them. Sound production was frequent during courtship interactions and two sound types could be distinguished, the thump and the

5

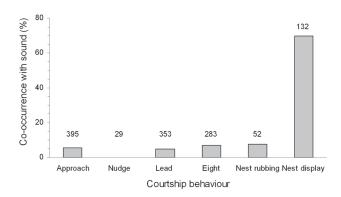


Figure 4. Percentage of courtship displays that were accompanied by the emission of thumps in *Pomatoschistus pictus* males. Total number of occurrences per recording sessions is depicted on top of the histogram bars. Eight – eight display.

drum. Thumps were relatively short (~80 ms) non-pulsed sounds of very low frequency (Figure 1, Table 1). Typical peak frequencies were below 100 Hz and most sound energy was under 1 kHz. Thumps were emitted in bursts of 4 to 12 sounds that lasted on average 4 s. Thump bouts were made up of a succession of typically 1 to 3 bursts and could last up to 42 s.

Thump parameters differed significantly between males, with the exception of thump intervals within a burst and the number of bursts in a bout (Table 1). Coefficients of variation (CV) showed that within male variability for all thump parameters was very high, with thump duration being the least variable characteristic (CV=13.4%). Thump acoustic parameters were not related with male traits (SL and CF) except for burst duration that was negatively related with CF (Spearman correlation: N=20, R=-0.47, P=0.04) and the number of thump bursts in a bout that decreased with male SL (Spearman correlation: N=20, R=-0.46, P=0.04); all other tests: R=-0.43-0.31, P>0.05). The number of thump bouts emitted per recording session was positively correlated with male SL (Spearman correlation: N=20, R=0.52, P=0.02) but not with his condition (N=20, R=0.047, P>0.05).

Drumming sounds were heard only rarely. On average, only two sounds (range = 1–5) were recorded per male (total N=33 sounds). This sound type consisted of low frequency pulse trains with mean dominant frequencies around 300 Hz [mean \pm SD (range)=297.9 \pm 69.9 (156–431)]. Most of the acoustic energy of drums was in the range of the 60–500 Hz (Figure 2). Typical drums had durations of approximately 663 ms [662.9 \pm 464.1 (211–2981)], with 29 pulses [28.5 \pm 17.8 (9–114)] and pulse periods of 23 ms [22.7 \pm 2.8 (19–31)]. Pulses were short, with mean durations of 8.0 ms [\pm 1.8 (6–14) ms]. Drums were usually emitted singly but drum bursts of up to 3 sounds were heard, lasting up to more than 4 s.

Association with behaviour

Pomatoschistus pictus males courted the females by series of vigorous displays that included exhibiting erected fins, darkening parts of the body, leading the female to the

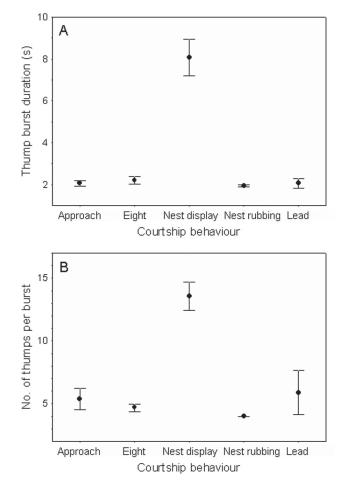


Figure 5. Mean ±SE of the duration of thump bursts (top) and the number of sounds per thump burst (bottom) observed in sounds emitted by *Pomatoschistus pictus* males during different courtship displays. Eight – eight display.

nest, exhibitions in the nest and making sounds. During the 20 behaviour recording sessions, 1244 behavioural acts were registered from which 154 were accompanied by the emission of thumps. All behavioural categories except nudge were observed to co-occur with sound production (Figure 4). The emission of thumps was significantly associated with the behaviour nest display (Chi-square test: $\chi^{2=448.83}$, df=6, P<0.001, Figure 4). While emitting thumps, males made downward thrusts with the head while closing the opercula rapidly. Although drums were not registered during behaviour recording sessions, this sound emission was only observed when the male was outside the nest near the female with erected dorsal fins, raised on the pelvic fins, and quivering his body.

The acoustic features of thumps that co-occurred with different courtship behaviours were compared. Thumps bursts were significantly longer (Kruskal-Wallis test: H=37.84, P<0.001; Figure 5A) and with a higher number of sounds (Kruskal–Wallis test: H=31.12, P<0.001; Figure 5B) when associated with nest displays than with other behaviours (approach, lead, eight display and nest display; nest rubbing was excluded from the analysis due to the small sample size). All other thump features did not differ between associated behaviours (Kruskal–Wallis tests, H=1.19–5.59, P>0.05).

Courtship intensity and male traits

Frequencies of total courtship behaviour, lead and nest display were positively correlated with male SL (Spearman correlation: N=20, total courtship, R=0.63, P=0.002; lead, R=0.72, P<0.001, nest display, R=0.67, P=0.001), but not with male CF (R=-0.15-0.19, P>0.05). The frequency of all other behaviours were not correlated with male traits (R=-0.25-0.44, P>0.05). When males courted females more intensively (i.e. showed a higher total courtship frequency), the visual displays that increased more markedly were approach, followed by lead and nest display (Spearman correlation: N=20, R=0.69-0.85, P<0.001; all other behaviours: nest rubbing, R=0.47, P=0.04; nudge, R=0.52, P=0.02; eight display, R=0.33, P>0.05). As expected, the frequency of sound production was also positively correlated with total courtship performed by each male (Spearman correlation: N=20, R=0.79, P<0.001).

DISCUSSION

Painted goby males emitted two sound types during early stages of courtship. The most common sound, the thump, was emitted when the male was displaying alone in the nest, but also while courting the female outside the nest. Drums were emitted more rarely and only outside the nest, when the male was stationary near a female, quivering and displaying the fins. Thumps were short (~80 ms) very-low frequency (below 100 Hz) non-pulsed sounds, whereas drums were longer (hundreds of ms) and consisted of low frequency (~300 Hz) pulse trains. Similarly to other sand gobies (Lindström & Lugli, 2000), sounds of *Pomatoschistus pictus* were organised in groups (sound bursts): thumps were organised in thump bursts and thump bouts (groups of bursts) and drums into drum bursts.

Thump acoustic characteristics varied significantly among painted goby males, with the exception of thump intervals and number of bursts in a bout. However, thump parameters showed low levels of stereotypy, especially in the number of thumps in a burst, burst duration, number of bursts in a bout and bout duration (CV>59%). Similar results have been found for the drums of P. minutus (Pallas, 1770) that also show inter-male differences and high within male coefficients of variation, in particular for sound duration and the number of pulses per sound (CV>60%) (Lindström & Lugli, 2000). In addition, sounds produced by males of P. minutus differ in the sound pressure level, which is positively correlated with male body length, and in *P. marmoratus*, drum pulse period also varies among males, suggesting that drums emitted by Pomatoschistus males could be used in mate choice based on male size or other male qualities (Lugli & Torricelli, 1999; Lindström & Lugli, 2000). Intra-specific variability in drums was not studied in *P. pictus* due to the small sample size.

Thump duration was the least variable acoustic feature in *P. pictus*, which could be limited by the mechanism of sound emission. Tavolga (1971) suggested a shared mechanism of sound emission for *Bathygobius soporator* (Valenciennes, 1837), *Neogobius melanostomus* (Pallas, 1814) and *Gobius jozo* (= *Gobius niger* Linnaeus, 1758), that consists in the rapid ejection of strong jets of water through the opercula, occurring during downward thrusts of the head (also see Stadler, 2002).

Thump-like sounds that also accompany head shakes have also been described for *Tridentiger obscurus* males (Temminck & Schlegel, 1845) (Kishi, 1979), suggesting that this sound type and associated mechanism of sound production is shared by several goby species, including *P. pictus*.

The number of thump bouts and courtship behaviour (total courtship, lead and nest display) observed per recording session were positively correlated with male size but not with male condition. Thump acoustic parameters were not related with male traits except for thump burst duration and the number of bursts in a bout that decreased with male CF and SL, respectively. The smaller number of thump bursts per bout found in larger males probably represents a trade-off with the concomitant increase in acoustic activity. A similar trade-off has been described in other fish species (e.g. Thorson & Fine, 2002), suggesting the existence of physiological constraints on sound production.

Thump acoustic parameters also varied with the associated visual display. Thump bursts were significantly longer and with a higher number of sounds when associated with nest display than with other behaviours. These acoustic variables were however highly correlated. Nest display seems to signal a high motivation for mating as it significantly increases with total courtship frequency and male size, and it is associated with longer emissions of thumps. Taken together, these results suggest that larger males court females more intensively than smaller ones, both in terms of visual and acoustic displays. This indicates that courtship activity (including sound production) and male size may be under sexual selection in *P. pictus*. Consistent with this suggestion, females of P. minutus and other gobies chose mates on the basis of multiple traits including courtship intensity (e.g. Forsgren, 1997; Takahashi & Khoda, 2004) and male size (e.g. Lindström, 1992; Forsgren, 1997). Goby females are thought to prefer males with higher courtship intensity because of their higher genetic quality and parental abilities, as displaying is energetically costly and correlated with parental care (e.g. Svensson et al., 2004; Takahashi & Khoda, 2004). Male size is also an important trait in the mating success of sand gobies. Larger P. minutus males are more successful in nest competition, provide more parental care and are preferred by females (e.g. Lindström, 1992). Thumps emitted by *P. pictus* males at a higher rate and in longer bursts, as observed in larger and more active males during nest displays, could thus signal male quality and perhaps parental abilities.

Thump-like sounds have never been reported for *Pomatoschistus* spp. or other sand gobies, but drums are similar to the breeding sounds emitted by other congeneric species and by *Knipowitschia* spp. (Lugli et al., 1995; Lugli & Torricelli, 1999). Although drumming emission was not registered for *P. pictus* with both male and female in the nest, the extension of sound production throughout spawning cannot be ruled out since no female was observed to spawn in the present study.

In conclusion, the ability that the painted goby shows to emit two different sound types associated with different courtship behavioural patterns, and the positive correlation found between courtship intensity (including sound production) and male size, indicates that acoustic signalling may play a major role in mate assessment and male mating success in *P. pictus*, as suggested for other sand gobies.

The authors would like to thank Frederico Almada, Ines Tojeira, António Vitorino and Gonçalo Jesus for the help with fish collection. Miguel Simões also advised on behavioural recording with the Observer. MCPA thanks FCT, Portugal (grant POSI SFRH/BPD/14570/2003) for financial support.

REFERENCES

- Amorim, M.C.P., Knight, M.E., Stratoudakis, Y. & Turner, G.F., 2004. Differences in sounds made by courting males of three closely related Lake Malawi cichlid species. *Journal of Fish Biology*, 65, 1358–1371.
- Bass, A.H. & McKibben, J.R., 2003. Neural mechanisms and behaviors for acoustic communication in teleost fish. *Progress in Neurobiology*, **69**, 1–26.
- Bouchereau, J.-L., Houder, V., Marques, A., & Rebelo, J.E., 2003. A new distribution record and the reproductive strategy of *Pomatoschistus pictus adriaticus* (Pisces: Gobiidae) in the Mediterranean Sea. *Journal of the Marine Biological Association of the* United Kingdom, 83, 1157–1161.
- Forsgren, E., 1997. Mate sampling in a population of sand gobies. *Animal Behaviour*, 53, 267–276.
- Gerald, J.W., 1971. Sound production during courtship in six species of sunfish (Centrarchidae). *Evolution*, 25, 75–87.
- Hawkins, A.D. & Amorim, M.C.P., 2000. Spawning sounds of the male haddock, *Melanogrammus aeglefinus. Environmental Biology of Fishes*, **59**, 29–41.
- Kishi, Y., 1979. Social behaviour of the goby, *Tridentiger obscurus*. *Hiyoshi Science Review*, **15**, 127–146.
- Lindström, K., 1992. Female spawning patterns and male mating success in the sand goby *Pomatoschistus minutus*. *Marine Biology*, 113, 475–480.
- Lindström, K. & Lugli., M., 2000. A quantitative analysis of the courtship acoustic behaviour and sound patterning in male sand goby, *Pomatoschistus minutus*. *Environmental Biology of Fishes*, 58, 411–424.
- Locatello, L., Mazzoldi, C. & Rasotto, M.B., 2002. Ejaculate of sneaker males is pheromonally inconspicuous in the black goby, *Gobius niger* (Teleostei, Gobiidae). *Journal of Experimental Zoology*, 293, 601–605.
- Lugli, M., 1997. Response of male goby, *Padogobius martensii*, to aggressive sound playback following pre-experimental visual stimulation. *Behaviour*, **134**, 1175–1188.
- Lugli, M. & Torricelli, P., 1999. Prespawning sound production in mediterranean sand-gobies. *Journal of Fish Biology*, 54, 691–694.
- Lugli, M., Pavan, G., Torricelli, P. & Bobbio, L., 1995. Spawning vocalizations in male freshwater gobies (Pisces, Gobiidae). *Environmental Biology of Fishes*, **43**, 219–231.
- Lugli, M., Pavan, G. & Torricelli, P., 1996. The importance of breeding vocalizations for mate attraction in a freshwater goby with a composite sound repertoire. *Ethology, Ecology and Evolution*, 8, 343–351.
- Lugli, M., Torricelli, P., Pavan, G., & Mainardi, D. 1997. Sound production during courtship and spawning among freshwater gobiids (Pisces, Gobiidae). *Marine and Freshwater Behaviour and Physiology*, **29**, 109–126.

Lugli, M., Pavan, G. & Torricelli, P., 2004. The response of male freshwater goby to natural and synthetic male courtship sound playback following exposure to different female sexual stimuli. *Ethology, Ecology and Evolution*, **16**, 55–70.

7

- Marshall, J.A., 1972. Influence of male sound production on oviposition in female *Tilapia mossambica* (Pisces, Cichlidae). *American Zoologist*, **12**, 663–664.
- Martin, P. & Bateson, P., 1993. Measuring Behaviour. An Introductory Guide, 2nd edn. Cambridge: Cambridge University Press.
- Miller, P.J., 1986. Gobiidae. In Fishes of the north-eastern Atlantic and the Mediterranean. Vol. 3 (ed. P.J.P. Whitehead et al.), pp. 1019– 1085. Paris: Unesco.
- Myrberg, A.A., Jr, 1997. Sound production by a coral reef fish (*Pomacentrus partitus*): evidence for a vocal, territorial "keep-out" signal. *Bulletin of Marine Science*, **60**, 1017–1025.
- Myrberg, A.A., Jr & Lugli, M., 2006. Reproductive behaviour and acoustical interactions. In *Communication in fishes. Vol. 1* (ed. F. Ladich et al.), pp. 149–176. Enfield: Science Publishers.
- Myrberg, A.A., Jr., Spanier, E. & Ha, S.J., 1978. Temporal patterning in acoustical communication. In *Contrasts in Behaviour* (ed. E.S. Reese and F.J. Lighter), pp. 137–179. New York: John Wiley & Sons.
- Myrberg, A.A., Jr., Mohler, M. & Catala, J., 1986. Sound production by males of a coral reef fish (*Pomacentrus partitus*): its significance to females. *Animal Behaviour*, **24**, 923–933.
- Stadler, J.H., 2002. Evidence for a hydrodynamic mechanism of sound production by courting males of the notchtongue goby, *Bathygobius curacao* (Metzelaar). *Bioacoustics*, **13**, 145–152.
- Svensson, O. & Kvarnemo, C., 2005. The importance of sperm competition risk and nest appearance for male behavior and female choice in the sand goby, *Pomatoschistus minutus. Behavioral Ecology*, 16, 1042–1048
- Svensson, O., Nyman, A. & Kvarnemo, C., 2004. Costly courtship or dishonest display? Intensely displaying sand goby males have lower lipid content. *Journal of Fish Biology*, 64, 1425–1429.
- Takahashi, D. & Kohda, M., 2004. Courtship in fast water currents by a male stream goby (*Rhinogobius brunneus*) communicates the parental quality honestly. *Behaviour, Ecology and Sociobiology*, 55, 431–438.
- Tavolga, W.N., 1958. The significance of under-water sounds produced by males of the gobiid fish, *Bathygobius soporator*. *Physiological Zoology*, **31**, 239–271.
- Tavolga, W.N., 1971. Sound production and detection. In Fish Physiology. Vol. 5 (ed. W.S. Hoar and D.J. Randall), pp: 135–205. New York: Academic Press.
- Thorson, R.F. & Fine, M.L., 2002. Crepuscular changes in emission rate and parameters of the boatwhistle advertisement call of the gulf toadfish, *Opsanus beta. Environmental Biology of Fishes*, 63, 321–331.

Submitted 2 January 2007. Accepted XXXX.