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Mating sounds in the two-spotted goby, *Pomatoschistus flavescens*: Effects of water temperature on acoustic features[a]

Morgane Millot,[1,b] Ana M. Faria,[2] (iD) and M. Clara P. Amorim[1] (iD)

[1]*Departamento de Biologia Animal, Faculdade de Ciências, MARE—Marine and Environmental Sciences Centre/ARNET, Aquatic Research Network, Universidade de Lisboa, Lisbon, Portugal*

[2]*MARE—Marine and Environmental Sciences Centre/ARNET—Aquatic Research Network, ISPA—Instituto Universitário, Lisbon, Portugal*

ABSTRACT:

Acoustic signals in teleost fishes play a fundamental role in reproduction. As fish are ectothermic animals, temperature has the potential to change their signal production and detection, with further implications for mating interactions. In this study, we describe the mating sounds made by the two-spotted goby, *Pomatoschistus flavescens*, for the first time and further investigate the effect of temperature on the acoustic features. Courtship sounds of 15 two-spotted goby males were recorded at three different temperatures: 16 °C, 19 °C, and 21 °C. As seen for other marine gobies, two-spotted goby produced two courtship sounds: drums and thumps. Drums showed similar acoustic features to other *Pomatoschistus* species already studied. Calling rates for both kinds of sound were not affected by the increases in temperature. However, pulse rate increased from 16 °C to 19 °C and stabilised between 19 °C and 21 °C, suggesting that two-spotted gobies reached their physiological limits at 19 °C. Spectral features were also affected by temperature, presenting higher values at 19 °C. Whether or not the observed changes in acoustic features with temperature lead to changes in mating remains to be addressed. Studies like the present one are fundamental to better comprehend how reproduction will be affected by global warming in soniferous fishes.

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I. INTRODUCTION

Acoustic communication of teleost species is the subject of numerous studies, highlighting the diversity of sounds (Amorim, 2006), the associated mechanisms (Fine and Parmentier, 2015), the production contexts (Kasumyan, 2009), and its function (Amorim *et al.*, 2015). Particularly, acoustic signals play a fundamental role in providing information about size, sex, age, or reproductive quality of the producer (e.g., Colleye *et al.*, 2009; Amorim *et al.*, 2010; Tellechea and Norbis, 2012; Amorim *et al.*, 2013; Millot *et al.*, 2021). Furthermore, these signals can elicit gonads' development in females (Rosenthal and Marshall, 2011; Crovo *et al.*, 2022), likely trigger gamete release (Hawkins and Amorim, 2000), and influence reproductive success (Vasconcelos *et al.*, 2012; Amorim *et al.*, 2013; Oliver and Lobel, 2013; Pedroso *et al.*, 2013; Amorim *et al.*, 2016).

As ectotherms, acoustic communication in fish is dependent on temperature (Ladich, 2018). Temperature effects are known on both peripheral and central mechanisms of signal production and detection, as well as on behaviour (Warren *et al.*, 2017; Ladich, 2018). Previous studies have reported changes on temporal and spectral features of fish sounds associated with temperature (Torricelli *et al.*, 1990; Lugli *et al.*, 1996; Vicente *et al.*, 2015). Acoustic features, such as sound duration, pulse period (PP) (duration between peak-to-peak interval of consecutive pulses, ms) or pulse repetition rate, sound amplitude, and spectral characteristics, have been reported to change with temperature (e.g., Connaughton *et al.*, 2000), but the effect may depend on species (Ladich, 2018). For example, sound duration may increase or decrease in different species or even within species when considering different sound types (Torricelli *et al.*, 1990; Amorim, 2005). Also, temperature may not affect the different acoustic features in the same way; some may be more affected than others (Ladich and Maiditsch, 2020). In general, the pulse repetition rate or the fundamental frequency of sounds is the feature most affected by temperature, with pulse rate (or fundamental frequency) increasing in different species, such as batrachoidids, triglids, and sciaenids (Connaughton *et al.*, 2000; Connaughton, 2004; Amorim, 2005; Maruska and Mensinger, 2009). This pattern reflects the temperature dependence of the firing rate of hindbrain central pattern generators controlling the activity of sonic muscles, as well as the speed of the muscle twitch (Bass *et al.*, 2015).

The intra- and inter-specific variability in the effect of temperature on acoustic signals within and between species raises important concerns in the face of a global warming scenario and the increase in ocean temperature (+4 °C estimated before the end of the century; IPCC, 2021).

The prevalence of acoustic communication in teleost fishes is likely related to its role in reproduction (Looby *et al.*, 2022). Thus, the effect of temperature in acoustic signalling during mating interactions needs to be further investigated in fishes.

This study describes the acoustic signals produced by males of the two-spotted goby, *Pomatoschistus flavescens*, during courtship and further examines how temperature impacts these signals. Acoustic communication has been well studied in gobies (Table I), highlighting that two types of sounds are commonly produced during courtship: drums (pulsed) and thumps (non-pulsed) (e.g., Lugli and Torricelli, 1999; Malavasi *et al.*, 2009; Amorim *et al.*, 2013; Pedroso *et al.*, 2013). These sounds likely result from the contraction of muscles connected to the pectoral girdle (Parmentier *et al.*, 2013; Parmentier *et al.*, 2017). The two-spotted goby is a small-size, semi-pelagic goby, with parental care and distinct sexual dimorphism. The species is easily kept under laboratory conditions, where it reproduces and displays the natural courtship behaviour (e.g., Lopes *et al.*, 2022). This goby is well known for its dynamic sexual role (Amundsen, 2018), with a marked sexual selection on males in the early breeding season (operational sex ratio heavily male-biased at the start of the season), and a complete reversal of sex roles by the end of the season (female-biased operational sex ratio) (Forsgren *et al.*, 2004). This species displays an elaborate visual courtship (Amundsen and Forsgren, 2001; Forsgren *et al.*, 2004), and males are also known to produce sounds (drums and thumps) close to the nest just prior to mating (de Jong *et al.*, 2018). However, drums and thumps have not been characterised thus far. Here, mating sounds produced by a total of 15 males were recorded under three temperatures (16 °C, 19 °C, and 21 °C), representative of the natural variability experienced by the species during the breeding season.

II. MATERIALS AND METHODS

A. Fish collection and experimental setup

Specimens of two-spotted goby, *P. flavescens*, were collected, via scuba diving, at the Arrábida Marine Park, Portugal (38° 28′ N; 8° 59′ W), in December 2021. Fish were immediately transported to the fish facilities of the Animal Biology Department of University of Lisbon, where they were placed in a 200-litre tank filled with artificial filtered seawater and equipped with filtration systems. Fish were kept at 16 °C, salinity of 35, and provided with sand, shelters, and artificial algae as environmental enrichment. Temperature was controlled using a chiller (HC300A, Hailea Group Co., Ltd., Chaozhou, China). The photoperiod

TABLE I. Species of Gobiidae known to be vocal and contexts of sound production.

Species	Agonistic	Reproduction	References
Periophthalmodon septemradiatus	Yes	—	Polgar *et al.* (2011)
Padogobius nigricans	No	Yes	Lugli *et al.* (1996); Lugli *et al.* (1997); Malavasi *et al.* (2008)
Padogobius bonelli (previously *Padogobius martensii*)	Yes	Yes	Torricelli and Romani (1986); Torricelli *et al.* (1990); Lugli *et al.* (1995); Lugli *et al.* (1997); Lugli *et al.* (2003); Malavasi *et al.* (2008)
Knipowitschia panizzae	No	Yes	Lugli and Torricelli (1999); Malavasi *et al.* (2008)
Gobius paganellus	Yes	Yes	Malavasi *et al.* (2008); Parmentier *et al.* (2013)
Gobius cobitis	Yes	Yes	Malavasi *et al.* (2008)
Gobius niger	Yes	Yes	Kinzer (1961); Malavasi *et al.* (2008)
Gobius cruentatus	Yes	—	Sebastianutto *et al.* (2008)
Zosterisessor ophiocephalus	Yes	Yes	Malavasi *et al.* (2003); Malavasi *et al.* (2008)
Pomatoschistus minutus	Yes	Yes	Lindström and Lugli (2000); Malavasi *et al.* (2008); Pedroso *et al.* (2013); Blom *et al.* (2022)
Pomatoschistus marmoratus	Yes	Yes	Lugli and Torricelli (1999); Malavasi *et al.* (2008)
Pomatoschistus flavescens (previously *Gobiusculus flavescens*)	—	Yes	de Jong *et al.* (2016); de Jong *et al.* (2018) + present study
Pomatoschistus pictus	Yes	Yes	Amorim and Neves (2007, 2008); Amorim *et al.* (2013); Bolgan *et al.* (2013); Pedroso *et al.* (2013); Vicente *et al.* (2015); Parmentier *et al.* (2017)
Pomatoschistus microps	—	Yes	Bolgan *et al.* (2013); Blom *et al.* (2016)
Neogobius melanostomus	Yes	Yes	Protasov *et al.* (1965); Rollo *et al.* (2007); Horvatić *et al.* (2019)
Neogobius fluviatilis	Yes	Yes	Horvatić *et al.* (2016)
Bathygobius soporator	—	Yes	Tavolga (1958)
Bathygobius curacao	—	Yes	Stadler (2002)
Bathygobius fuscus	—	Yes	Zhang and Takemura (1989)
Proterorhinus marmoratus	Yes	Yes	Ladich and Kratochvil (1989)
Gobiosoma bosc	Yes	Yes	Mok (1981)
Ponticola kessleri	Yes	No	Horvatić *et al.* (2019)
Tridentiger obscurus	—	Yes	Kishi (1979)
Orsinigobius punctatissima (previously *Knipowitschia punctatissima*)	No	Yes	Lugli *et al.* (1995); Lugli *et al.* (1997); Malavasi *et al.* (2008)
Ninnigobius canestrinii (previously *Pomatoschistus canestrinii*)	Yes	Yes	Lugli and Torricelli (1999); Malavasi *et al.* (2008); Malavasi *et al.* (2009)

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followed a natural light cycle (12 h:12 h until the start of June and then 14 h:10 h light-dark). Fish were daily fed *ad libitum* with frozen *Artemia*. Temperature and salinity were measured daily, and other water quality parameters, such as ammonia, nitrates, and nitrites, were monitored weekly and kept below critical levels.

We used three experimental temperatures: 16 °C, 19 °C, and 21 °C. Before introducing males and females in the experimental tanks at 19 °C and 21 °C, they were placed in 35-litre tanks and progressively acclimated to these temperatures as follows: temperature was increased by 1 °C on the first day and 2 °C on the following days until the target temperature was reached. Water temperature was controlled and adjusted with aquaria chillers, one per tank (Hailea HC300A). Then fish were introduced and left undisturbed in the experimental tanks for 48 h before being tested.

Experimental tanks (35 litres $26 \times 51 \times 31\,cm^3$) were divided into three compartments by two transparent and perforated plexiglass partitions to allow water circulation and filtration. Two ripe females were placed in the central compartment and one male in each lateral compartment. Artificial nests made with polyvinyl chloride (PVC) tubes [as in Amorim *et al.* (2013)] were placed on top of bags of gravel (5 cm high) and added to each male compartment (Fig. 1). For a maximum noise insulation, each experimental tank was positioned on top of two 3-cm thick marble slabs interspaced with two levels of rubber foam shock absorbers, which significantly minimised the conduction of floor born vibrations. All pumps and chillers were also turned off during the recordings.

B. Experiments

Each male was used in a single tested temperature. Recordings were carried out from April to July 2022; the experimental protocol followed Amorim *et al.* (2013) and Vicente *et al.* (2015). In each recording day, we tested fish from the three temperature treatments, to exclude the influence of different breeding conditions throughout the 3-month period of experiments. Experiments were started by positioning two hydrophones:one (94 SSQ, sensitivity of −165 dB re 1 V/µPa, flat frequency response up to 6 kHz ± 1 dB, High Tech Inc., Gulfport, MS) at the junction of the females and the tested male compartments and one (HTI-96-Min, sensitivity of −165 dB re 1 V/µPa, High Tech Inc.) in the nest chimney (Fig. 1). The hydrophone in the nest chimney aimed to optimise the recording of sounds made by the male inside the nest, by placing it as close as possible to the male (ca. 1 cm). Although artificial shelters used in laboratory studies can affect the characteristics of fish sounds when made within the shelters, the PVC chimney and remaining nest structure are not expected to significantly change the spectral properties of male sounds due to their similar density to water (Lugli, 2012). Lugli (2012) studied the frequency response of different artificial shelters and concluded that PVC shelters should be preferred over other materials when characterising low-frequency acoustic signals, i.e., with main frequency below 400–500 Hz. Then the partition between the focal male and the females was removed, allowing male-female interactions during 30 min. An opaque partition was added in the non-focal male compartment to prevent visual contact during recordings. Experimental sessions were filmed with a video camera (DCR SR15E, Sony, Tokyo, Japan). Sounds were captured by the hydrophones, digitised with an audio interface (Cakewalk UA25EX UA25, 16-bit, 6 kHz acquisition rate; Roland, Hamamatsu, Japan) to a laptop controlled by Cool Edit Pro (version 2.0, Cool Record Edit, Cool Media LLC, Gainesville, FL). Video and audio signals (derived from the audio recording chain) were synchronised and digitised with
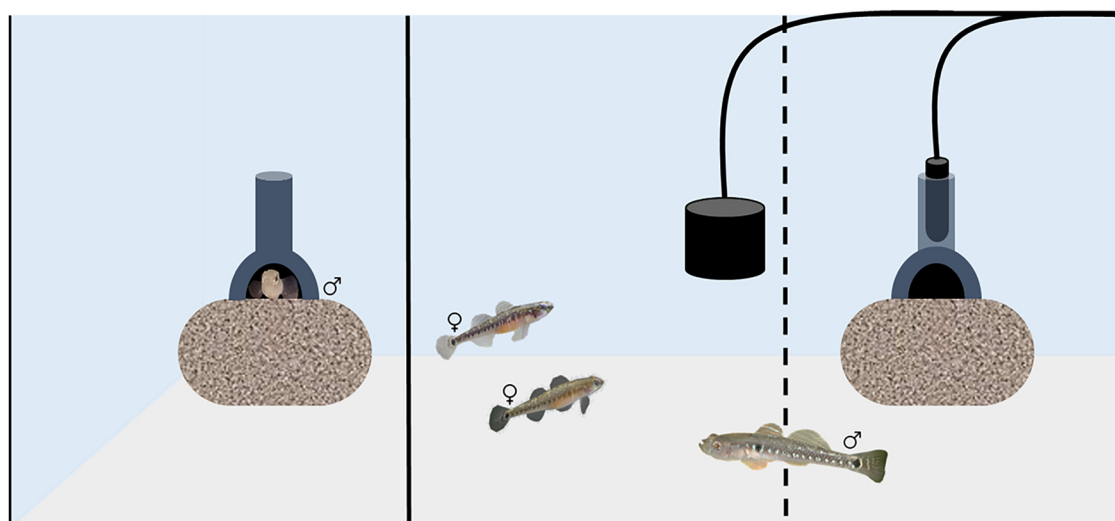
FIG. 1. (Color online) Representation of an experimental tank and the setup used to record courtship sound of males of the two-spotted goby *P. flavescens*. Black line, the opaque partition (added to the transparent one) was placed during the experiment to avoid visual interactions between males; dotted line, the transparent partition was removed for the experiment. Females and male on the right part of the tank can physically interact. Two hydrophones are positioned, one in the chimney of the nest of the tested male and one on the middle of the experimental side on the tank, to record sounds produced during male-female interactions outside and inside the nest.

an acquisition card (Pinnacle Dazzle DVD Recorder Plus, Pinnacle Systems, Mountain View, CA) to the laptop used for audio recordings. At the end of the 30-min session, males and females were measured for total length (TL) and standard length (SL) in mm and weighed (weight in g, ± 0.01 g). Males were placed in individual holding tanks after being recorded.

C. Sound analyses

Only recordings with a minimum number of sounds with a good SNR were chosen for analysis. In this study, two types of sounds produced by males of *P. flavescens* during courtship were analysed using Raven Pro software version 1.6 (Cornell Lab of Ornithology, Ithaca, NY): drums and thumps, the latter typically emitted in sequences (Fig. 2).

Temporal features were measured from oscillograms and spectral parameters were obtained from power-spectra (FFT size 1024 points, time overlap 50%, Hanning window, Hz). Durations of the sound (ms) and peak frequency (the frequency where the sound has maximum energy, Hz) were measured for the two types of sounds. For the drums, number of pulses (NP) and pulse period (PP, duration between peak-to-peak interval of consecutive pulses, ms) were also measured. Then pulse rate (NP/drum duration*1000, Hz) and pulse rate modulation (PRM) (ratio between average PP of 13–16 and 3–6 pulses, measuring the decrease in pulse rate within one sound) were calculated for the drums that were composed of more than 16 pulses. Additionally, the centre frequency, the first and third quartile frequencies (Q1 and Q3 frequency, Hz), and frequency bandwidth 90% were also measured for drums. The centre frequency is the median frequency, whereas Q1 and Q3 are the frequencies that divide the selection into two frequency intervals containing 25% and 75% of the energy in the selection. The frequency bandwidth 90% is the difference between the 5% and 95% frequencies, i.e., the frequencies that divide the selection into two frequency intervals containing 5% and 95% of the energy in the selection.

The calling rate per male was calculated for each type of sound (total number of sounds produced/recording time, sounds min^{-1}).

Sounds produced by five males per temperature were analysed, with a maximum of 20 sounds per type and per individual. Only sounds with a good signal-to-noise ratio (SNR) were considered. In the case of an individual who produced more than 20 sounds with a good SNR, they were randomly selected along the recording.

D. Statistical analyses

Statistical analyses were performed with Rstudio software (R Core Team, 2022), with a significant level $\alpha = 0.05$ for all the tests. Mean and standard deviation (SD) were calculated, for each type of sound, per male and per temperature, for the measured acoustic features. Coefficients of variation within and between males were calculated for each acoustic feature at a given temperature, following Amorim *et al.* (2013).

The effect of temperature on sounds' acoustic parameters was only measured for the drums, the most frequent sound type. When normality and homoscedasticity were met, parametric tests were used. To test the effect of temperature on drum acoustic features, analysis of variance (ANOVA) tests were done, followed by a *post hoc* Tukey test when applicable. If normality and/or homoscedasticity were not met, non-parametric tests were used: Kruskal–Wallis tests followed (when applicable) by a *post hoc* Dunn test.

III. RESULTS

Two-spotted goby males measured [mean $\pm$ SD (range)] 4.0 cm $\pm$ 0.4 (3.3–4.7 cm), weighed 1.1 g $\pm$ 0.4 (0.4–1.9), and had a condition factor of 1.7 $\pm$ 0.6 (0.4–1.9). Males' SL, weight, and K factor did not differ between the three temperature conditions [one-way ANOVA, respectively: F(2,12) = 0.76, $p = 0.49$; F(2,12) = 0.13, $p = 0.88$, and F(2,12) = 1.09, $p = 0.37$].

A total of 1788 drums and 497 thumps were produced by the 15 specimens (five specimens per temperature), of which 248 drums [17 $\pm$ 6.4 (3–20) drums per male] and 151
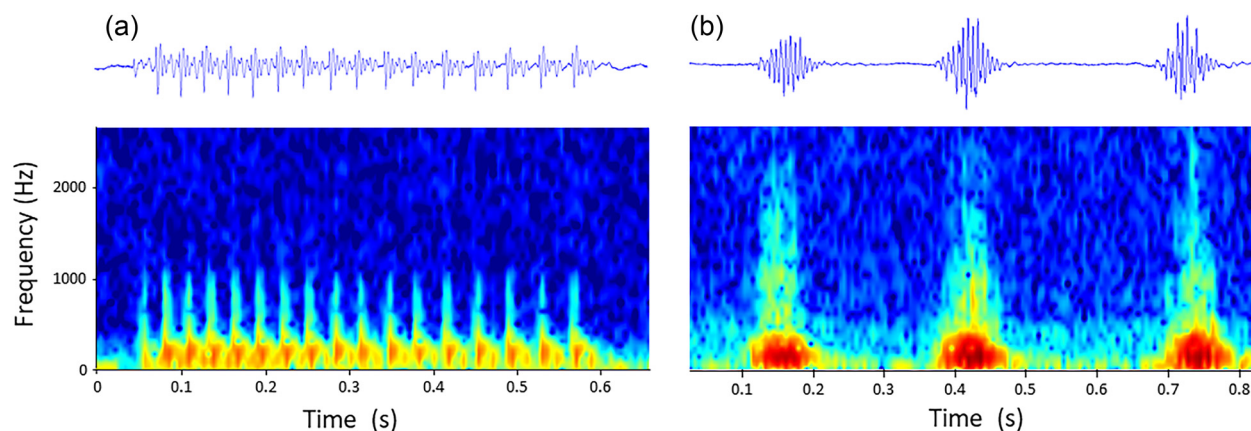
FIG. 2. (Color online) Oscillograms and spectrograms of sounds produced by males of two-spotted gobies, *P. flavescens*, during courtship: (a) a drum and (b) a sequence of thumps. Spectrogram configuration: fast Fourier transform (FFT) size: 128 points; time overlap: 50%, Hanning window.

thumps [17 ± 4.7 (8–20) thumps per male] were analysed. The average features for each type of sound at the three temperatures are presented in Table II.

Drum and thump calling rate were not different between the three temperatures [respectively, Kruskal–Wallis: $\chi^2 = 4.37$, $p = 0.1$, degrees of freedom (df) = 2 and $\chi^2 = 1.26$,

$p = 0.5$, df = 2]. Regardless of temperature, the majority of drums had between 10 and 20 pulses [Fig. 3(a)]. For the three temperatures, PPs increased until the 30th pulse was reached and then stabilised [Fig. 3(b)]. Pulse rate modulation was not affected by the increase in the temperature [ANOVA: F(2,12) = 0.05, $p = 0.95$].

TABLE II. Acoustic features of two kinds of sounds, (a) drums and (b) thumps produced during courtship by males of two-spotted gobies *P. flavescens*. Mean, SD, range, within-male (CVw), and between male coefficient of variation (CVb) were calculated for each temperature on male mean analysed sounds except for total of sounds produced and calling rate per minute because there was only one value per male. The absolute range values (Range$_{abs}$) concern all data analysed. Five males were considered per temperature. (a) Descriptive statistics are based on sounds produced by five males per temperature, T (°C) (total of sounds produced/number of sounds analysed): 16 °C (254/20, 178/20, 293/20, 6/4, 23/20), 19 °C (257/20, 315/20, 37/20, 73/20, 140/20), 21 °C (129/20, 15/14, 3/3, 58/20, 7/7). (b) Descriptive statistics are based on sounds produced by two males at 16 °C, three males at 19 °C, and four males at 21 °C. T (°C) (total of sounds produced/number of sounds analysed): 16 °C (2/0, 44/20, 29/20, 2/0, 0/0), 19 °C (0/0, 0/0, 101/20, 8/8, 12/12), 21 °C (12/12, 22/19, 0/0, 91/20, 174/20).

(a)								Drums
Acoustic parameters	T (°C)	Mean	SD	Range	Range$_{abs}$	CVw	CVb	CVb/CVw
	16	150.8	131.3	—	6–293	—	0.87	—
Total of sounds produced	19	164.4	118.8	—	37–315	—	0.72	—
	21	42.4	53.1	—	3–129	—	1.25	—
	16	5	4.4	—	0.2–9.8	—	0.88	—
Calling rate per min	19	5.5	4	—	1.2–10.5	—	0.73	—
	21	1.4	1.8	—	0.1–4.3	—	1.29	—
	16	783.4	222.7	579.5–1101.4	176.0–4421.1	0.79	0.28	0.35
Sound duration (ms)	19	532.2	112.2	398.5–643.0	181.0–3367.5	0.69	0.21	0.30
	21	541.1	154.2	338.5–711.4	165.0–1490.5	0.48	0.28	0.58
	16	23.4	6.3	17–32	6–118	0.71	0.27	0.38
NP	19	19.6	4.9	14–25	7–131	0.64	0.25	0.39
	21	20	5.9	11–25	7–53	0.46	0.30	0.65
	16	32.80	2.61	28.88–35.62	25.27–44.15	0.10	0.08	0.8
PP (ms)	19	27.06	1.50	25.32–28.73	20.88–36.39	0.07	0.06	0.86
	21	27.59	3.26	25.44–33.05	22.26–37.3	0.08	0.12	1.5
	16	31.55	2.54	29.14–35.45	23.28–42.08	0.10	0.08	0.80
Pulse rate (Hz)	19	37.65	2.03	0.035–0.040	27.90–48.88	0.07	0.05	0.71
	21	37.33	3.41	0.032–0.040	28.99–45.89	0.07	0.09	1.29
	16	1.21	0.08	1.07–1.29	0.99–1.57	0.09	0.07	0.78
Pulse rate modulation	19	1.22	0.06	1.16–1.33	1.04–1.46	0.07	0.05	0.71
	21	1.21	0.03	1.16–1.24	1.06–1.43	0.08	0.02	0.25
	16	183.4	31.5	149–227	70–311	0.23	0.17	0.74
Peak frequency (Hz)	19	252.6	80	138–363	88–457	0.27	0.32	1.19
	21	180.2	38.7	124–231	64–334	0.30	0.21	0.70
	16	180.0	27.7	142–210	123–275	0.12	0.15	1.25
Centre frequency (Hz)	19	262.7	59.1	200–359	152–439	0.15	0.22	1.47
	21	188.3	32.2	146–230	146–316	0.12	0.17	1.41
	16	135.1	25.1	94–160	59–223	0.21	0.19	0.90
Q1 (Hz)	19	191.1	46.6	124–251	47–369	0.26	0.24	0.92
	21	126.1	41.6	57–165	47–234	0.18	0.33	1.83
	16	220.9	39.3	183–272	152–551	0.19	0.18	0.95
Q3 (Hz)	19	327.4	58.7	271–414	211–469	0.14	0.18	1.29
	21	248.7	33.4	209–290	182–387	0.12	0.13	1.08
	16	259.8	61.6	173–323	117–662	0.30	0.24	0.80
FBW90	19	404.7	88.7	285–498	193–750	0.17	0.22	1.29
	21	294.0	57.0	220–374	182–563	0.16	0.19	1.19

(b)								Thumps
Acoustic parameters	T (°C)	Mean	SD	Range	Range$_{abs}$	CVw	CVb	CVb/CVw
	16	15.4	20.0	—	0–44	—	1.30	—
Total of sounds produced	19	24.2	43.2	—	0–101	—	1.79	—
	21	59.8	73.0	—	0–174	—	1.22	—

TABLE II. (*Continued*)

(b) Acoustic parameters	Thumps							
	T (°C)	Mean	SD	Range	Range$_{abs}$	CVw	CVb	CVb/CVw
Calling rate per min	16	0.5	0.7	—	0–1.5	—	1.40	—
	19	0.8	1.5	—	0–3.4	—	1.88	—
	21	2.0	2.4	—	0–5.8	—	1.20	—
Sound duration (ms)	16	126.8	9.3	120.2–133.3	90.4–159.4	0.15	0.07	0.47
	19	103.8	25.7	82.7–132.4	50.9–168.5	0.16	0.24	1.5
	21	110.6	26.1	93.3–149.3	61.6–192.1	0.18	0.25	1.39
Peak frequency (Hz)	16	110.0	29.7	89–131	53–228	0.39	0.27	0.69
	19	102.7	38.0	59–128	59–246	0.15	0.37	2.47
	21	115.0	24.3	91–148	59–275	0.26	0.21	0.81

Sound duration and NP were not significantly affected by temperature [respectively, ANOVA: $F_{(2,12)} = 3.54$, $p = 0.06$ and $F_{(2,12)} = 0.63$, $p = 0.55$; Figs. 3(c) and 3(d)]. On the contrary, mean PPs decreased between 16 °C and 19 °C and stabilised between 19 °C and 21 °C [ANOVA: $F_{(2,12)} = 7.65$, $p = 0.007$; Figs. 3(b) and 3(e)]. Pulse rate, which was a redundant metric of PP, followed the opposite pattern, increasing between 16 °C and 19 °C, and was stable between 19 °C and 21 °C [ANOVA: $F_{(2,12)} = 7.96$, $p = 0.006$; Fig. 3(f)].

In general, spectral parameters were higher at 19 °C than at 16 °C and 21 °C. These differences were significant for centre frequency, frequency bandwidth 90%, and Q3 frequency [ANOVA: centre frequency: $F_{(2,12)} = 5.88$, $p = 0.017$; frequency bandwidth 90%: $F_{(2,12)} = 5.78$, $p = 0.02$, Q3 frequency: $F_{(2,12)} = 7.49$, $p = 0.008$; Figs. 4(a), 4(c), and 4(e)].

Peak frequency and Q1 frequency were not significantly different among the three temperatures (respectively, ANOVA: $F_{(2,12)} = 2.80$, $p = 0.1$ and $F_{(2,12)} = 4.1$, $p = 0.4$).

IV. DISCUSSION

Here, we describe the sounds made by the two-spotted goby during courtship and investigate the effect of water temperature on sound production for the first time. Two-spotted goby produced two sound types—drums and thumps—that are common to other gobies of the genus *Pomatoschistus* (Malavasi *et al.*, 2009; Bolgan *et al.*, 2013; Pedroso *et al.*, 2013). Temperature increased pulse rate in drums and affected spectral features.

Drums consisted of pulse trains lasting on average ca. 600 ms, were made of ca. 20 pulses repeated every 29 ms (mean pulse rate of 36 Hz) and had a typical peak frequency around 200 Hz (considering the three temperatures). In contrast, thumps were shorter (ca. 115 ms) non-pulsed sounds with lower peak frequency around 100 Hz. In general, drums were produced more frequently than thumps (1788 vs 497 for all males). Drums made by the two-spotted goby males had similar temporal features to other *Pomatoschistus* species (sand gobies) at similar temperature ranges (Amorim

and Neves, 2007; Malavasi *et al.*, 2008; Amorim *et al.*, 2013; Pedroso *et al.*, 2013).

Temperature can affect sound production in fishes through changes in the calling activity, namely, number of sounds emitted in a certain period, as well as changes in the temporal and spectral characteristics of acoustic signals, such as sound duration, PPs, pulse repetition rates, and sound frequencies (Kéver *et al.*, 2015; Ladich, 2018).

In this study, we found that PP and pulse rate (which are redundant metrics) were influenced by water temperature. Pulse rate increased from 16 °C to 19 °C and stabilised between 19 °C and 21 °C. Pulse rate is the acoustic feature that is most frequently affected by temperature (Ladich, 2018). In fish species in which one contraction of the sonic muscles results in a sound pulse, increasing water temperature, and therefore body temperature, will result in a sound with a higher pulse rate due to its effect on the hindbrain central pattern generators controlling the activity of sonic muscles and on sonic muscle contraction speed (Bass *et al.*, 2015). This is typically the case of drumming sounds resulting from the fast contraction of muscles acting on the swim bladder (e.g., Connaughton *et al.*, 2000) but is also observable in drums produced by pectoral sonic muscles in gobies (Torricelli *et al.*, 1990; Parmentier *et al.*, 2013; Vicente *et al.*, 2015; Parmentier *et al.*, 2017). Indeed, in the closely related painted goby (*P. pictus*), pulse rate also shows a positive linear relation with temperature, from 14 °C to 22 °C (Vicente *et al.*, 2015). Yet why did pulse rate plateau around 19 °C in the two-spotted goby? It is possible that sonic muscle contraction rate could be maximal at 19 °C in this species, meaning that they reached their physiological limits and cannot contract their sonic muscles faster.

However, based on temperature dependency of sonic muscle contraction, we predicted longer sound duration at the lower temperature compared to the highest, as seen for *P. pictus*, which showed a mean duration about twice as long at 14 °C as at 22 °C (Vicente *et al.*, 2015). Nevertheless, graphically, it is possible to observe that sound duration tends to be higher at 16 °C than at higher temperatures, but there is a lot of variability in this parameter. It is likely that the number of males analysed per temperature was too low to highlight any temperature effect on
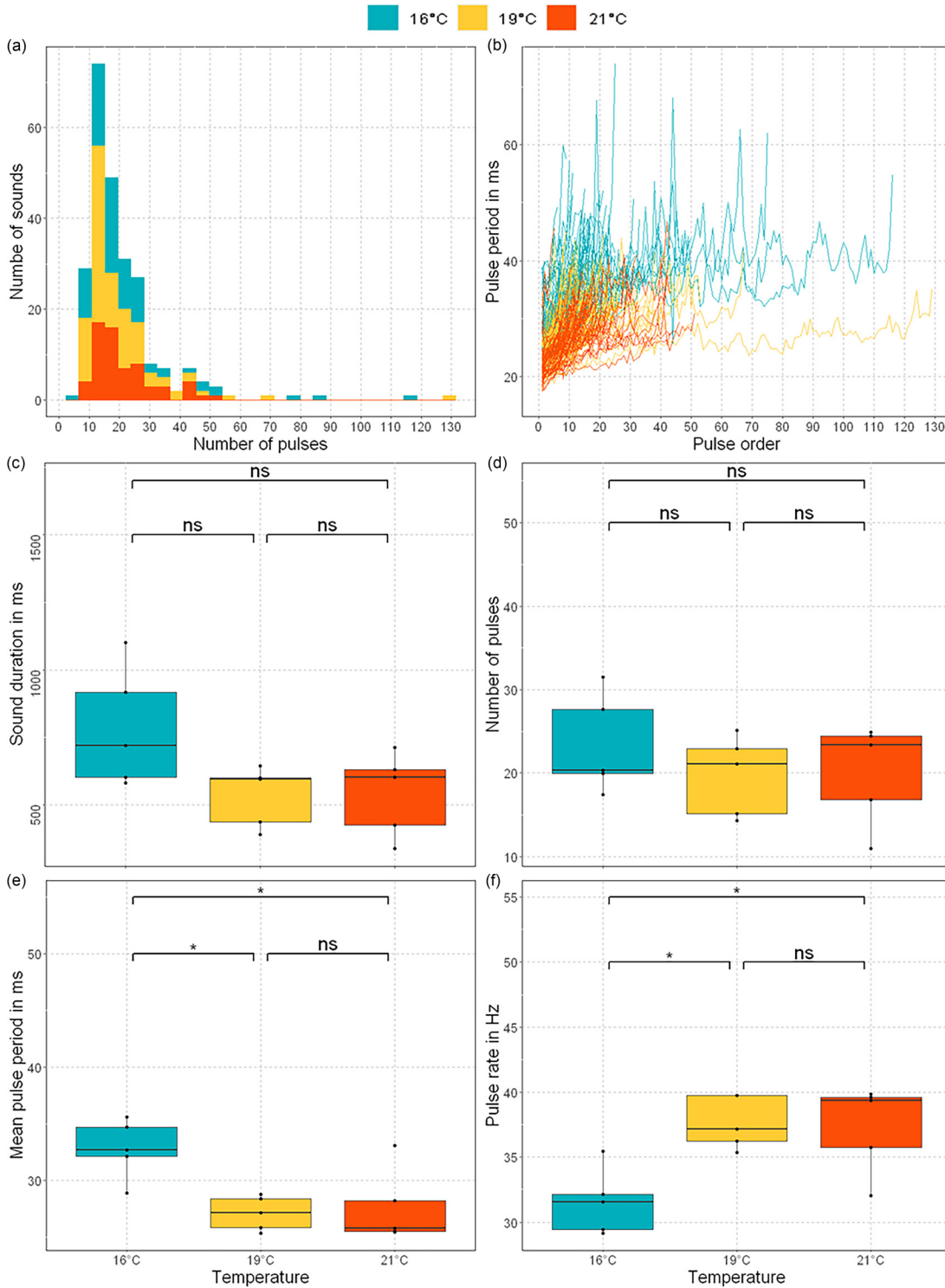
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FIG. 3. (Color online) Effect of the temperature (16 °C in blue, 19 °C in yellow, 21 °C in red) on temporal acoustic features (average per male) of drums produced by *P. flavescens* males during courtship. (a) Number of sounds as a function of the NP. (b) Representation of the PP succession within a drum (i.e., PP as a function of the pulse order within the pulse train). Each line represents a sound ($n = 248$). [(c)–(f)] Comparisons of temporal features under the three temperatures. (c) Drum duration (ms). (d) NP in a drum. (e) Mean PP (ms). (f) Pulse rate (Hz). Tukey's *post hoc* test: *, $p < 0.05$.

this parameter. Also, sound duration is correlated with the NP in a sound, and both are highly dependent on motivation (Amorim 2006), making temperature effects less obvious.

Whether or not the observed changes in PP and pulse rate with temperature lead to changes in mating and reproductive success remains to be addressed. Pulse period has been suggested to be a key feature in mate choice (Amorim *et al.*, 2010; Amorim *et al.*, 2013), which could imply that changes in this feature due to temperature can impact mating and, hence, reproductive success. However, the observed changes were on the order of 5 ms when comparing 16 °C vs 19 °C/21 °C, which are unlikely to be resolved by their
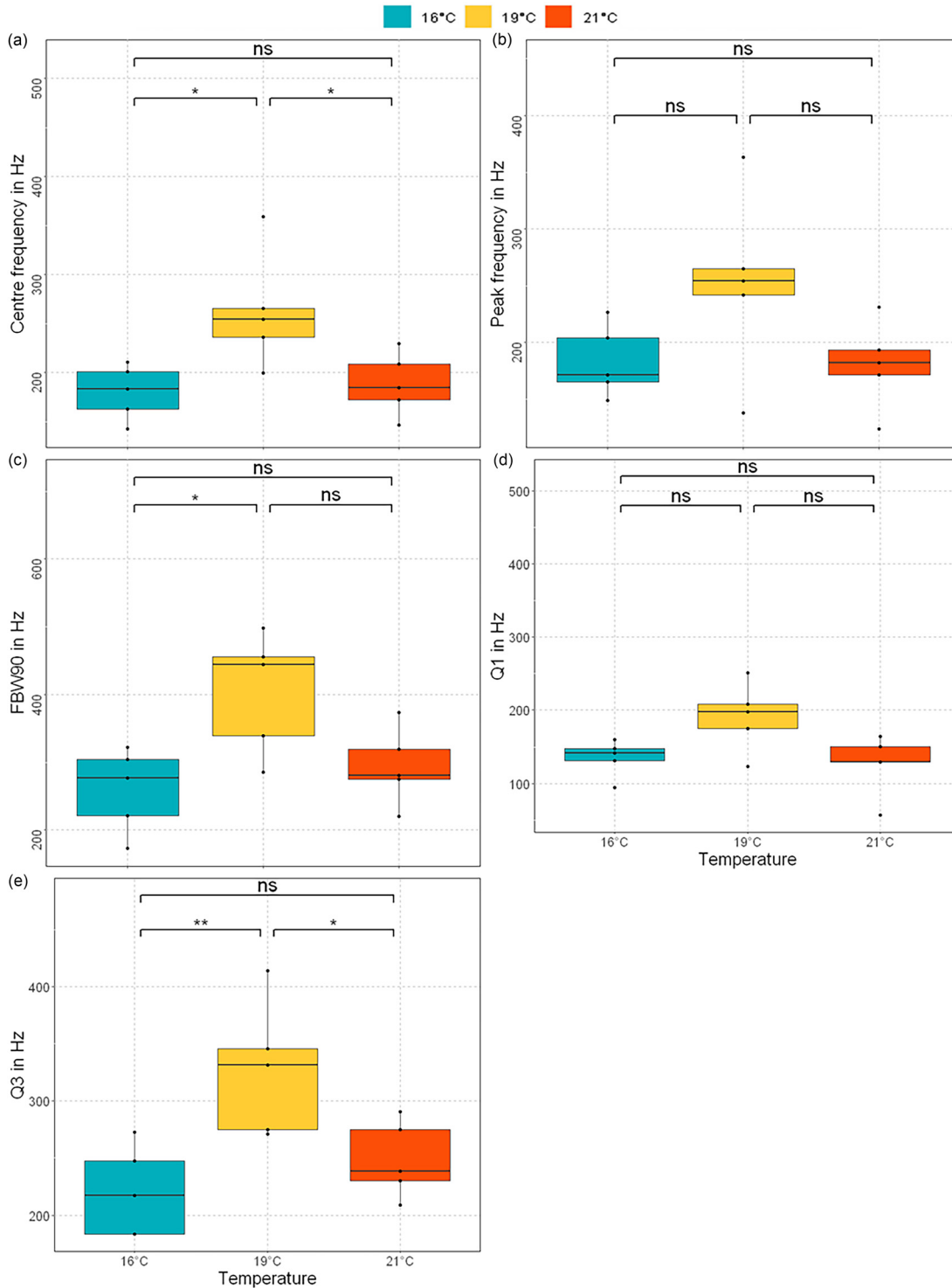
FIG. 4. (Color online) Effect of the temperature on spectral acoustic features of drums produced by *P. flavescens* males during courtship. (a) Centre frequency in Hz. (b) Peak frequency in Hz. (c) 90% frequency bandwidth in Hz. (d) Q1 frequency in Hz. (e) Q3 frequency in Hz. Tukey's *post hoc* test: *, $p < 0.05$; **, $p < 0.01$.

auditory system (Amorim *et al.*, 2018). Consistently, a recent study failed to detect significant differences in spawning success of this species under temperatures within the range of the tested temperatures of the current study. Lopes *et al.* (2022) exposed breeding adults of two-spotted goby to ambient temperature and $+3\,°C$ above ambient temperature (higher temperature $\sim 20.5\,°C$) and concluded that warming

did not lead to changes in reproductive output. However, it did lead to smaller eggs, increased lipid peroxidation levels in recently hatched larvae, lower gonadosomatic index (GSI) in males, and a decrease in the expression of cyp11b1 gene in males, which is involved in the synthesis of the most important fish androgen, 11-ketotestosterone. The authors did not examine courtship behaviour or parental care, but

considering the overall results, it seems that warming did not affect spawning activity, but there were costs for males and offspring. A different study with the two-spotted goby (Albouy *et al.*, 2023) showed that, as seen in the current study, the numbers of drums and thumps were not affected by temperature (16 °C and 20 °C), but acoustic activity proved to be a good proxy for reproductive success in this species, as spawning success and number of laid eggs were positively correlated with number of drums and negatively correlated with number of thumps.

Considering all the above, it is likely that the observed changes with temperature in PP/pulse rate will not lead to changes in mating success in this species, at least within the range of tested temperatures. However, pulse rate could be relevant for species recognition (e.g., Amorim and Vasconcelos, 2008; Malavasi *et al.*, 2008), and if temperature affects this feature dissimilarly in different species, then conspecific recognition could be impaired—a hypothesis that warrants further investigation. Further studies should also aim at testing temperatures outside the thermal variability that the species is used to experiencing in the wild and further detailing and relating the acoustic features with reproductive success. Also, the effect of temperature on hearing abilities should be addressed, as it is known to affect the hearing sensitivity of fishes (Papes and Ladich, 2011).

Some spectral drum parameters, namely, the centre frequency, frequency bandwidth 90%, and Q3 frequency, were higher at 19 °C than at 16 °C and 21 °C. In other species, the effect of temperature on sound frequency can be variable, from no effect to an increase in the fundamental or the peak frequency (Ladich, 2018). In *P. flavescens*, no effect of temperature on peak frequency was found, consistent with findings for *P. pictus* (Vicente *et al.*, 2015), which produces similar sounds. The apparent non-linear effect of temperature on the remaining spectral features warrants further investigation.

V. CONCLUSION

This study provides the first description of the vocalisations of two-spotted goby *P. flavescens* males in a courtship context. As other marine gobies, they produced two kinds of sounds to attract females: drums and thumps. Drum acoustic features were similar to other sand goby species recorded in the same temperature range. Water temperature affected pulse rate in drums and some spectral (centre frequency, frequency bandwidth 90%, and Q3 frequency) drum features. In a global warming scenario, it is paramount to increase our knowledge of its effect on traits, such as acoustic signals, that are key in mediating reproduction outcome.

AUTHOR DECLARATIONS
Conflict of Interest

The authors declare no conflict of interest.

Ethics Approval

Experiments were authorised by the Portuguese National Authority for Animal Health—Direção Geral de Alimentação e Veterinária (DGAV reference 0421/000/000/2021) and performed in strict accordance with the EU Directive 2010/63/EU for animal experiments. The study also followed the recommendations of the Animal Care and Use Committee of the University of Lisbon.

DATA AVAILABILITY

Data are available from the authors upon request.

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