

RESEARCH ARTICLE

Acoustic communication in marine shallow waters: testing the acoustic adaptive hypothesis in sand gobies

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ABSTRACT

Acoustic communication is an important part of social behaviour of fish species that live or breed in shallow noisy waters. Previous studies have shown that some fish species exploit a quiet window in the background noise for communication. However, it remains to be examined whether hearing abilities and sound production of fish are adapted to marine habitats presenting high hydrodynamism. Here, we investigated whether the communication system of the painted (*Pomatoschistus pictus*) and the marbled (*Pomatoschistus marmoratus*) gobies is adapted to enhance sound transmission and reception in Atlantic shallow water environments. We recorded and measured the sound pressure levels of social vocalisations of both species, as well as snapshots of ambient noise of habitats characterised by different hydrodynamics. Hearing thresholds (in terms of both sound pressure and particle acceleration) and responses to conspecific signals were determined using the auditory evoked potential recording technique. We found that the peak frequency range (100–300 Hz) of acoustic signals matched the best hearing sensitivity in both species and appeared well adapted for short-range communication in Atlantic habitats. Sandy/rocky exposed beaches presented a quiet window, observable even during the breaking of moderate waves, coincident with the main sound frequencies and best hearing sensitivities of both species. Our data demonstrate that the hearing abilities of these gobies are well suited to detect conspecific sounds within typical interacting distances (a few body lengths) in Atlantic shallow waters. These findings lend support to the acoustic adaptive hypothesis, under the sensory drive framework, proposing that signals and perception systems coevolve to be effective within local environment constraints.

KEY WORDS: Gobiidae, *Pomatoschistus*, Acoustic communication, Acoustic window, Ambient noise, Auditory sensitivity

INTRODUCTION

Sensory systems have evolved to increase survival and reproduction success, playing a crucial role in detection and discrimination of

relevant stimuli from background noise, including mates' signals and cues from predators or prey (Stevens, 2013). Likewise, communication signals, which are central in social behaviour, should be adapted to the local environment to enhance transmission and reception (Bradbury and Vehrencamp, 2011). Because habitat properties impose selective pressures in all stages of communication (signal production, transmission and reception), Endler (1992) proposed a sensory drive framework to explain the coevolution of sensory systems, signals, signalling behaviour and microhabitat choice. The author postulated that natural selection should favour signals, behaviour and receptors that will maximise detection and recognition of the received signals against the background noise and minimise signal attenuation and degradation.

Evidence from the sensory drive framework is derived largely from terrestrial organisms, and mainly from visual systems, with fewer studies focussing on the effect of environmental constraints on acoustic signals and auditory reception (Bradbury and Vehrencamp, 2011). Much work on acoustic systems comes from studies testing the acoustic adaptation hypothesis (enclosed in the sensory drive framework) on birds, frogs and insects (Boncoraglio and Saino, 2007; Ey and Fischer, 2009; Wilkins et al., 2013). This hypothesis predicts that local habitat attributes influence signal evolution through effects on signal transmission (Morton, 1975).

Although acoustic systems are privileged in the aquatic environment because sound propagates faster and is much less attenuated in water than in air (making it particularly suitable to extract information from distant sources; Rogers and Cox, 1988), little is known on how environmental pressures act on the evolution of acoustic communication in aquatic animals (Lugli, 2015). Among aquatic organisms, fish constitute excellent candidates to examine the effects of various environmental pressures, such as background noise, on the evolution of communication systems. Teleost fishes inhabit an immense variety of aquatic habitats, ranging from extremely shallow water to open ocean and deep sea habitats, and have evolved the most diverse sound-generating mechanisms among vertebrates to produce vocalisations, which are crucial for social communication, including mate choice (Amorim et al., 2015; Ladich and Fine, 2006; Parmentier and Fine, 2016). This variety in sonic organs results in diverse sound types, which differ in both the temporal and the spectral domain (Ladich and Fine, 2006). The diversity of hearing abilities is also exceptional, suggesting that, along the evolutionary process, species have found ways to specialise to gather more information about their highly diverse environments (Braun and Grande, 2008).

In particular, the coevolution of acoustic signalling and hearing abilities in communication-challenging marine habitats is poorly understood. Shallow water habitats are perhaps the most unfavourable for fish acoustic communication. They are typically characterised by high noise levels, originating from surf, wind, shipping, industrial and biological noises, that vary greatly in time

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and among places (Urick, 1983), and impose serious constraints to sound propagation, especially for wavelengths larger than the water depth (Roger and Cox, 1988). However, most soniferous fish species use low-frequency pulsed sounds (under 500 Hz, i.e. wavelengths >3 m) and inhabit or reproduce in noisy shallow waters (Lugli, 2015). Solutions to optimise sound detection [i.e. higher signal-to-noise ratio (SNR)] may involve using short communication distances, concentrating signal energy within a more 'silent window' of the ambient noise (AN) spectrum and/or matching the signal dominant frequencies with the most sensitive hearing range of the species (Lugli et al., 2003; Bradbury and Vehrencamp, 2011). Matching both best hearing sensitivity and main sound frequencies with quiet AN has been observed for freshwater gobies only by Lugli et al. (2003), but the exploitation of a quiet AN window for acoustic signalling has been reported in other fishes, including marine species (Lugli, 2010; Speares et al., 2011). However, it remains to be examined whether hearing abilities and fishes' sound spectra have evolved to match quiet AN levels in coastal areas with high hydrodynamics.

The present study investigates the correlation between sound spectra and hearing sensitivities in two small goby species with the prevalent AN of these species' habitat. Specifically, it: (1) investigates the spectral content of acoustic signals and the auditory sensitivity of two sympatric goby species, the painted goby *Pomatoschistus pictus* (Malm 1865) and the marbled goby *Pomatoschistus marmoratus* (Risso 1810); (2) examines the spectral composition of AN in shallow brackish and marine goby habitats in the Eastern Atlantic coast with different local ocean exposures; and (3) compares sound spectra of both communication signals and habitat noises with the species auditory sensitivities to evaluate the potential role of the acoustic environment shaping vocal communication at the level of the sender (sound signal) and the receiver (sound detection).

MATERIALS AND METHODS

Study species

The painted goby *P. pictus* and the marbled goby *P. marmoratus* are short-lived (up to 1–2 years), small-bodied coastal and brackish benthic species inhabiting shallow gravel and sand substrate areas, overlapping their distribution range in the Eastern Atlantic, including the Portuguese shoreline (Miller, 1986). Like other Gobiidae, males of these two species are polygynous, build nests under shells (Bouchereau et al., 2003), use low-frequency pulsed sounds to defend their breeding territories and to court the females, and have exclusive paternal care (Lugli and Torricelli, 1999; Amorim and Neves, 2007, 2008; Malavasi et al., 2008). In *Pomatoschistus* spp., courtship sounds are related to male quality and influence male reproductive success (Lindström and Lugli, 2000; Amorim et al., 2013; Pedrosa et al., 2013).

Test subjects

The methods for animal collection, housing, handling and experimental protocols comply with Portuguese and European animal welfare laws, guidelines and policies, and were undertaken under the supervision of an accredited expert in laboratory animal science (following FELASA category C recommendations). Permission for capturing fish at the field site was granted by the National Maritime Authority – Port of Cascais (Autoridade Marítima Nacional – Capitania do Porto de Cascais) and the National Institute for the Conservation of Nature and Forests (ICNF).

Fish from both species were captured with hand nets during low spring tides at Parede beach (38°41'N, 9°21'W) and by scuba diving in shallow waters in Arrábida (38°28'N, 8°58'W), Portugal. They

were then brought to the laboratory and kept in small aquaria (24×24×32 cm, ca. 18 l). Each aquarium was provided with sand substrate, shelters and a closed circuit flow of filtered artificial seawater, maintained at approximately 16°C. The stock system was provided with a natural day–night light cycle (12 h:12 h light:dark) and food, consisting of finely chopped shellfish, was provided daily.

We tested six adult males from each species for the hearing threshold measurements: painted goby (values given as mean, range): 34.3, 30–38 mm standard length (SL); 0.59, 0.41–0.75 g total weight (Wt); and marbled goby: 38.5, 35–45 mm SL; 0.85, 0.52–1.10 g Wt. We tested a different set of six painted goby males (35.2, 30–43 mm SL; 0.65, 0.39–1.20 g Wt) to assess the auditory response to conspecific sounds.

For characterisation of the acoustic signals made by the painted goby, we considered courtship sounds produced by 11 males (mean, range: 35, 30–43 mm SL, 0.72, 0.36–1.33 g Wt; 2011 recordings from Amorim et al., 2013) and agonistic sounds made by six males (36, 31–40 mm SL, 0.64, 0.46–0.97 g Wt; recordings from Bolgan et al., 2013). We additionally recorded courtship sounds from three marbled goby males (37, 33–40 mm SL, 0.73, 0.55–0.89 g Wt; present study).

Fish sound recordings and analysis

Marbled goby sound recordings were obtained in 35 l aquaria at 16°C, following the methods previously used for painted gobies (Amorim et al., 2013). Briefly, after a minimum of a 24 h acclimation period, each male was allowed to interact with one or two conspecific females for ca. 20 min, while sounds were registered with a hydrophone (8104, Brüel & Kjær, Naerum, Denmark; sensitivity –205 dB re. 1 V μPa^{-1} ; frequency response from 0.1 Hz to 180 kHz). The hydrophone was housed inside a structure of the male's nest (a chimney), which allowed the distance to the sound-producing male inside the nest to be minimised (ca. 1 cm from the hydrophone tip, i.e. ca. 3 cm from the acoustic centre of the hydrophone). The signal from the hydrophone was then conditioned through a Brüel & Kjær Mediator sound level meter (2238, Brüel & Kjær) and digitised with an A/D converter device (M-Audio Fast Track Ultra 8R, M-Audio, Irwindale, CA, USA; 16 bit, 48 kHz acquisition rate per channel) and stored in a laptop.

The amplitudes of acoustic signals were measured as average root mean square (RMS) values of the recordings. Sound pressure level (SPL; dB re. 1 μPa) values were obtained by comparison with readings in the sound level meter (Brüel & Kjær Mediator 2238, broadband linear frequency weighting, instantaneous time weighting) during fish sound production. Sounds were further analysed regarding sound duration (ms), the number of pulses, pulse period (average peak-to-peak interval of consecutive pulses; ms) and sound peak frequency [the frequency where the sound has maximum energy, measured from power spectra: 48 kHz, fast Fourier transform (FFT) size 8192 points, time overlap 60%, Hamming window; Hz]. Following Lugli (2010), we determined the range of sound peak frequency (hereafter referred to as peak frequency range), encompassing the 10th–90th percentiles of the peak frequency of the species' sounds, considering the peak frequency of individual sounds of each male. The sounds of the marbled goby are described for the first time here for Atlantic populations but have been previously described for the Mediterranean populations (Malavasi et al., 2008).

Ambient noise recordings

We characterised snapshots of the acoustic scene encountered by gobies while communicating in Atlantic coastal marine habitats

during the breeding season. The sites were chosen based on their varied hydrodynamic characteristics and included brackish lagoons, estuarine beaches and Atlantic beaches from the Portuguese coast (Fig. 1A,B, Table 1), inhabited by both species: Parede beach, Carcavelos beach, Portinho da Arrábida beach, Figueirinha beach, Albarquel beach and Albufeira Lagoon (da Cunha and Antunes, 2008). Parede and Carcavelos are characteristic Atlantic beaches, situated close to Lisbon, presenting a southwest orientation and moderate hydrodynamics (with waves typically up to 3 m high). Carcavelos beach is sandy, delimited by a fort and a beach break, whereas Parede is characterised by having sand patches intermingled by rock substrate. Portinho da Arrábida and Figueirinha are sandy/rocky beaches with little wave action as they are facing south, being protected by the adjacent mountain chain of Arrábida from the prevailing north and northwest winds. Figueirinha beach, however, is affected by tidal currents coming from the nearby Sado Estuary. Albarquel is an estuarine sandy beach and Albufeira Lagoon is a small body of water that, at times, is in contact with the sea, characterised by sand/mud sediments and a high density of aquatic vegetation (*Zostera* sp.). Both are brackish water systems with natural noise sources mainly consisting of the wind action on the water surface, and tidal currents in the case of Albarquel.

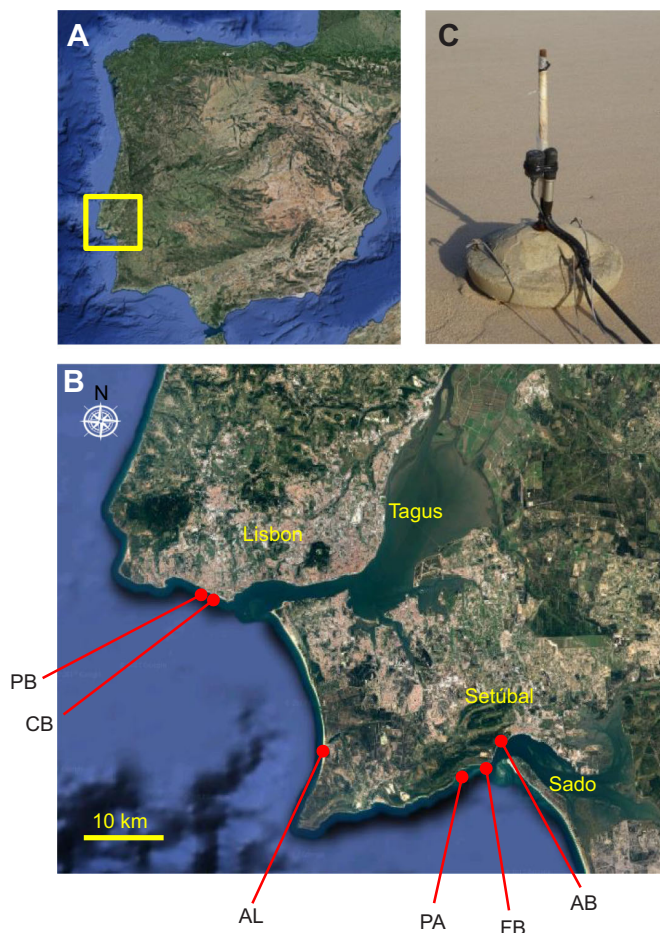


Fig. 1. Recording locations and setup. Aerial photo map of the Iberian Peninsula (A) and a detailed map (B; boxed area in A) showing the recording locations. (C) A hydrophone, attached to a metal rod inserted in a concrete slab used to minimise hydrophone drifting underwater. PB, Parede beach; CB, Carcavelos beach; AL, Albufeira Lagoon; PA, Portinho da Arrábida beach; FB, Figueirinha beach; AB, Albarquel beach.

AN was recorded during the gobies' breeding season (January–May; Amorim et al., 2013) for 3 min at one to three sites within each location (Table 1). While these snapshots do not characterise the soundscape temporal variability within a location, they nevertheless provide a good picture of the AN variability during the breeding season. Wind speed was measured using a handheld digital anemometer, while wave crest height was estimated visually always by the same observer to eliminate inter-observer variability. Recordings were made using a hydrophone (Brüel & Kjær 8104) conditioned through the Mediator sound level meter (2238) and a High Tech 94 SSQ hydrophone (High Tech Inc., Gulfport, MS, USA; sensitivity -165 dB re. $1 \text{ V } \mu\text{Pa}^{-1}$; frequency response within ± 1 dB from 30 Hz to 6 kHz) and stored in a 4-channel audio recorder (R-4, Roland, Japan, 16-bit, 96 kHz sampling frequency). The hydrophones were positioned at ca. 20 cm from the substrate, attached to a metal rod that was inserted in a concrete slab to minimise hydrophone drifting underwater (Fig. 1C). AN was recorded with common weather conditions (weak to moderate wind and no rain) and, when possible, at 1.0 m water depth (range 0.7–2 m) (Table 1). Recordings were made at intermediate tide levels except for Parede (low tide) and Figueirinha (full tide). At Carcavelos beach, the recording was made at 2 m depth as it was made from a beach break. SPLs (dB re. $1 \mu\text{Pa}$) were measured using the Mediator settings L_{LSInst} (linear frequency weighting, 5 Hz–20 kHz and a slow integration time, i.e. 1 s). Six SPL measurements were taken every 10 s during 60 s at each site. The equivalent continuous SPL (L_{Leq}), which measures the averaged energy in a fluctuating sound field and is commonly used to assess environmental noise (ISO 1996-1: 2016), was calculated, following Codarin et al. (2009), by averaging the instantaneous SPL values over 60 s, i.e. by averaging the six SPL readings.

Average sound power spectra of three 60 s recordings were obtained for each recording location, using an FFT filter bandwidth of 6 Hz (Hamming window) with Adobe Audition 3.0 (Adobe Systems Inc., CA, USA). Absolute spectra were calculated following Amoser and Ladich (2005) and using the SPL (L_{Leq}) values (see above).

In addition to the average sound spectra, for each location, we computed sound spectra (as above) for five 2 s AN samples containing elevated noise or intense noise bursts, such as breaking waves (following Lugli, 2010), as sources of high background noise are expected to be important selective forces shaping acoustic signals (Lugli et al., 2003). We also computed power spectra from another five 2 s AN samples with non-elevated noise levels. Note that, for Albufeira Lagoon and Albarquel beach, we did not calculate elevated noise sound spectra as there were no loud events. To explore the potential match between the goby sounds and the AN spectrum, we compared the courtship drum peak frequency range from both goby species with the quietest frequency window bandwidth from the AN samples with non-elevated and elevated noise events.

Auditory sensitivity measurements

The method used to measure auditory sensitivity was the auditory evoked potential (AEP) recording technique. Sound stimuli were presented through a custom-made sound stimulation device (for a detailed description see Vasconcelos et al., 2011a) calibrated before each experiment. Sound measurements were performed using a mini-hydrophone (8103, Brüel & Kjær; sensitivity -211 dB re. $1 \text{ V } \mu\text{Pa}^{-1}$; frequency response from 0.1 Hz to 180 kHz) positioned 7 cm above the disc, a position normally occupied by the fish's inner ears, during the recordings. The hydrophone was connected to an amplifier (2692 Nexus, Brüel & Kjær) and the acoustic signal digitised (Edirol UA-25, Roland Corporation, Japan) and monitored

Table 1. Recording locations with habitat type, typical sources of AN and average L_{Leq} (full spectrum) for the recording locations

Recording location	GPS coordinates	Habitat type	N	Mean water depth (m)	Mean wave crest height (m) (from substrate)	Wind speed (km h ⁻¹)	Typical sources of AN	L_{Leq}
Parede beach	38°41.158'N 09°21.172'W; 38°41.143'N 09°21.161'W	Atlantic beach, sand +rock substrate	2	0.9	0.2	10–12	Breaking waves typically up to 3 m high, waves splashing against rock and boulders, rip currents, water motion associated with waves	112.6
Carcavelos beach	38°41.143'N 09°21.161'W	Atlantic beach, sand	1	2	0.8	14–18	Similar to Parede, water action against rocks are restricted to beach breaks	119.7
Portinho da Arrábida beach	38°28.769'N 08°58.883'W; 38°28.827'N 08°58.758'W; 38°28.870'N 08°58.748'W	Calm beach, sand +scattered rocks	3	1	0.2		Small breaking waves, waves splashing against rock and boulders	112.1
Figueirinha beach	38°29.156'N 08°56.526'W; 38°29.127'N 08°56.887'W; 38°29.104'N 08°56.804'W	Calm beach, sand+ scattered rocks	3	0.9	0.6	2–7	Small breaking waves, waves splashing against rock and boulders, tidal currents	137
Albarquel beach	38°30.864'N 08°54.575'W; 38°30.975'N 08°54.442'W; 38°30.895'N 08°54.539'W	Estuarine beach, sand	3	1	Flat	3–13	Tidal currents	108.1
Albufeira Lagoon	38°30.535'N 09°10.618'W; 38°30.557'N 09°10.574'W; 38°30.575'N 09°10.490'W	Brackish lagoon, sand, mud, vegetation	3	0.9	Flat	14–20	Small breaking waves	111.1

N, number of recording sites within each recording location; GPS, global positioning system; AN, ambient noise; L_{Leq} , equivalent continuous sound pressure level (SPL). See Materials and Methods for details on SPL measurements.

by a laptop running Audition 3.0, which was used to verify stimuli spectra and control the relative amplitudes of auditory stimuli. SPLs were measured using the Mediator sound level meter 2238 connected to the mini-hydrophone. We additionally calibrated the sound field with a tri-axial accelerometer (M20-040, sensitivity 1–3 kHz, GeoSpectrum Technologies, Dartmouth, Canada). Particle acceleration levels were determined for all sound stimuli at various levels, including the hearing threshold level of the species, and in the three orthogonal directions. Pressure and particle acceleration varied similarly below the water surface in the same position occupied by the test subjects. Most of the stimuli energy was present in the vertical axis, where 6 dB changes in SPL were generally accompanied by a 6 dB change in particle acceleration level for all stimuli. Particle acceleration at the two horizontal axis was at least 15–20 dB below the value measured in the vertical axis within stimulation frequencies and amplitudes.

Specimens from both species were first mildly anaesthetised in a tricaine methanesulfonate bath (PharmaQ, Hampshire, UK) buffered with sodium bicarbonate and then immobilised by an intramuscular injection of gallamine triethiodide (PharmaQ, Hampshire, UK) following Vasconcelos and Ladich (2008). Similarly to Vasconcelos et al. (2011a), test fish were positioned below the water surface in the middle of a round plastic experimental tank (diameter: 36 cm, water depth: ca. 18 cm), with the inner ears kept at about 7 cm above the vibrating disc of the sound-generating device (see above). The tank was placed on a vibration-isolated table inside a Faraday cage. All recording and sound-generating equipment was located outside the recording room. Fish gills were perfused with saltwater through the mouth, using a simple temperature-controlled (24.2±0.9°C) gravity-fed water system.

We assessed hearing thresholds in both species with sound stimuli consisting of tone pulses presented 1000× at opposite polarities (180 deg phase shifted). Hearing thresholds were estimated at 15 Hz (stimuli repetition rate 5 s⁻¹), 30 and 60 Hz (repetition rate 10 s⁻¹), and 100, 200, 300, 400, 500, 800 and 1000 Hz (stimuli repetition rate 20 s⁻¹), presented randomly. Tone stimuli ranged from two

(15–100 Hz) up to five complete cycles. Stimuli were presented at increasing amplitudes in 4 dB steps, from 86 up to 136 dB re. 1 µPa depending on the frequency sensitivity. We further analysed the auditory responses (temporal and frequency representation) to conspecific sounds in the painted goby. One courtship and one agonistic sound with typical durations (respectively, 690 ms and 410 ms) were used as stimuli, presented in increasing amplitudes using three 4 dB steps, from 122 to 130 dB re. 1 µPa. Analysis of response latencies (interval between stimulus presentation and response onset) while decreasing stimuli amplitude served as an additional confirmation of the biological response. Sounds were presented 600× at opposite polarities and at a repetition rate of 1.0 and 1.6 sounds s⁻¹ for courtship and agonistic drums, respectively.

The recording electrode was placed firmly against the fish skin above the location of the brainstem and the reference electrode close to the nares. The signal from the electrodes was differentially amplified (50,000×; AC amplifier CP511, Grass Instruments, USA). The AEP signals were monitored with an oscilloscope and digitised using the above-mentioned equipment (Edirol UA-25). AEP signals were recorded along with the respective trigger (that represented the stimuli onset) into a stereo WAV file (48 kHz sampling rate). AEPs from each stimulus were aligned using the trigger signal (±0.02 ms) and averaged by a custom-made software (P.J.F.).

Gobies possess no hearing specialisations and thus are primarily sensitive to particle motion (Lugli et al., 2003); therefore, we report both sound pressure and particle acceleration hearing thresholds for both species.

RESULTS

Fish acoustic signals

Both the painted and the marbled gobies produced low-frequency sounds (drums) consisting of repeated fast-transient pulses with a characteristic temporal patterning (Fig. 2, Table 2). While painted goby males emitted sounds in both agonistic and courtship contexts, marbled goby males produced sounds only during mating, when the female approached the male and typically from inside the nest.

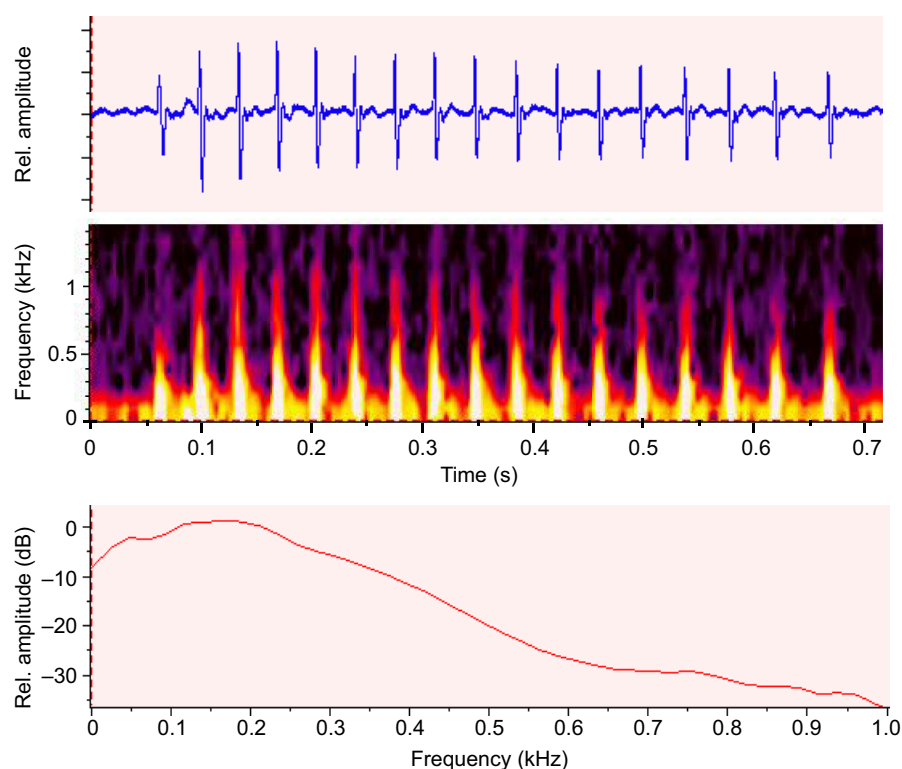


Fig. 2. Courtship sounds made by marble goby males. Oscillogram, spectrogram and power spectrum [2048 points fast Fourier transform (FFT)] of a courtship drum made by a marble goby male. Sampling frequency 48 kHz, 512 points FFT for spectrogram and 2048 points FFT for power spectrum, 60% overlap, Hanning window.

Sounds made by both species presented a peak frequency range (10th–90th percentiles) of 150–300 Hz centred at 200 Hz and with SPLs of about 130 dB re. 1 μ Pa at ca. 1 cm (Fig. 2, Table 2).

Ambient noise

AN spectral levels varied considerably between recording locations, with Figueirinha beach being the loudest habitat, with considerably higher SPLs across a wide frequency range, followed by Carcavelos (Fig. 3A, Table 1). Albufeira Lagoon, Portinho da Arrábida and Albarquel beaches presented the lowest SPLs and the most flat spectral profiles especially above 150 Hz, while Parede beach presented intermediate levels and a clear quiet window around 100–300 Hz (Fig. 3A, Table 1). The recordings made within each location did not show significant variability in their frequency spectral characteristics except in Praia da Figueirinha, where the recording made near a beach break (sand substrate) showed louder spectra, peaking around 450 Hz (Fig. 3B).

When looking at 2 s samples of elevated AN levels from the different locations, three groups emerge, with Figueirinha beach presenting the loudest events, Carcavelos and Parede beaches presenting intermediate levels and very similar spectra with a quieter low-frequency region until about 300/350 Hz, and a third group consisting of Albufeira Lagoon and Portinho da Arrábida and Albarquel beaches with lower AN spectra (Figs 4A and 5). Overall,

the loud sample AN spectra (Fig. 4A) were very similar to the average power spectra (Fig. 3) with the exception of Carcavelos, which did not show less energy in the low-frequency range (<500 Hz) when considering the full recordings (Fig. 3A).

The variability among spectra from quiet samples was considerably smaller than the observed for elevated noise samples, and the loudest quiet spectrum was observed in Carcavelos beach. Low noise spectra of Albufeira Lagoon and Arrábida beach were very similar and the lowest of all samples (Fig. 4B).

Interestingly, the spectral peak around 450 Hz observed in Parede and Carcavelos (elevated and quiet AN) is similar to the one found in Figueirinha beach in the recording made near a beach break (Fig. 3B), suggesting that this elevation in noise around that frequency is associated with water moving and splashing against big boulders that are either isolated (Parede) or part of a beach break (Carcavelos and Figueirinha).

Figure 5 examines in more detail the elevated noise events in the louder habitats. The main source of noise is water movement associated with wave action and breaking waves in both Parede and Figueirinha beaches; in the latter, water movement may also be related to incoming currents from the estuary. As waves became larger, the quieter window of the spectra that can be used for communication got smaller, disappearing in larger waves (Fig. 5A–E), but was still present in smaller waves. In contrast with

Table 2. Acoustic features of drums produced during courtship and agonistic contexts by *Pomatoschistus pictus*, and during courtship by *Pomatoschistus marmoratus*

	Drum duration (ms)	Number of pulses	Pulse period (ms)	Peak frequency (Hz)	SPL (dB)
Agonistic drums <i>P. pictus</i>	933 (234.1–2085.2)	28.8 (8–59.8)	29.6 (25.0–35.2)	156.9 (105.4–221)	–
Courtship drums <i>P. pictus</i>	833.5 (335.0–1489.6)	32.4 (14–53)	23.5 (17.6–28.7)	187.2 (146.5–236.1)	129.3 (123.2–136.0)
Courtship drums <i>P. marmoratus</i>	740.5 (560.8–894.6)	18.6 (13.0–24.6)	35.4 (32.0–41.4)	221.4 (171.2–300.0)	133 (127.7–136.2) ^a

Pomatoschistus pictus: courtship ($N=11$ males, 16–26 sounds per male, total no. of sounds=273) and agonistic ($N=6$ males, 11–101 sounds per male, total no. of sounds=238); *Pomatoschistus marmoratus*: courtship ($N=3$ males, 3–12 sounds per male, total no. of sounds=23).

Mean and ranges (10th–90th percentiles) are depicted and were quantified for individual sounds, i.e. for the total number of sounds.

^aMeasured for 15 sounds from only two males measuring 3.7 cm and 4.0 cm standard length (SL).

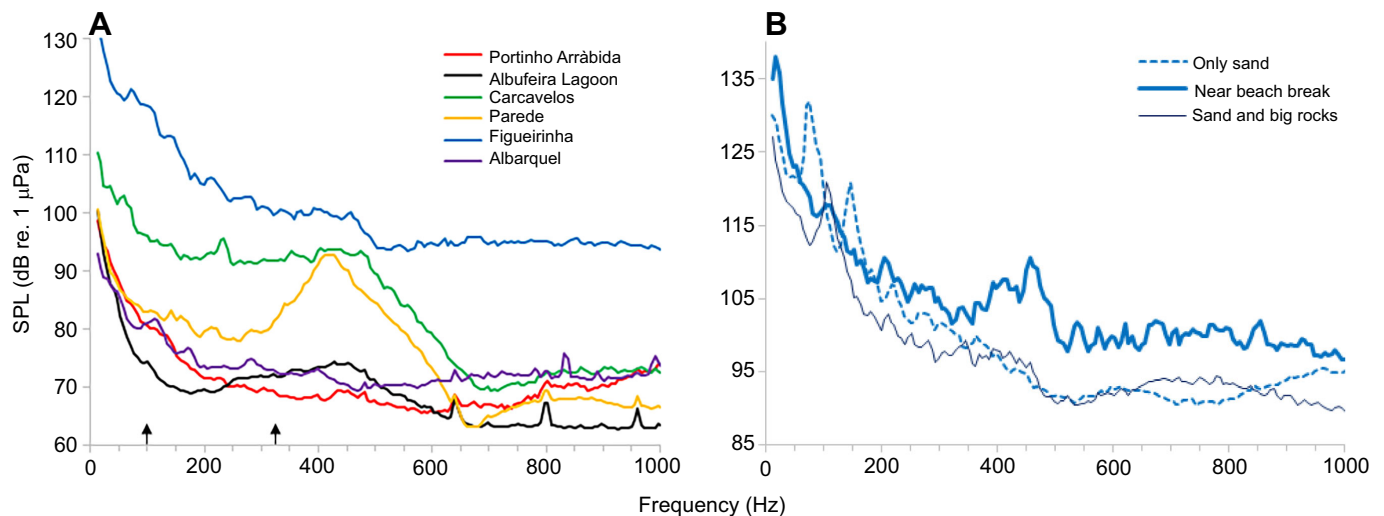


Fig. 3. Ambient noise (AN) in the recording locations. (A) Average sound power spectra of AN from the different studied locations (1–3 sites within each location). (B) Sound spectra from three different recording sites at Figueirinha beach. Note the peak at around 450 Hz in the recording near the beach break, delimiting an area with sand substrate. Arrows depict the lower and upper values of an AN quiet window.

Parede, the recordings from Carcavelos (Fig. 5F) presented a constant elevated energy in frequencies below 600 Hz (also observable in Fig. 4), probably due to the permanent water movement against the boulders from the beach break that also likely caused small pebbles and sand to shuffle back and forth constantly. However, this is likely a peculiarity of the exact location of the hydrophone deployment and not really a characteristic of Carcavelos beach, which is a wide sandy beach.

The peak frequency range of courtship sounds of both goby species, depicted by the grey rectangle, was above the AN spectra in most locations, especially when considering quiet moments (Fig. 4B), and fell within the low-frequency quiet region of Parede and Carcavelos beaches during loud events (Fig. 4A).

Hearing sensitivity and response to conspecific sounds

Mean auditory thresholds obtained with AEPs under quiet laboratory conditions indicated higher sensitivity from 100 to 300 Hz in both

goby species and a gradual sensitivity decrease towards 1000 Hz (Fig. 6). The hearing thresholds increased from (means \pm s.d.): 94 ± 4.4 dB re. 1 μ Pa (-58 ± 3.9 dB re. 1 m s^{-2}) at 200 Hz (best hearing frequency) up to 126 ± 2.1 dB re. 1 μ Pa (-28 ± 1.9 dB re. 1 m s^{-2}) at 1000 Hz in the painted goby, and from 94 ± 2.5 dB re. 1 μ Pa (-58 ± 2.3 dB re. 1 m s^{-2}) at 200 Hz (best hearing frequency) up to 124 ± 3.3 dB re. 1 μ Pa (-31 ± 3.0 dB re. 1 m s^{-2}) at 1000 Hz in the marbled goby.

Moreover, auditory responses of painted goby males to courtship and agonistic drums showed a representation of sound pulses and overall call duration (Fig. 7A; only responses to courtship sounds are depicted as courtship and agonistic drums are very similar but with a different number of pulses; Bolgan et al., 2013). The frequency content of the sound was represented through a double frequency response component observed in the AEPs (Fig. 7B). This indicates that the species is not only able to detect the pulsed structure of the conspecific signal but is also sensitive to its call peak frequency.

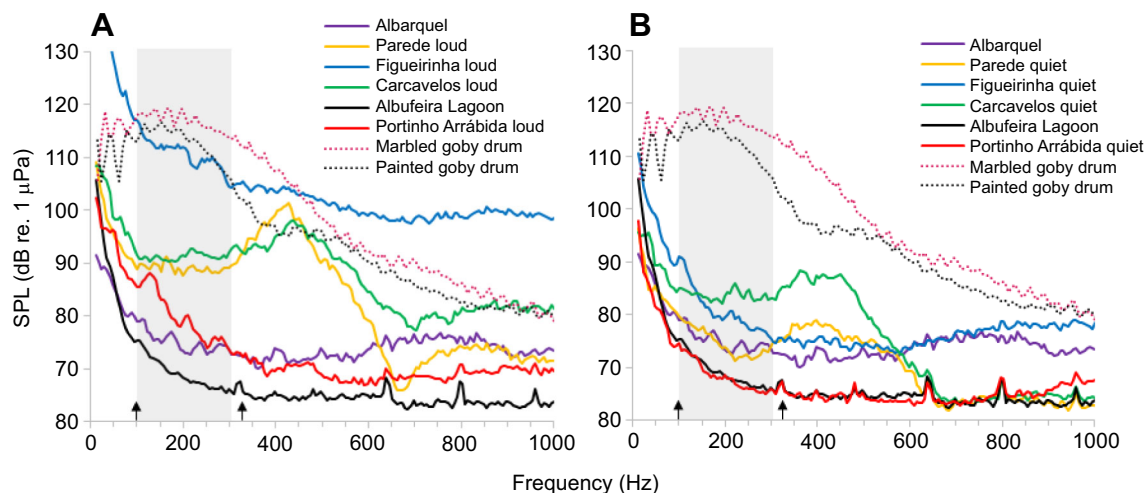


Fig. 4. AN during quiet and loud moments. Power spectra of (A) elevated ($N=5$ per location) and (B) low ($N=5$ per location) AN of 2 s samples from the studied sites and sound spectra from courtship drums of the painted and the marbled gobies. Note that for Albufeira Lagoon and Albarquel beach, the 2 s samples are the same in both panels as there were no loud events (see Material and Methods). The grey rectangles represent the peak frequency range of drums made by both species as shown in Table 2. Arrows depict the lower and upper values of an AN quiet window.

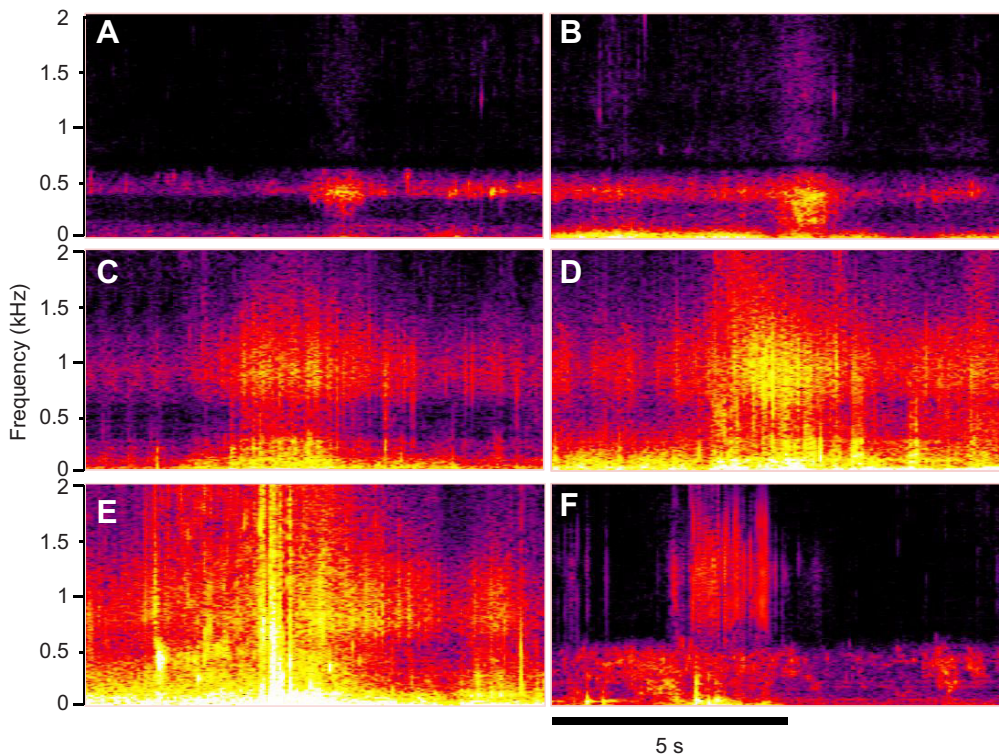


Fig. 5. Sonograms of typical elevated AN events. (A,B) Parede beach and (C–E) Figueirinha beach, showing water movement and waves of increasing intensity. (F) Water movement, noise from moving sand/pebbles and waves at Carcavelos. Note that, as wave action increases, the silence frequency window is lost during wave breaking (A–E).

DISCUSSION

Here, we tested the hypothesis that acoustic signals and hearing abilities in two small goby species are well adapted to maximise acoustic communication in different habitats. These included exposed Atlantic coastal areas, characterised by moderate to high

hydrodynamism and elevated noise in the low-frequency domain. We have shown that the main frequencies of the sounds made by painted and marbled gobies in a social context match their best hearing abilities. Importantly, both acoustic signals and hearing abilities appear well adapted to Atlantic habitats as the sound peak frequency range and best hearing matched quieter frequencies of the background noise, including during elevated noise events (e.g. breaking waves) in all but one location. Consistent with other studies, we have found a quiet window in the AN in some of the studied habitats (Crawford et al., 1997; Lugli and Fine, 2003; Wysocki et al., 2007; Lugli, 2010; Speares et al., 2011).

Acoustic signals

The painted and the marbled gobies made low-frequency pulsed courtship sounds with main energies (peak frequency range) between 150 and 300 Hz, and SPLs of about 130 dB re. 1 μ Pa at ca. 1 cm. The mating sound spectrum of these species is comparable to those of other goby species, which also present dominant frequencies below 300 Hz; exceptions are *Zoosterisessor ophiocephalus* and *Gobiosoma boscii* (reviewed in Lugli, 2015). Interestingly, most other vocal teleosts also inhabit or breed in shallow water and similarly make low-frequency acoustic signals (Amorim, 2006; Ladich, 2013; Lugli, 2015), although there is a great lack of knowledge regarding pelagic (Ladich and Winkler, 2017) and deep-water (Fine et al., 2018) species.

The amplitude of the mating sounds made by our study species (130 dB at ca. 1 cm) is similar to that of the sand goby, *Pomatoschistus minutus* (SPL range of 121–138 dB at <3 cm in ten fish ranging in SL from 45 to 54 mm; Lindström and Lugli, 2000), and likely louder than tonal sounds made by *Padogobius bonelli* (91–101 dB at 5 cm measured in three males ranging in SL from 58 to 79 mm; Lugli and Fine, 2003). Owing to scale effects, gobies typically make quiet sounds when compared to other larger fish. As an example, the mating sound level of the oyster toadfish, *Opsanus tau* (Batrachoididae), is ca. 125 dB at 1 m (Barimo and Fine, 1998),

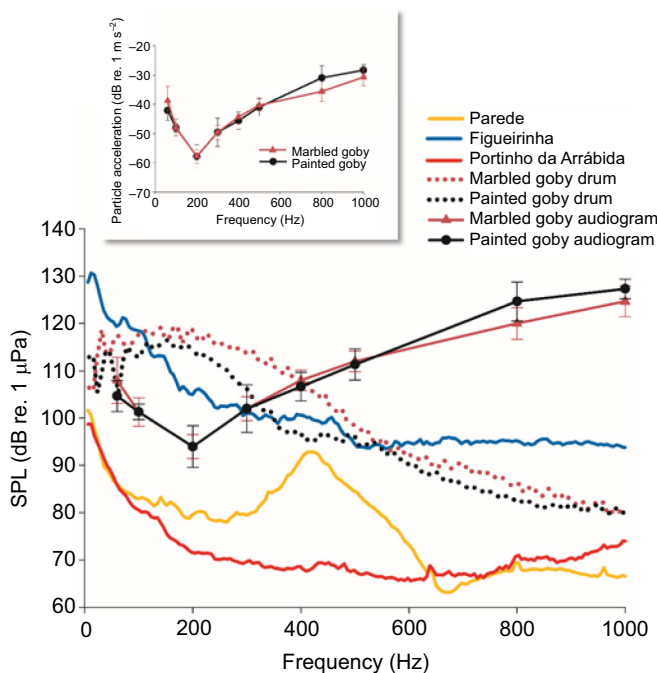


Fig. 6. Mean (\pm s.e.m.) hearing thresholds of the painted and the marble gobies. Six adult males from each species were tested. The average sound power spectra from courtship drums made by the two species as well as of typical habitats (Portinho da Arrábida, Figueirinha and Parede beaches) where specimens were collected are also depicted. Inset depicts hearing thresholds in particle acceleration units.

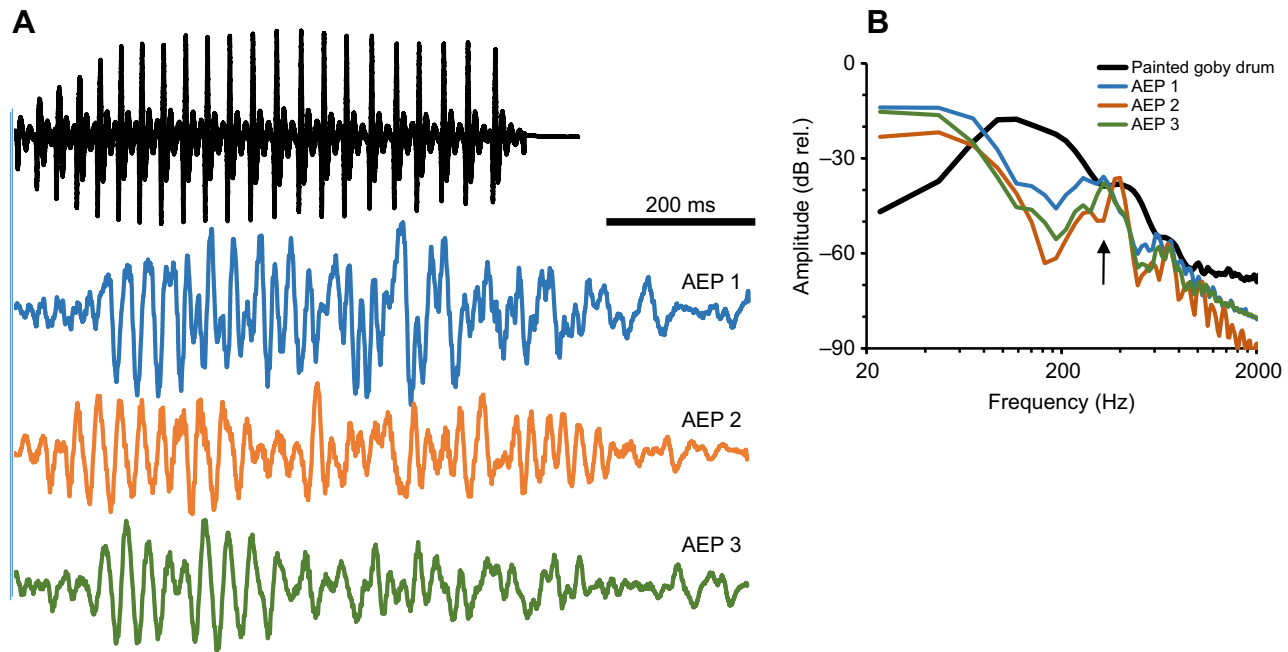


Fig. 7. Hearing response to conspecific sounds. (A) Oscillogram of the courtship sound stimulus (upper black trace) and corresponding auditory evoked potential (AEP) response recorded from three painted goby males (lower traces). (B) Power spectra of the sound stimulus (black trace; main frequency; 3 dB bandwidth around peak: 94–164 Hz) and of AEP responses (colour traces) to conspecific courtship drums in the same three males. The arrow depicts the double frequency response in the AEP. Sampling frequency 16 kHz, 2048 points FFT, 50% overlap, Hanning window.

and the estimated mating sound level for mullet *Argyrosomus japonicus* (Sciaenidae) is ca. 160 dB at 1 m (Parsons et al., 2012). Because of their low amplitude, goby sounds will attenuate to the background level even at shorter distances than for most other fishes (reviewed in Amorim et al., 2015), considering the same propagation conditions. Acoustic communication active space is additionally reduced by the water depth in which gobies breed (Lugli, 2015). In very shallow waters, fish sounds (depending on the main frequency) often show a steeper transmission loss than predicted theoretically with either the cylindrical (3 dB per doubled distance) or the spherical (6 dB per doubled distance) transmission loss models (e.g. Lugli and Fine, 2003; Alves et al., 2016). For example, the sounds from *P. bonelli* attenuate around 15–20 dB from 5 to 20 cm and are likely not detected further than 20–30 cm from the fish (Lugli and Fine, 2003). This probably explains why male gobies, including the studied species, only make sounds when females are in close proximity or inside the nest (Amorim et al., 2013). What is the acoustic communication distance under prevalent AN conditions in our study species? A loss from spherical spreading would predict that goby sound level would be 96 dB at 16 cm (four doubling distances). Assuming that the smallest detectable amplitude change may be quite low in fish (for example, the cod *Gadus morhua* is able to discriminate changes in sound amplitude of 3.7–6.7 dB in the frequency range of 110–250 Hz; Chapman and Johnstone, 1974), a drum of 96 dB at 16 cm could still be detectable even during loud events at Parede, as the average AN level at 200 Hz at the referred location was 90 dB during noisy events (Fig. 4A). In a more realistic transmission loss scenario for the extreme near field (steeper than theoretical models), it is possible that acoustic communication during loud events is restricted to shorter distances but would likely be possible when the female is very close to the male's nest or inside it. Notably, sound amplification in the low frequencies by goby natural nests (shells with sand piled on top of it) could help maximise communication active space in these shallow water environments (Lugli, 2015).

Ambient noise

Because AN can mask or impair the ability to detect and extract accurate information from an acoustic communication signal (Erbe et al., 2016), we asked whether AN levels in the Atlantic natural goby habitats, characterised by particularly challenging high levels of hydrodynamism, allow acoustic communication in these species.

The studied locations presented variable AN levels. Under reasonably calm weather conditions, Albufeira Lagoon, and Portinho da Arrábida and Albarquel beaches, were the quietest of the studied habitats (Table 1). The habitats with higher exposure to the Atlantic wave action, Parede and Carcavelos, presented intermediate noise levels, while, surprisingly, Figueirinha, a beach with reasonably low exposure, presented the loudest AN levels at all relevant frequencies for goby species (<1 kHz). The main sources of noise in the habitats with intermediate and high AN levels were likely bubble noise produced by travelling and breaking waves, and water and sediment movement associated with wave action (Lugli, 2010), as well as the turbulent water movement against big boulders and beach breaks. The latter probably caused the spectral peak around 450 Hz observed for Parede, Carcavelos and Figueirinha (Fig. 3B, recording made near the beach break; Fig. 4A). Consistently, Wysocki et al. (2007) and Speares et al. (2011) detected that increasing flow regimes in freshwater habitats elevated noise levels at low frequencies but left a quiet window at frequencies from about 150 to 400/450 Hz, i.e. they observed a similar noise level increase at around 450 Hz. Lugli (2010) found that the noise burst from a distant breaking wave in a brackish lagoon also showed an elevation of noise levels around 450 Hz. The AN levels in Figueirinha were surprisingly high considering that it is fairly protected from prevailing winds and ocean action. However, this beach is exposed to incoming currents from the Sado estuary, which likely caused an increase in AN levels. In addition, the recordings in Figueirinha were made at high tide, which must have increased AN

levels. Coers et al. (2008) showed that, in a rock-pool environment of the Atlantic island of Faial (Azores), the AN increases up to 40 dB during high tide and up to 16 dB in the range of 50–300 Hz.

It is clear that aquatic soundscapes vary considerably not only between but also within habitats. Also, within the same microhabitat, noise can fluctuate considerably with time: seasonally (Amoser and Ladich, 2010) and with lunar or tidal rhythms (Coers et al., 2008; Radford et al., 2015), but also in a very short time frame, as highlighted by our 2 s samples taken from 3 min recordings (Figs 4 and 5). In general, our 2 s elevated noise spectra were very similar to the average power spectra, indicating that average spectra are dominated by loud events in most locations (as observed by Lugli, 2010), which is expected because power spectra are represented in a log-scale. This highlights the need to characterise both short-term quiet and loud noise events when studying the adaptation to a particular habitat, as the quiet events may be predominant but still not depicted in the overall AN spectrum. In addition, although snapshots can be quite informative, to acquire a more complete picture of the temporal variability of these Atlantic soundscapes, continuous recordings over long periods of time should be made.

Noise levels in the studied Atlantic habitats (generally >110 dB re. 1 μ Pa) were higher than in freshwater habitats (mostly <100 dB; e.g. Wysocki et al., 2007), but, even in areas of freshwater habitats with fast water movement, such as in rapids and riffles, noise levels significantly increase by as much as 40–60 dB in the lower frequency range (e.g. Lugli and Fine, 2003; Wysocki et al., 2007; Speares et al., 2011). Lugli (2010) studied the AN of typical goby habitats in the Mediterranean Sea and brackish lagoons. As in our study, the soundscape in Mediterranean beaches presented higher AN levels than in the brackish lagoon. Interestingly, this author observed a quiet window in sandy and rocky Mediterranean beaches in the low frequencies (below 250–300 Hz) with a low-noise peak around 100 Hz, coincident with the peak frequency of sounds made by local gobies. Comparing these results with our data, we also observed a quiet window in the exposed Atlantic beaches (Parede and Carcavelos), with quieter frequencies centred around 200 Hz, also coincident with the main frequencies of the painted and the marbled goby mating sounds. Apart from tide, one major difference between Mediterranean and Atlantic beaches is likely wave size and period. However, we observed that, even during wave breaking, there was a quiet window, which only disappeared when waves became larger (Fig. 5), suggesting that gobies are well adapted to the prevailing ambient conditions of both the Mediterranean and the Atlantic. Considering that auditory thresholds will shift up when fish are exposed to AN (compared with quiet lab conditions), it is possible that hearing is masked by short noisy events, which may include not only large but also medium waves.

Hearing abilities

The AEP technique showed that both goby species had very similar auditory abilities, with best hearing sensitivity from 100 to 300 Hz both in terms of sound pressure and particle motion, thus matching the peak frequency of conspecific sounds and the quiet AN window found in the exposed Atlantic beaches. Note that, although behavioural audiograms are considered the most valid method to establish a species's hearing ability, AEP hearing thresholds provide useful information when comparing hearing curves between species (Ladich and Fay, 2013). Hearing sensitivity in the studied species is comparable to that of other fish species living in near-shore marine habitats, including other gobies (see figure 5 in Lugli, 2010). For example, *Gobius cruentatus* and *Gobius melanostomus* have best hearing sensitivities at frequencies below 300 Hz, also matching the

main conspecific sound frequencies (Rollo and Higgs, 2008; Codarin et al., 2009; Zeyl et al., 2013). Nevertheless, regardless of being vocal or mute, fish inhabiting noisy environments typically lack hearing specialisations, have low hearing sensitivities and are thus less affected by noise, suggesting that hearing sensitivities may have been shaped mainly by AN regimes (Ladich, 2013).

Besides assessing a species' ability to detect pure tones, it is useful to investigate auditory sensitivity to conspecific sounds because stimulation of the auditory system is probably different with complex natural stimuli (Vasconcelos et al., 2007, 2011b; Maruska and Tricas, 2009; Belanger et al., 2010; Zeyl et al., 2013). Here, we showed that the auditory system of the painted goby is able to resolve the temporal structure of conspecific mating and agonistic drums. Encoding drum temporal structure is key in goby communication as it provides information on the sender's motivation (aggressive versus courtship), quality and species identity (Amorim and Neves, 2008; Amorim et al., 2013; Pedroso et al., 2013). This result is supported by similar work carried out in other hearing generalists, fish that lack accessory hearing structures that allow pressure detection. For example, Vasconcelos and colleagues showed that the Lusitanian toadfish, *Halobatrachus didactylus*, is able to perform fine temporal resolution of complex conspecific sounds (Vasconcelos et al., 2011b).

In addition, to investigate whether comfortable communication is possible (sensu Dooling et al., 2015), it is also important to consider whether, besides signal detection, the signal information content is perceived (Alves et al., 2016). To allow comfortable communication and therefore a good representation of the sound structure in the auditory system, the received sound levels should be well above the species' hearing thresholds. Because AEP hearing thresholds are typically higher than behavioural hearing thresholds (Ladich and Fay, 2013; Maruska and Sisneros, 2016), it is reasonable to assume that, in the case of our study species, this is likely possible when the receiver is within <3 body lengths from the emitter during quiet moments (see spreading loss calculations above).

Concluding remarks

Here, we investigated whether the acoustic communication system from two small marine gobies from Atlantic populations are adapted to prevailing environmental conditions. We have found that hearing abilities are tuned to main frequencies of acoustic signals and both species seem well adapted to detect acoustic information under local AN. These findings are consistent with the acoustic adaptive hypothesis, within the sensory drive framework, which predicts that communication systems adapt to environmental characteristics (Endler, 1992; Boughman, 2002).

Research that simultaneously correlates acoustic signalling and hearing abilities with AN is generally lacking, especially in fish (but see Lugli et al., 2003). However, a few studies lend support to the acoustic adaptation hypothesis and have shown that gobies as well as other shallow-water vocal teleosts, including batrachoidids, cottids, cyprinids, percids and mormyrids, seem to take advantage of a quiet window in the background noise to communicate, both in freshwater and marine environments (Crawford et al., 1997; Speares et al., 2011; Lugli, 2015; but see Coers et al., 2008). These works provide strong evidence that habitat noise may exert important selective pressure acting on the low frequencies used in acoustic communication in shallow-water fish species. Additionally, environmental characteristics (such as water depth) may have exerted additional pressures to signalling behaviour as sounds are typically emitted in close proximity of the receiver.

Other studies have highlighted that, in marine habitats, fish auditory abilities are often tuned to the main frequency of acoustic

signals as shown in gobies and other fishes (reviewed in Ladich, 2013; Lugli, 2015; Maruska and Sisneros, 2016). Moreover, in noisy environments with variable masking conditions, such as in shallow marine waters and in some freshwater microhabitats, fish hearing thresholds are typically above the prevailing AN levels, probably to avoid or minimise masking of acoustic signal recognition (Lugli, 2015). It thus seems that, in such habitats, there is support that acoustic environmental pressures have shaped the acoustic communication systems of fishes.

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Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: M.C.P.A., P.J.F.; Methodology: All authors; Validation: M.C.P.A., R.O.V., P.J.F.; Formal analysis: M.C.P.A., P.J.F., M.B., S.S.P.; Investigation: All authors; Writing - original draft: M.C.P.A., R.O.V.; Writing - review & editing: M.C.P.A., R.O.V., M.B., P.J.F.; Supervision: M.C.P.A., P.J.F.

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