Environ Biol Fish (2026) 109:115
https://doi.org/10.1007/s10641-026-01883-z

Sound amplification by the sand goby nests in the field and comparison with laboratory results

Marco Lugli

Received: 17 April 2025 / Accepted: 12 July 2026
© The Author(s) 2026

Abstract Male sand gobies call and spawn inside cavities beneath stones, shells, and other submerged objects (including artificial shelters) which they cover by piling sand on them. The male emits low-frequency courtship sounds only during the mating interactions taking place in the nest hollow. These vocalizations are crucial for female spawning decisions. A previous laboratory study showed shelters used as a nest amplify the sound pressure in the frequency range of 50–150 Hz. Another laboratory study showed the sand pile further increases the low-frequency amplitude gain of the hollow by up to 12 dB. In the present study, the role of nest hollow and the sand pile in sound amplification were examined using two types of bivalve shells in the field. Results were similar to those obtained in laboratory for the shelters with and without the nest pile, both in terms of frequencies enhanced and amplitude gain. The relationship between shell weight and sound amplification was examined by pooling field and laboratory data. Results showed the amplitude gain increased with the weight of the shell, whereas peak frequency was not affected. These results provide further support to the conclusions from early laboratory studies that (1) the amplification properties of the nest hollow may contribute to explain the evolution of the low-frequency acoustic communication among sand gobies and that (2) sand digging and piling is an activity of environmental manipulation performed by the male sand goby to increase sound amplitude and efficiency of the acoustic signaling in the nest.

Keywords Acoustic communication · Gobiidae · Sand pile · Nest cavity · Shell weight · Environmental manipulation

Introduction

Many shallow water teleosts (e.g., blennies, gobies, toadfishes, and darters) use submerged objects, crevices, or burrows as calling and spawning sites (i.e., benthic cavity-spawning species; reviewed in Myrberg and Lugli 2006; Zeyl et al. 2016). Sounds are usually emitted by the male from the nest (e.g., a hollow below a stone) toward an approaching female and/or when the female is inside the hollow (Lugli et al. 1995). Vocalizations emitted by these species are, with few exceptions, low-frequency pulsatile/tonal or knocking sounds with dominant frequencies below 300 Hz (e.g.,Lugli et al. 1997; Malavasi et al. 2008; Zeyl et al. 2016). Low frequencies do not propagate well in the shallow waters due to the frequency cutoff phenomenon, i.e., the acoustic energy decays exponentially with distance when the water depth is less than about one-fourth the wavelength of the sound (Rogers and Cox 1988; see also

M. Lugli (✉)
Department of Chemistry, Life Sciences and Environmental Sustainability, University of Parma, Parma, Italy
e-mail: Marco.lugli@unipr.it

Published online: 25 July 2026

the Discussion). Consequently, acoustic communication among these species often only occurs over short distances.

In a previous laboratory study (Lugli 2012), I showed that natural (flat stones, bivalve shells) and artificial (e.g., clay flowerpots) shelters used by gobies as nest sites may "amplify" the acoustic pressure of a sound source placed inside the nest hollow. Significant amplitude gains (i.e., how much the hollow increases the amplitude of the probe/imput signal), up to 20–25 dB, always occurred only at frequencies below 300 Hz, the typical acoustic communication range of these fishes. Analogous tests conducted in the field (a stony stream) on submerged flat stones (the type of shelters used by the freshwater goby, *Padogobius bonelli* (Bonaparte, 1846; formerly *P. martensii*), as nest sites) confirmed the results obtained in the laboratory (Lugli 2012). These findings suggest that sound amplification properties of the nest cavity might have promoted low-frequency communication among these species (Lugli 2015). The reason why sound amplification occurs only at lower frequencies is unclear.

Sand gobies of the genus *Pomatoschistus* and *Knipowitschia* are small-sized coastal marine or brackish water fishes whose males build nests by excavating sand below and around small submerged objects (empty bivalve shells, pebbles, or other suitable covers). Males also cover the shelter by digging sand and piling it on top of it. Furthermore, the male sand goby emits low-amplitude sounds during the mating activities taking place inside the nest cavity (Lugli and Torricelli 1999; Lindström and Lugli 2000). Typically, these sounds are trains of sound pulses with dominant frequencies of 60–250 Hz (Lugli et al. 1997; Malavasi et al. 2008), i.e., the frequencies amplified by the nest (Lugli 2012). In the sand goby *P. minutus* (Pallas, 1770), sound amplitude is a predictor of male size and quality (Lindström and Lugli 2000; Amorim et al. 2013). Furthermore, a louder sound, resulting in a higher signal-to-noise ratio, may provide more reliable information to the receiver in the presence of adverse noise conditions (Brumm and Slabbekoorn 2005). Therefore, exploiting the amplification properties of the nest cavity could provide benefits to the male in the context of sexual selection operating in the presence of the noisy conditions typical of marine/brackish shallow water habitats (Lugli 2010). Among gobies, the role of male vocalizations in the context of mate choice has received some attention in the last few years (e.g., Pedroso et al. 2013). Unfortunately, the role of sound amplitude in female mate choice and mate attraction has not yet been examined with playback experiments.

Unlike sound, the role of the sand pile in the context of both sexual and natural selection has been the focus of many studies in the past (reviewed in Svensson and Kvarnemo 2023), sometimes with contradictory results (Jones and Reynolds 1999, Lehtonen and Wong 2009). However, until recently, no study had examined the presence of a possible relationship between the male vocalizations and the sand-piling activity.

Following the same experimental procedure used to examine the acoustical response of the shelter cavity, I (Lugli 2013) conducted laboratory tests to examine a possible effect of the sand pile on sound amplification by the sand goby nests. Results showed the sand pile (artificially created by piling sand on top of the shelter and leaving a single opening to simulate the nest preparation behavior of the male) may further amplify (up to 8–10 dB) the sound frequencies amplified by the cavity, including the dominant frequencies of the sound emitted by the male sand goby, *P. minutus* (Lugli 2013). Notably, the sand pile enhanced these frequencies also in shelters without amplification properties (e.g., light plastic tiles, *Mytilus* shells, Lugli 2013). Finally, sound amplification was higher in nests constructed using larger amounts of sand. These findings explain well the results of mate choice experiments in the sand goby *P. minutus* and in the common goby *P. microps* (Krøyer, 1838), which showed that reproductive females of these species spawn significantly more often in the nests covered by larger amounts of sand (Lehtonen and Lindström 2009; Svensson and Kvarnemo 2005). Thus, the sand digging activity might be considered an activity of environmental manipulation performed by the sand goby male to enhance the amplitude of sounds emitted in the nest hollow. This conclusion is based on the results of laboratory tests conducted within small laboratory tanks, however. It is well known that the small-sized aquaria are closed environments where the sound waveform may be easily distorted, and sound propagation constrained, by a variety of factors (see the "Discussion" section). Therefore, assessing the acoustic response of the nest cavity and the effect of the sand pile at spawning locations of sand gobies in the field is necessary to validate conclusions based on the results obtained in the laboratory.

The aim of the present field study is to investigate the acoustic properties of the hollow below different types of bivalve shells, alone or covered with an artificially created sand pile, at a location known to be used by sand gobies (*Pomatoschistus* spp., *K. panizzae* (Verga 1841)) as a spawning site. As done in early studies by the same author, shells are acoustically stimulated using a small custom-built waterproof buzzer placed inside the shell cavity (a sound source mimicking a sand goby male calling inside the nest) and pure tones as input stimuli to drive the acoustical response of the system. The separate contribution of the shell with or without the sand pile to the sound amplification by the shell hollow is determined, and results are compared with those from previous laboratory studies. Given that the amplification properties of the nest hollow are similar for both the laboratory-tested stones and those in the stream (Lugli 2012), it is expected that this finding will hold true for shells as well. This result would strengthen the conclusion from early laboratory tests that sand digging and piling are activities of environmental manipulation performed by the male sand goby to increase sound amplitude and efficiency of the acoustic signaling in the nest.

Materials and methods

This study was carried out in a brackish water lagoon in Northern Italy (the "Sacca del Canarin," Po river delta (N: 44° 55′ 47″, E: 12° 29′ 27″), where nesting sand gobies (genera *Pomatoschistus*, *Knipowitschia*) are locally abundant. Acoustical tests were conducted in April (water temperature, 12–15 °C; salinity, ~ 25 ‰) in a location with a sandy-muddy bottom and the same water depth (15–20 cm) of laboratory tests (Lugli 2013). At such depths, no frequency below 2 kHz propagates, i.e., the energy decays exponentially with losses of about 20 dB/20 cm (Rogers and Cox 1988; Akamatsu et al. 2002; Lugli and Fine 2007).

Acoustical stimulation tests were carried out on seven bivalve shells ($n = 4$, *Crassostrea gigas* (Thunberg, 1793), the Japanese oyster; $n = 3$, *Scapharca inaequivalvis* (Bruguiére, 1789), the Ark clam)), collected in situ and known to be used as nest sites by Mediterranean sand gobies of the genus *Pomatoschistus,* Lugli and Torricelli 1999), within a 0.25 m^2 area of the bottom under non-windy conditions.

Before testing, the shell was placed on the substrate at a slightly oblique angle, above a small pit created by manually removing sand. This arrangement allowed an opening connecting the pit to the outside, thereby mimicking the hollow used as a nest cavity by the male sand goby.

All shells were acoustically stimulated with pure tones following the procedure described in Lugli (2012) for the field tests on flat stones. Briefly, a sequence of 14 pure tones (the probe signal) in 1/3 octave steps in the range of 50–1000 Hz (i.e., 50, 65, 80, 100, 125, 165, 200, 250, 315, 400, 500, 630, 800, 1000 Hz) was generated with a portable analog signal generator (MINIRATOR MR1; NEUTRIK AG, Shaan, Liechtenstein) connected to an output transformer in turn connected to a small underwater buzzer (Lugli 2013) acting as sound source (note: the use of white-noise probe signals for acoustical stimulation tests was not possible in the field due to the low voltage output of the signal generator, Lugli 2012). The buzzer was positioned on the substrate in the center of the pit. Then, the shell to be tested was placed above the pit as described above.

Tones were recorded with a small hydrophone (GLG 9190, Edmund Scientific Co., Barrington, NJ) positioned at 2–3 cm in front of the shell opening and connected to a DAT recorder (TASCAM DR-2D, TEAC Corp.). The level of sound stimulation was set to produce peak levels of tones (> 100 dB sound pressure level re:1 µPa) comparable to the sand goby sound levels measured at 1–2 cm from the male in laboratory (120–140 dB, Lugli and Torricelli 1999).

The acoustical test (Lugli 2012, 2013) consisted of recording the probe signal from the buzzer in the pit twice: without the shell and with the shell above the pit, the recording sequence being randomly assigned. Two oyster shells were also tested for the effect of the sand pile. The sand pile was created in the pause after the record with the shell by manually pouring sand on top of the shell until it was fully covered except for the opening (care was taken not to obstruct the opening or allow the sand to enter the cavity) (Lugli 2013). Then, the probe signal was recorded as usual.

All records were digitally analyzed (sampling rate, 44,100 Hz) using the real-time spectrogram function of AvisoftSASLab ProTM (R. Specht, Berlin, Germany) and stored as WAV files for later analysis. Fast Fourier transform (FFT) of the whole probe signal was computed (FFT length, 1024 Hz; frame size,

100%, Hamming window), and the amplitude of test tones was measured.

The frequency response (=gain function) of the shell alone and that due to the sand pile was estimated by computing the pressure amplitude difference (AD, dB) of each tone between the recording with and without the shell, and between the recordings with and without the sand pile above the shell, respectively (Lugli 2013). Assuming the frequency response of the buzzer does not change between subsequent recording sessions of each acoustical test, the AD values can be used to assess the independent contribution of the shell and the sand pile to the acoustical response of the hollow to sound stimulation. Thus, a positive value of AD for a given tone indicates an amplitude gain by the shell, or the sand pile, at that particular frequency, whereas a negative value indicates an amplitude loss (see Lugli 2013 for examples of calculation of AD values). The amplitude (G_{peak}) and frequency (F_{peak}) of the highest positive AD value (always under 150 Hz in the frequency response of the shelter alone; Lugli 2013) were measured for comparisons with laboratory values. A preliminary inspection of the results showed that all the significant deviations from 0 dB gain (either as amplitude gains or losses) occurred only at tones below 500 Hz, thus confirming conclusions from Lugli (2012, 2013). Consequently, all the frequency responses are shown for tones in the range of 50–500 Hz.

The mean frequency response of the shell hollow was assessed by averaging the AD values of all the tested shells. The 95% confidence interval for the mean AD of each tone was determined using the corresponding standard error of the *t*-distribution (Sokal and Rohlf 1981).

Comparisons with laboratory data

The amplification properties of the shells tested in the field were compared to those determined in the laboratory (Lugli 2012) for five *Crassostrea* shells and five *Scapharca* shells. In the laboratory (Lugli 2012), the frequency response of the shelter (stones, bivalve shells, and artificial shelters) was determined following the same experimental protocol used in the field, except that the main probe signal was white noise band-passed from 0.1 to 2 kHz. Consequently, the frequency response of laboratory shells was obtained by plotting the AD values for each 8 Hz wide band in the range of 0.1–2 kHz (Lugli 2012). However, the frequency response of a subsample of shelters (stones and shells) was also determined using pure tones as probe stimuli and compared to that obtained using filtered white noise. Results showed the gain function of these shelters was similar in both cases; the dB differences between the two probe stimuli for corresponding frequencies (i.e., the tone frequency and the frequency band of the white noise spectrum including the tone) rested in the ±2 dB range (Lugli 2012). This finding allows to compare the low-frequency response of fish shelters determined using different types of probes both in laboratory and in the field. This was accomplished by recalculating the frequency response of each of the ten shells measured in the laboratory from the original recordings using the frequency band with maximum gain in the range of 0.05–0.5 kHz. The values of G_{peak} and F_{peak} were then measured and compared with those of the shells measured in the field. Of course, the value of F_{peak} of a shell measured in the laboratory might not match exactly the F_{peak} of a shell measured in the field.

The differences between mean G_{peak} and F_{peak} values measured in the laboratory and in the field were examined using the Student *t*-test. The relationship between G_{peak}, F_{peak}, and shell weight (all shells were weighed in laboratory using a precision analytical balance measuring the shell's mass in grams) was examined using the Pearson product-moment correlation test (Siegel and Castellan 1988). All statistical significances were two-tailed. Further details on statistical analysis of data are reported in the "Results" section.

As to the effect of the sand pile, the frequency responses of the two oyster shells tested in the field were compared with those of two oyster shells tested in another laboratory study (Lugli 2013). The effects of the sand pile in field and laboratory shells (*Crassostrea*) were only compared qualitatively.

Results

Frequency response of the shell hollow

The two types of bivalve shell differed markedly in shape, size (Fig. 1), and weight range (clam shell, 26.2–36.1 g; oyster shell, 33.8–50 g). Despite these differences, all shells showed a similar response to sound stimulation: the amplitude gain (AD > 0) of the cavity increased at frequencies below 200 Hz (Fig. 2;

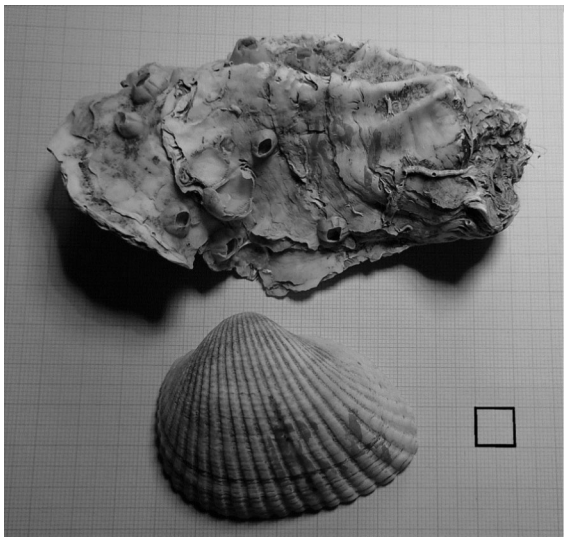


Fig. 1 The two types of bivalve shell used for the experiments (top: *Crassostrea gigas*; bottom: *Scapharca inaequivalvis*) laid on a sheet of regular graph paper (the area of the unit square marked on the grid is 1 cm^2)

see also Fig. 4 for more examples) and peaked in the range 60–100 Hz. These features also characterized the average response obtained by pooling the data obtained from the seven tested shells: gain values were maximal (around 7 dB) at frequencies in the 60–100 Hz range (the only ones significantly different from 0 dB, Fig. 3, shadowed area) and fluctuated randomly around 0 dB above 200 Hz.

Differences in the frequency response between the two types of shell were also observed, however. In the examples shown in Fig. 2, the frequency response of the heavier oyster shell (*Crassostrea*) is characterized by larger amplitude gains (in the range of 50–200 Hz) and a lower F_{peak} compared to the lighter clam shell (*Scapharca*). To test this effect, G_{peak} and F_{peak} were both correlated to shell weight, irrespective of shell type. Results showed that G_{peak} increased significantly with shell weight ($r=0.957$, $p<0.001$; $n=7$), whereas F_{peak} was not affected ($r=-0.01$, ns, $n=7$) (see also Fig. 5).

Effect of the sand pile

In the two oyster shells examined, the presence of the sand pile further enhanced the amplitude gain by the hollow at frequencies in the range 60–125 Hz (Fig. 4, black lines). For both shells with the sand pile above, the gain peaked below 100 Hz (Fig. 4, light-gray lines); for one of them (Fig. 4B), the presence of the sand pile determined a second major gain peak at around 250 Hz followed by an amplitude loss peaking just above 300 Hz. The presence of two gain peaks at lower frequencies was also observed in the frequency response of shells with the sand pile tested in laboratory (Lugli, unpublished data).

Comparison with laboratory experiments

The mean F_{peak} of field (79.3 Hz ± 15.7 standard deviations) and laboratory (98.3 Hz ± 20.7) shells was not statistically different (Student $t=2.04$, df = 15, not statistically significant (NS)). Conversely, the mean G_{peak} was significantly higher in the field shells (field

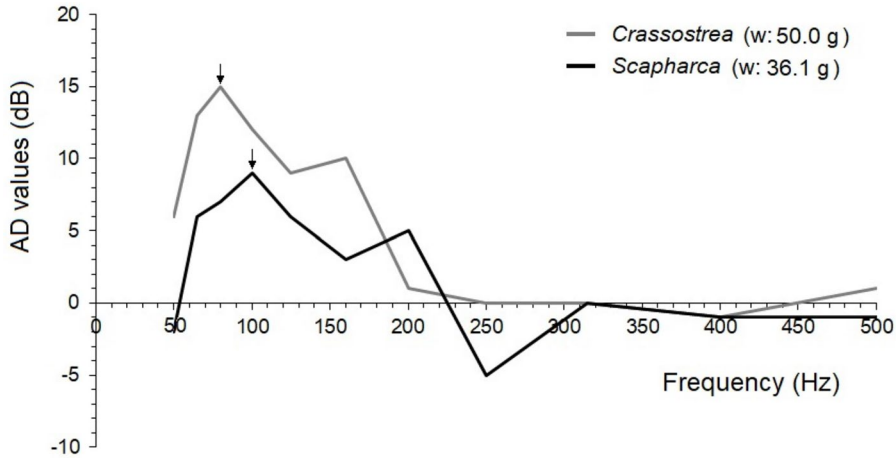


Fig. 2 Frequency response (AD values, dB) of the cavity below one oyster shell (*Crassostrea*) and one clam shell (*Scapharca*), taken as an example. Arrows mark the frequency value (F_{peak}) of maximum gain

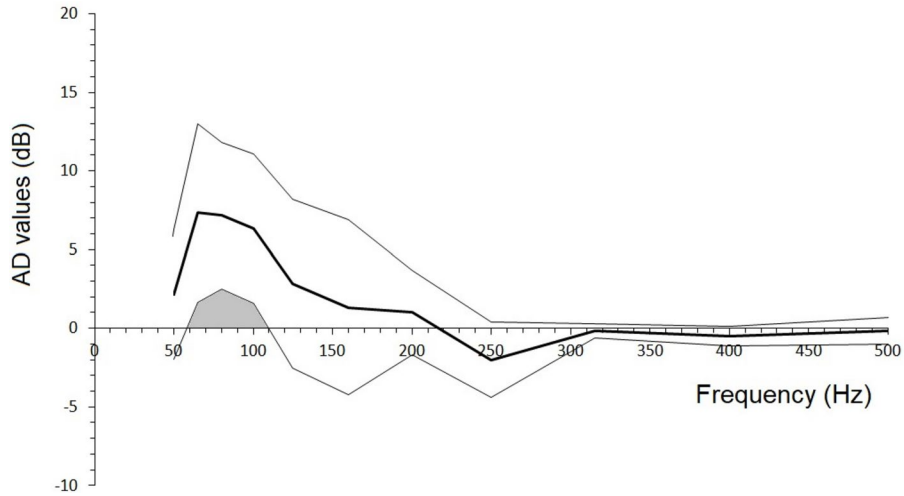


Fig. 3 Mean values (thick line) (±95% confidence interval of the mean, thin lines) of the frequency response (AD values, dB) of the seven bivalve shells tested in the field. The shadow area marks the (interpolated) frequency range with statistically significant amplitude gains

shells, 9.6±3.4 dB; laboratory shells, 6.1±1.6 dB; Student $t=2.86$, df=15, $p=0.012$). However, this result might be explained by the effect of shell weight (Lugli 2012, this study) since the shells tested in the field were significantly heavier than those tested in the laboratory (field shells, 36.0±9.3 g; laboratory shells, 21.1±10.4 g; Student $t=3.3$, df=15, $p=0.008$). Therefore, the relationship between the shell weight and the response variables was examined by pooling field and laboratory data. The results showed G_{peak} increased significantly with shell weight ($r=+0.888$, $n=17$, $p<0.01$; Fig. 5), whereas the relationship between F_{peak} and shell weight was not significant ($r=-0.396$, n=16, NS). The relationships between G_{peak}, F_{peak}, and shell weight were also examined for oyster and clam shells separately. In both cases, G_{peak} increased significantly with shell weight ($r=+0.930$, $n=9$, $p<0.01$, *Crassostrea*; $r=+0.903$, $n=8$, $p<0.01$, *Scapharca*; Fig. 5) whereas F_{peak} was not affected ($r=-0.529$, $n=9$, NS, *Crassostrea*; $r=-0.143$, $n=8$, NS, *Scapharca*).

As to the effect of the sand pile, the response curve of the two oyster shells tested in the field was compared with that of two oyster shells tested in laboratory (Lugli 2013). The response of the oyster hollow to the presence of the sand pile was similar in the two environments: the gain values due to the pile peaked around 100 Hz (peak gain magnitude for laboratory shells, 5.7 dB) and were most significant below 250 Hz (see Fig. 1 of Lugli 2013 for an example).

Discussion

Results of the present field study confirmed those obtained for different types of shell (including the oyster shell, *Crassostrea gigas*, the clam shell *Scapharca inaequivalvis*) tested in laboratory (Lugli 2012): acoustic stimulation of the shell hollow determines significant amplitude gains at frequencies below 250 Hz and maximum gains at around 100 Hz (range, 70–110 Hz). Indeed, the frequency of maximum gain (F_{peak}) did not differ between the field shells and those of the same type tested in the laboratory. Differences in the frequency response between field and laboratory shells were also observed: the acoustical stimulation of field shells yielded greater maximum gains (G_{peak}) in comparison to laboratory shells. However, this result was well explained by the larger size of shells tested in the field because the magnitude of sound amplification by the hollow increases with shell weight (Lugli 2012, this study). Analogous conclusions can be drawn on the effect of the sand pile: its presence above the shell further increased sound amplification by the cavity of both field and laboratory shells in a similar way, both in terms of amplitude gain and frequencies enhanced.

The conclusions of the current study on shells are similar to those obtained in a previous study on flat stones used by stream gobies as shelters and nest sites (Lugli 2012): the measurement of the frequency response of the hollow under stones tested

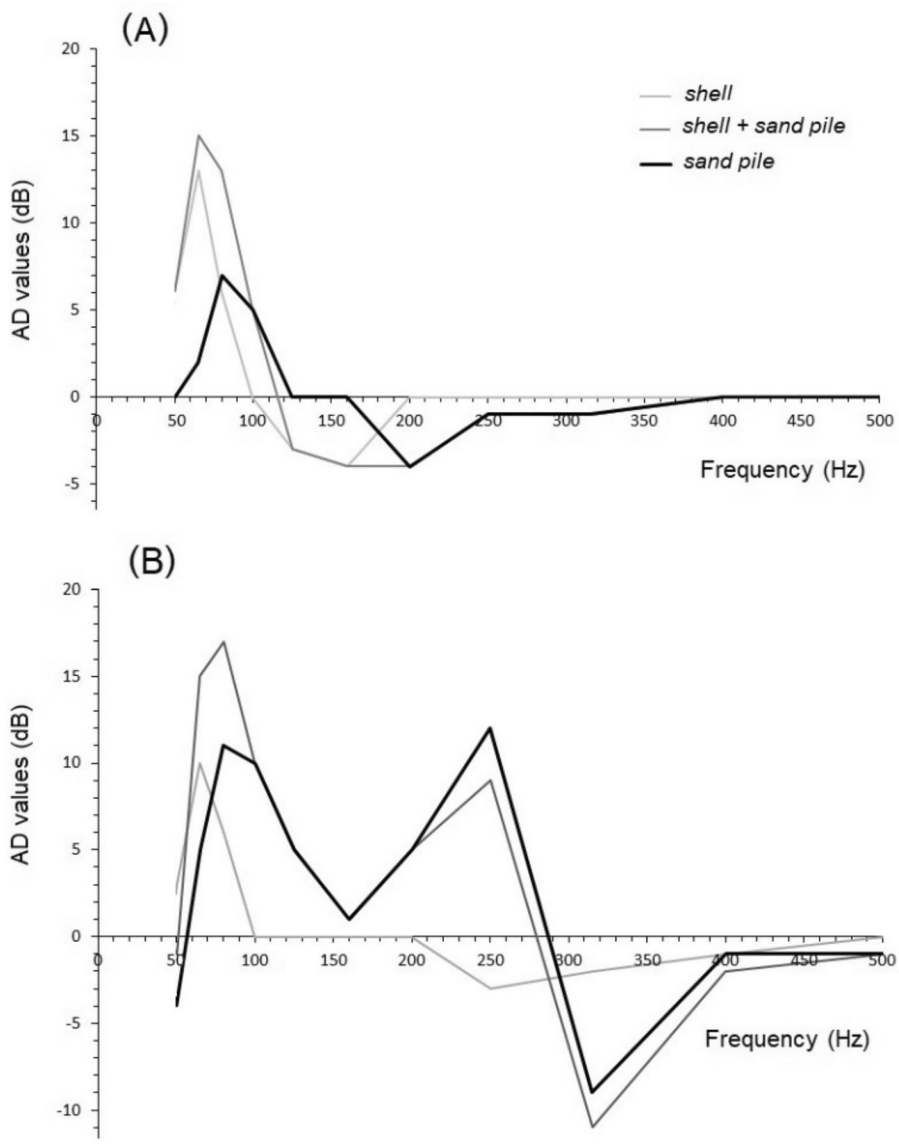


Fig. 4 Frequency response of the hollow below two *Crassostrea* shells (weight, 42.6 g (**A**), 34.3 g (**B**)), with (dark-gray line) and without (light-gray line) the sand pile on it. The effect of the sand pile alone (dark line) is the difference between the two curves

in laboratory and in a stream yielded comparable results. These findings are notable considering that laboratory shelters (both shells and flat stones) were tested within a small-sized tank (Lugli 2012, 2013), i.e., a closed environment where the sound may be distorted as a result of reverberation and resonances (Parvulescu 1967; Akamatsu et al. 2002; Rogers et al. 2016). However, the importance of such effects was likely minimal in the laboratory and lagoon, because in both test environments, sound propagation was constrained by the very shallow depth (25 cm) at which acoustical tests were carried out. It is known that water depth strongly constrains low-frequency communication underwater because no frequency corresponding to a wavelength longer than approximately four times the water depth will propagate, i.e., the frequency cutoff phenomenon over a rigid bottom (Rogers and Cox 1988). For example, frequencies below 750 Hz will not propagate in water with a depth of 50 cm or less, and gobies (including the sand gobies) typically emit sounds with main frequencies well below 500 Hz (Lugli et al. 1995, 1997, 2003). This phenomenon has been observed in the field for the sounds emitted by the stream goby, *P. bonelli*, from the nest cavity (a hollow under a stone) (Lugli and Fine 2003, 2007). Thus, all field and laboratory

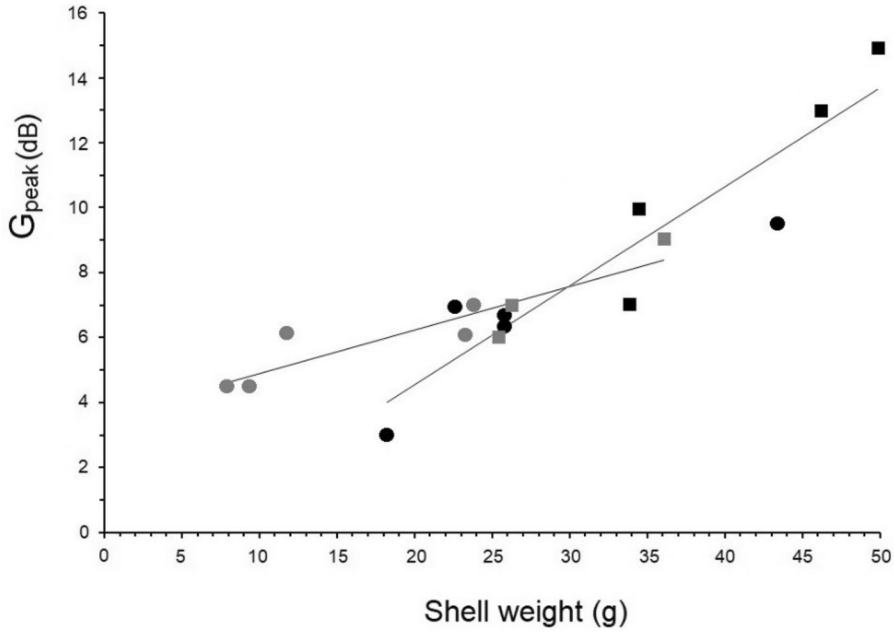


Fig. 5 The relationship between G_{peak} and shell weight (*Crassostrea*, black points; *Scapharca*, gray points) shown by pooling field (squares) and laboratory (circles) data. The graph also shows the regression (best-fit) line between G_{peak} and shell weight calculated separately for the *Crassostrea* and *Scapharca* shells

tests (Lugli 2012, 2013, this study) were conducted under non-propagating conditions of the water-borne sound pressure energy because all probe frequencies used were below the cutoff value, i.e., sound amplitude decayed exponentially at increasing distance from the source. Hence, the similarity in the frequency response of shelters tested in laboratory and field.

Unfortunately, exploiting the cutoff phenomenon for obtaining reliable acoustic measurements does not solve all the pitfalls of sound recording in small tanks. In the present study, the acoustical response of shells was determined by measuring the pressure component of the probe frequencies. However, most fishes, including gobies, respond to particle motion (Popper and Hawkins 2018). The problems associated with the correct measurement of particle motion in small tanks have been repeatedly emphasized by several authors (Parvulescu 1967; Duncan et al. 2016; Popper et al. 2019) and need not be summarized here (note: field measurements conducted on flat stones in the stream using a pressure (p)-velocity (u) sensor anchored to the substrate and facing the cavity below the stone as described in Lugli and Fine (2007) showed comparable amplitude gains by the cavity for both p and u components of the probe tone stimulus; Lugli, unpublished data). A further complication arises when, as in the case of the present study, the sound source is near the boundary between two mediums with different acoustic impedances, such as the water-substrate boundary (Roberts and Rice 2023). In this situation, part of the water-borne sound energy is transmitted to the substrate (e.g., the sandy bottom), where it propagates with much less attenuation due to the higher acoustic impedance of the sand (Bradbury and Vehrencamp 2011; Whang and Janssen 1994). During all the acoustic stimulation tests conducted in the field and laboratory, the buzzer was directly in physical (mechanical) contact with the bottom (Lugli 2012). Consequently, the transmission of a fraction of acoustic energy of the test frequencies into the sand substrate was expected. Three findings of the acoustic stimulation tests conducted in the laboratory (Lugli 2012, 2013) and in the field (Lugli 2012, current study) indicate that acoustic vibrations travel through the bottom, adding energy to the water-borne component of the sound, thereby determining the amplification properties of the shelter hollow. First, the shelter–substrate coupling plays a key role in the amplification of the sound since the amplitude gain is drastically reduced if the shelter is decoupled from the bottom (Lugli 2012). Second, the observed increase in the peak of amplitude gain (G_{peak}) with increasing weight of the stone and shell (clam shell, oyster shell) may be similarly interpreted since a heavier shelter likely provides a better coupling to the

substrate. Third, the presence of the sand pile further increases the amplitude gain, likely in consequence of the increased substrate-shelter coupling. Unfortunately, the amount of energy transmitted into the substrate by the probe at each test frequency, as well as its propagation through the bottom, is unknown.

The propagation of acoustic waves through the substrate is a potentially important aspect of the acoustic communication among bottom-dwelling fishes (Whang and Janssen 1994; Hawkins et al. 2021). In the male goby, there is a physical connection between the substrate and the pectoral and (possibly) pelvic girdles (which are physically connected to the sonic muscle) when the sound-emitting fish rests on the bottom (Parmentier et al. 2013, 2017). Therefore, the importance of substrate-shelter coupling for sound amplification might greatly favor the emission of low-frequency vibrational sound stimuli transmitted by the fish to the substrate as biotremor inside the nest. In this way, the amplification mechanism of the shelter, the sound-production mechanism, and the sand-piling activity by the male sand goby would be logically connected. In the present study, the acoustical response of the shell hollow was assessed by recording the probe stimulus with the receiver outside of the shell opening. Gains are expected to be higher (e.g., > 20 dB) when both source and receiver are inside the hollow (Lugli 2014), the typical context of sound emission in male sand gobies.

In the previous laboratory study (Lugli 2013), I concluded that sand piling by the male sand goby might be an adaptation to increase sound amplitude inside the nest hollow and, hence, the efficiency of acoustical signaling in the nest (with possible positive effects on male attractiveness). Behavioral activities aimed at increasing the amplitude of vocal signals have been documented in a variety of species. For example, burrows or leaves are used as acoustic baffles by crickets to increase the efficiency of sound radiation (Forrest 1982). Also, Bornean tree-hole frogs boost the volume of their mating calls by tuning their vocalizations to the specific resonant frequency of the water-filled tree holes they inhabit (Björn and Maklarin 2002). Results of this field experimental study on the sand goby nests further strengthen the conclusion that the construction of a sand pile may be considered an activity of environmental manipulation performed by a fish, analogous to those adopted by other animals to solve similar problems.

Acknowledgements The author wishes to thank Mr. Romano Romani for his help in the collection of field data. This ms greatly benefited from comments from two anonymous reviewers.

Funding Open access funding provided by Università degli Studi di Parma within the CRUI-CARE Agreement. Publication charges were covered by funds of the University of Parma.

Data availability All data supporting the findings of this study are available within the paper and are saved as an Excel file by the author's lab upon reasonable request.

Declarations

Competing interests The author declares no competing interests.

Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit http://creativecommons.org/licenses/by/4.0/.

References

Akamatsu T, Okumura T, Novarini N, Yan HY (2002) Empirical refinements applicable to the recording of fish sounds in small tanks. J Acoust Soc Am 112:3073–3082. https://doi.org/10.1121/1.1515799

Amorim MCP, Pedroso SS, Bolgan M, Jordao JM, Caiano M, Fonseca PJ (2013) Painted gobies sing their quality out loud: acoustic rather than visual signals advertise male quality and contribute to mating success. Funct Ecol 27:289–298. https://doi.org/10.1111/1365-2435.12032

Björn L, Maklarin L (2002) Animal communication: tree-hole frogs exploit resonance effects. Nature 420:475. https://doi.org/10.1038/420475a

Bradbury JW, Vehrencamp SL (2011) Principles of animal communication, 2nd edn. Sinauer Associates, Massachusetts

Brumm H, Slabbekoorn H (2005) Acoustic communication in noise. In: Slater PJB, Snowdon CT, Brockman HJ, Roper TJ, Naguib M (eds) Advances in the study of behavior, vol Vol. 35. Elsevier, San Diego, pp 151–209

Duncan AJ, Lucke K, Erbe C, McCauley RD (2016) Issues associated with sound exposure experiments in tanks. Proc Mtgs Acoust 27:070008. https://doi.org/10.1121/2.0000280

Forrest TG (1982) Acoustic communication and baffling behaviors of crickets. Fla Entomol 65:33–44. https://doi.org/10.2307/3494144

Hawkins AD, Hazelwood RA, Popper AN, Macey PC (2021) Substrate vibrations and their potential effects upon fishes and invertebrates. J Acoust Soc Am 149:2782–2790. https://doi.org/10.1121/10.0004773

Jones JC, Reynolds JD (1999) The influence of oxygen stress on female choice for male nest structure in the common goby. Anim Behav 57:189–196

Lehtonen TK, Lindström K (2009) Females decide whether size matters: plastic mate preferences tuned to the intensity of male-male competition. Behav Ecol 20:195–199. https://doi.org/10.1093/beheco/arn134

Lehtonen TK, Wong BBM (2009) Should females prefer males with elaborate nests? Behav Ecol 20:1015–1019. https://doi.org/10.1093/beheco/arp091

Lindström K, Lugli M (2000) A quantitative analysis of the courtship acoustic behavior and sound patterning in male sand goby, *Pomatoschistus minutus*. Environ Biol Fish 58:411–424. https://doi.org/10.1023/A:1007695526177

Lugli M (2010) Sounds of shallow water fishes pitch within the quiet window of the habitat ambient noise. J Comp Physiol A 196:439–451

Lugli M (2012) Acoustics of fish shelters: frequency response and gain properties. J Acoust Soc Am 132:3512–3524. https://doi.org/10.1121/1.4754581

Lugli M (2013) Sand pile above the nest amplifies the sound emitted by the male sand goby. Environ Biol Fish 96:1003–1012. https://doi.org/10.1007/s10641-012-0097-z

Lugli M (2014) Acoustics of fish shelters: background noise and signal-to-noise ratio. J Acoust Soc Am 136:3382–3388. https://doi.org/10.1121/1.4901707

Lugli M (2015) Habitat acoustics and the low-frequency communication of shallow water fishes. In: Ladich F (ed) Sound communication in fishes. Springer-Verlag, Wien, pp 175–206

Lugli M, Fine ML (2003) Acoustic communication in two fresh water gobies: ambient noise and short-range propagation in shallow streams. J Acoust Soc Am 114:512–521. https://doi.org/10.1121/1.1577561

Lugli M, Fine ML (2007) Stream ambient noise, spectrum and propagation of sounds in the goby, *Padogobius martensii*: sound pressure and particle velocity. J Acoust Soc Am 122:2881–2892. https://doi.org/10.1121/1.2783113

Lugli M, Torricelli P (1999) Pre-spawning sound production in mediterranean sand-gobies. J Fish Biol 54:691–694. https://doi.org/10.1006/jfbi.1998.0898

Lugli M, Pavan G, Torricelli P, Bobbio L (1995) Spawning vocalizations in male freshwater gobies (Pisces, Gobiidae). Environ Biol Fish 43:219–231. https://doi.org/10.1007/BF00005853

Lugli M, Torricelli P, Pavan G, Mainardi D (1997) Sound production during courtship and spawning in freshwater gobies (Pisces, Gobiidae). Mar Freshw Behav Physiol 29:109–126. https://doi.org/10.1080/10236249709379003

Lugli M, Yan HY, Fine M (2003) Acoustic communication in two freshwater gobies: the relationship between ambient noise, hearing thresholds and sound spectrum. J Comp Physiol A Neuroethol Sens Neural Behav Physiol 189:309–320. https://doi.org/10.1007/s00359-003-0404-4

Malavasi S, Collatuzzo S, Torricelli P (2008) Interspecific variation of acoustic signals in Mediterranean gobies (Perciformes, Gobiidae): comparative analysis and evolutionary outlook. Biol J Linn Soc 93:763–778. https://doi.org/10.1111/j.1095-8312.2008.00947.x

Myrberg AA Jr, Lugli M (2006) Reproductive behavior and acoustical interactions. In: Ladich F, Collin SP, Moller P, Kapoor BG (eds) Communication in fishes, Vol 1. Science Publishers, Enfield, NH, pp 149–176

Parmentier E, Kéver L, Boyle K, Corbisier Y-E, Sawelew L, Malavasi S (2013) Sound production mechanism in *Gobius paganellus* (Gobiidae). J Exp Biol 216:3189–3199. https://doi.org/10.1242/jeb.087205

Parmentier E, Petrinisec M, Fonseca PJ, Amorim MCP (2017) Sound-production mechanism in *Pomatoschistus pictus*. J Exp Biol. https://doi.org/10.1242/jeb.164863

Parvulescu A (1967) The acoustics of small tanks. In: Tavolga W (ed) Marine bio-acoustics Vol II. Pergamon Press, New York, pp 7–13

Pedroso SS, Barber I, Svensson O, Amorim MCP (2013) Courtship sounds advertise species identity and male quality in sympatric *Pomatoschistus* spp. Gobies. PLoS ONE 8(6):e64620

Popper AN, Hawkins AD (2018) The importance of particle motion to fishes and invertebrates. J Acoust Soc Am 143:470–486. https://doi.org/10.1121/1.5021594

Popper AN, Hawkins AD, Sand O, Sisneros JA (2019) Examining the hearing abilities of fishes. J Acoust Soc Am 146:948–955. https://doi.org/10.1121/1.5120185

Roberts L, Rice AN (2023) Vibrational and acoustic communication in fishes: the overlooked overlap between the underwater vibroscape and soundscape. J Acoust Soc Am 154:2708–2720. https://doi.org/10.1121/10.0021878

Rogers PH, Cox M (1988) Underwater sounds as a biological stimulus. In: Atema J, Fay RR, Popper AN, Tavolga WN (eds) Sensory biology of aquatic animals. Springer, New York, pp 131–149

Rogers PH, Hawkins AD, Popper AN, Fay RR, Gray MD (2016) Parvulescu revisited: small tank acoustics for bioacousticians. In: Popper AN, Hawkins AD (eds) The effects of noise on aquatic life II. Springer Science+Business Media, LLC, New York, pp 933–941

Siegel S, Castellan NJ Jr (1988) Nonparametric statistics for the behavioral sciences. McGraw-Hill, New York

Sokal RR, Rohlf FJ (1981) Biometry. Freeman, New York

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*. Behav Ecol 16:1042–1048. https://doi.org/10.1093/beheco/ari085

Svensson O, Kvarnemo C (2023) How sexual and natural selection interact and shape the evolution of nests and nesting behaviour in fishes. Philos Trans R Soc B Biol Sci 378:20220139. https://doi.org/10.1098/rstb.2022.0139

Whang A, Janssen J (1994) Sound production through the substrate during reproduction in the mottled sculpin, *Cottus*

bairdi (Cottidae). Environ Biol Fish 40:141–148. https://doi.org/10.1007/BF00002540

Zeyl JN, Malavasi S, Holt DE, Noel P, Lugli M, Johnston CE Covergent aspects of acoustic communication in darters, sculpins, and gobies. In: Sisneros JA (ed) Fish hearing and bioacoustics: An anthology in honor of Arthur N. Popper and Richard R. Fay. Advances in Experimental Medicine and Biology, vol 877. pp 93–120. https://doi.org/10.1007/978-3-319-21059-9_6

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.