

Acoustics of fish shelters: Frequency response and gain properties^{a)}

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Many teleosts emit sounds from cavities beneath stones and other types of submerged objects, yet the acoustical properties of fish shelters are virtually unexplored. This study examines the gain properties of shelters commonly used by Mediterranean gobies as hiding places and/or nest sites in the field (flat stones, shells belonging to five bivalve species), or within aquarium tanks (tunnel-shaped plastic covers, concrete blocks, concrete cylinder pipe, halves of terracotta flower pots). All shelters were acoustically stimulated using a small underwater buzzer, placed inside or around the shelter to mimic a fish calling from the nest site, and different types of driving stimuli (white noise, pure tones, and artificial pulse trains). Results showed the presence of significant amplitude gain (3–18 dB) at frequencies in the range 100–150 Hz in all types of natural shelters but one (*Mytilus*), terracotta flower pots, and concrete blocks. Gain was higher for stones and artificial shelters than for shells. Gain peak amplitude increased with the weight of stones and shells. Conclusions were verified by performing analogous acoustical tests on flat stones in the stream. Results draw attention to the use of suitable shelters for proper recording of sounds produced by fishes kept within laboratory aquaria.

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I. INTRODUCTION

Acoustic communication is widespread among both terrestrial and aquatic animals and may be limited by physical (e.g., body size) and environmental (e.g., ambient noise) constraints (reviewed in Bradbury and Vehrencamp, 1998). Small terrestrial animals (e.g., insects) have difficulties producing loud sounds because of the small dimensions of the sound producing organ, which decreases emission of acoustic pressure at lower frequencies (more suitable for long-range communication than higher frequencies) due to short-circuiting. In addition, differences in acoustic impedance between the body and the air do not allow an effective transfer of energy between the sonic apparatus and the transmission medium (Bradbury and Vehrencamp, 1998). Limitations due to different acoustic impedance of source and medium are more relaxed for marine animals. Fishes have approximately the same density as the water and, therefore, the coupling of the emitted sound to the transmission medium occurs with more efficiency than among terrestrial species. Many sound producing teleosts use the gas bladder for radiating the acoustic energy of the sound around the fish (Tavolga, 1971). However, the small size of the bladder is not appropriate for amplifying the low frequency sounds typical of so many teleost species. For instance, experimental deflation of the swim bladder does not affect sound amplitude in the stream goby *Padogobius bonelli* (Lugli et al., 2003).

Interestingly, in many hearing generalists (e.g., blennies, gobies, toadfishes, darters), most sound production occurs when the male is inside the nest cavity, e.g., a hollow under submerged objects (e.g., stones, shells), a hole or crevice between rocks. These enclosures have usually only one opening and, therefore, may be considered semi-open systems analogous to other enclosures (e.g., organ-pipes) with one or two open-ends. As such, they might affect the amplitude and frequency spectrum of the sound generated inside the enclosure. Similarly, the artificial shelters (e.g., concrete blocks, terracotta flower pots) commonly used in bioacoustical studies in the laboratory form tunnel-shaped enclosures that might affect the characteristics of sounds emitted inside them by the calling male. Quite surprisingly, however, to date no study has been conducted to explore the acoustic properties of these cavities and their effect on the sound spectrum. The only investigation available on this subject is the study of Barimo and Fine (1998) reporting the lack of interference of terracotta tiles open at both ends on the radiation pattern of the boat-whistle sound emitted by the male oyster toadfish (*Opsanus tau*) calling from these shelters in the field.

The large teleost family *Gobiidae* includes many species in which the male emits calls, mainly or exclusively, from the nest cavity (e.g., a hollow under a stone or shell) to attract and court ripe females (Tavolga, 1958; Torricelli et al., 1986; Lugli et al., 1997). Studies investigating goby sound production under laboratory conditions have employed either artificial shelters (i.e., tunnel-shaped plastic covers, Lugli et al., 1997; halves of terracotta flower pots, Lindström and Lugli, 2000), or natural shelters (bivalve shells, Lugli and Torricelli, 1999; Malavasi et al., 2008) as spawning sites for the male. Within the group of Mediterranean gobies, in particular, male sound production is tightly associated with mating and spawning activities occurring inside the nest cavity (e.g.,

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Torricelli *et al.*, 1986; Lugli *et al.*, 1997; Lugli and Torricelli, 1999; Malavasi *et al.*, 2008). Typically, these vocalizations are low-frequency pulse trains with dominant frequencies in the range 80–200 Hz (e.g., Lugli *et al.*, 1997; Malavasi *et al.*, 2008). These frequencies do not propagate under the very shallow conditions found in small laboratory tanks and in the species' natural environment (streams, brackish lagoons or marine sandy/rocky shores; typical water depths < 0.5 m) due to the frequency cutoff phenomenon [for instance, no frequency below 750 Hz will propagate in water with a depth < 0.5 m (Rogers and Cox, 1988)]. Thus, acoustic communication among gobies is generally limited to the nest cavity and a small area surrounding the shelter (Lugli and Fine, 2003; Myrberg and Lugli, 2006). The acoustic signals emitted by Mediterranean gobies and the types of shelters used by the male offer an excellent opportunity to explore the acoustical properties of these cavities and their effects on the sound spectrum.

In this study, the amplification properties of natural and artificial shelters are investigated using a small underwater buzzer as sound source (placed inside or around the shelter to mimic a fish calling from the nest site) and different types of driving stimuli (white noise, pure tones, and artificial pulse trains). The effects of the number of shelter openings, as well as the relative position of the receiver and the sound source on these properties, are also examined. Conclusions are verified by performing analogous acoustical tests on flat stones in a stream.

II. MATERIALS AND METHODS

A. Shelters

The natural shelters used for this study were flat stones, and the shell of five bivalve species: the Manila clam, *Tapes philippinarum* (Indopacific), *Crassostrea gigas* (Japanese oyster, Pacific), *Mytilus galloprovincialis* (common mussel), *Scapharca inaequivalvis* (Ark clam, Indopacific), and *Cerastoderma* (= *Cardium*) *edule* (common cockle) (Fig. 1). Three of these species (*Tapes*, *Scapharca*, *Cerastoderma*) had a heart-shaped shell (clam shells). Stones were collected in the stream (stream Stirone, Northern Italy) whereas bivalve shells were collected from two brackish lagoons (i.e., the Venice lagoon, and the “Sacca del Canarin” lagoon, River Po delta, upper Adriatic sea). All shelters were of suitable shape and size to be used as hiding places/nest sites by stream gobies [flat stones: *P. bonelli*, *Gobius nigricans* (Lugli *et al.*, 1992)] and lagoon gobies [stones and/or shells: *Pomatoschistus* spp., *Knipowitschia panizzae* (Lugli and Torricelli, 1999)]. The shape of stones was generally sub-rounded and approximated an irregular tetragon. Overall, ten flat stones (mean weight and range: 1950 g, 700–4100 g) and 25 bivalve shells (mean weight, range and species: 4.8 g, 3.7–5.8 g, *Cerastoderma*; 14.3 g, 7.9–23.8 g, *Scapharca*; 27.2 g, 18.2–43.4 g, *Crassostrea*; 12.6 g, 8.4–14.8 g, *Tapes*; 21.0 g, 12.6–25.8 g, *Mytilus*) were tested. Besides shelter total weight, the following dimensional parameters were measured to characterize the geometrical properties of shelters: area of substrate covered by the shelter (A , cm²), estimated by placing the stone, or the shell (convex side up), on regular graph paper and counting the number of

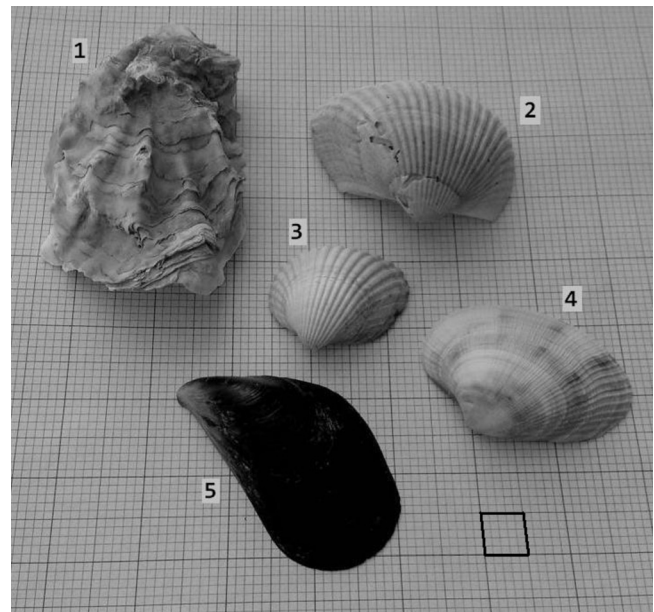


FIG. 1. The five types of bivalve shell used for the experiments (1. *Crassostrea gigas*, 2. *Scapharca inaequivalvis*, 3. *Cerastoderma edule*, 4. *Tapes philippinarus*, 5. *Mytilus edule*) laid on a sheet of regular graph paper (the area of the unit square marked on the grid is 1 cm²).

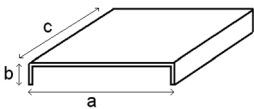
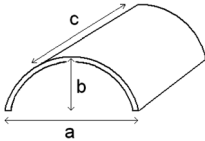
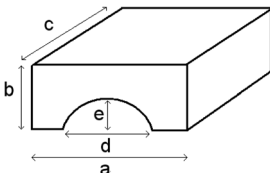
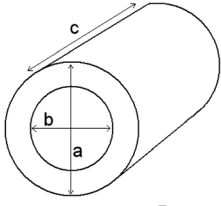
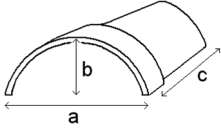
squared centimeters of the surface area delimited by the contour perimeter of the object; volume of the shell cavity (V^* , cm³), determined by measuring the amount of fine sand needed to fill the cavity of the valve held in the upside down position, i.e., with the convex side down; longest axis of the shelter (D , cm), measured with a caliper; volume of the stone (V , cm³), determined by measuring the amount of water displaced by the stone immersed into a graduated cylinder [note: V should not be confused with V^* , the former being the volume of a solid (i.e., the stone) whereas the latter being the volume of the empty space delimited by the inner surface of the valve].

Artificial shelters (Table I) consisted of two rectangular plastic [polyvinyl chloride (PVC)] covers with one and two open ends, respectively; two tunnel-shaped plastic (PVC) covers with one and two open ends, respectively; three squared concrete blocks of different size (i.e., small, medium, and large), each having a one-end open, tunnel-shaped cavity of same size; a one-end open concrete cylinder pipe; finally, two halves of a small terracotta flower pot, one having only the front opening (i.e., the one-end open terracotta shelter) the other one having an additional rear opening of smaller diameter than the front one, obtained by mechanical removal of the bottom of the flower pot (i.e., the two-ends open terracotta shelter); The tested artificial shelters were similar to those commonly used by experimenters for the study of sound production among bottom-dwelling teleosts (e.g., Lindström and Lugli, 2000; Amorim and Neves, 2007).

B. Experimental setup

All measurements were conducted within a 67 l laboratory plexiglass tank (55 × 55 × 25 cm, wall thickness: 0.8 cm). The bottom substrate was a 5 cm thick layer of coarse sand (all types of shelter) or fine gravel (stones,

TABLE I. Size parameters, weight, and shape of the ten artificial shelters used for the experiment.

Shelter type	Dimensions ^a (mm) and weight (g)				Schematic drawing (not to scale)
Rectangular plastic cover	Width (a) = 85 Height (b) = 22 Length (c) = 90 Thickness = 2 Weight (one-end open) = 37.7 Weight (two-ends open) = 32.0				
Tunnel-shaped plastic cover	Width (a) = 80 Height (b) = 23 Length (c) = 80 Thickness = 3 Weight (one-end open) = 37.6 Weight (two-ends open) = 32.0				
Concrete blocks		Small	Medium	Large	
	Width (a) =	90	30	90	
	Height (b) =	30	85	90	
	Length (c) =	90	125	150	
	Weight =	290	1875	3900	
	Cavity:				
	Width (d) = 80				
	Height (e) = 3				
	Depth = 85				
Concrete cylinder	Outer \varnothing (a) = 75 Cavity \varnothing (b) = 55 Total length (c) = 87 Cavity length = 70 Wall thickness = 10 Weight = 430				
Terracotta flower pot	Width ^b (a) = 80 Height ^b (b) = 40 Length (c) = 80 Thickness ^b = 5 Weight (one-end open) = 66.9 Weight (two-ends open) = 64.5				

^aIndicated by bold letters in the second and third columns.

^bFront side.

artificial shelters). The tank was filled with partially de-mineralized water to a depth of 20 cm. At such water depth no frequency below 2 kHz will propagate, i.e., the energy decays exponentially with theoretically and empirically determined losses of ~ 20 dB/20 cm (Akamatsu *et al.*, 2002). As all the test frequencies were below 2 kHz, all the experiments were conducted under conditions of no sound propagation (for acoustic waves travelling in the water medium). To minimize reflection effects from the tank walls and from the bottom of the tank, the portion of the side walls in contact with the substrate and the tank bottom were lined with 1 cm thick underwater sound-absorbing material (panels of reticulated open-cell foam). Finally the tank was set on vibration-absorbing material (rectangles of foam rubber) to minimize the transmission of background vibrations from the floor to the tank.

C. Sound sources and probe signals

In order to acoustically stimulate the shelter by simulating a fish calling inside the nest hollow, a custom-made,

specially constructed hemispheric transducer of very small size was used (Fig. 2). The acoustic near-field generated by the transducer was unknown. A complex dipole or quadrupole similar to the one generated by a calling fish might be reasonable assumptions.

The frequency response of the shelter was determined using artificial signals (probe signals), represented by white noise, pure tones and pulse trains. Random noise, which was mostly used, allows a quick assessment of the frequency response of a mechanical system. Pure tones were employed to verify the reliability of the frequency response determined with random noise stimulation and examine the low-frequency response of shelters (see the results discussed in Sec. III) by providing higher levels of excitation. Artificial pulse trains were used to examine the frequency response of the shelter to sounds signals mimicking the breeding sound emitted by gobies inside the nest hollow (Lugli *et al.*, 1995).

All artificial signals were generated using Avisoft SASLab ProTM software package for sound analysis (Raimund Specht, Berlin, Germany). A white noise sequence of

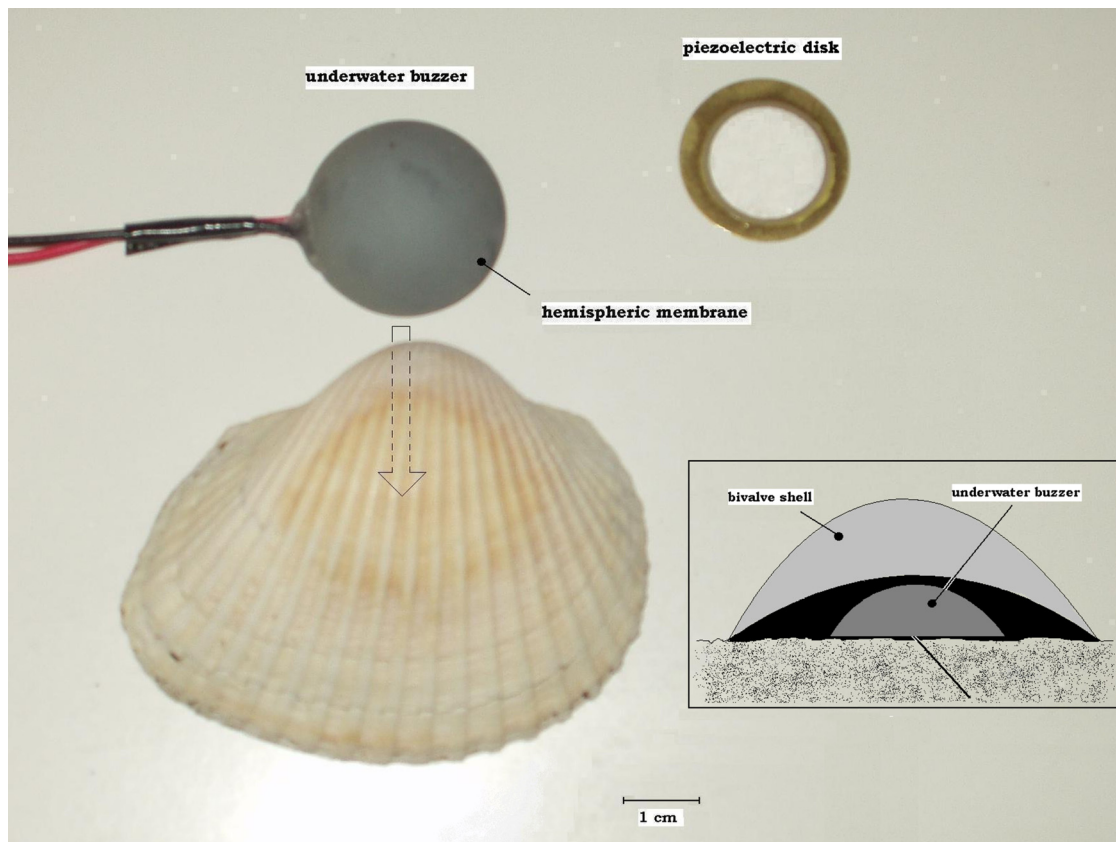


FIG. 2. (Color online) Picture of the underwater buzzer, i.e., a half of a small spherical rubber ball (outer \varnothing : 22 mm, thickness: 3 mm), acting as hemispheric membrane (convex part), glued around the circular edge of a piezoelectric metal disk (\varnothing : 20 mm, sensitive part up) (flat, or basal, part) acting as signal generator (shown to the right), and a bivalve shell (*Cerastoderma*) taken as an example (the arrow illustrates the positioning of the buzzer below the shell during the acoustic stimulation tests). The framed drawing illustrates the buzzer arranged inside the cavity of an hypothetical bivalve shell.

8 s (voltage amplitude: 0.5 V) was generated using the “synthesizer” function of Avisoft (sampling frequency 8 kHz). A sequence of ten-cycle tone bursts (100, 110, 120, 130, 140, and 150 Hz) separated by 0.5 s was constructed using the same function (voltage amplitude: 0.5 V). Finally, a train of 20 regularly spaced, artificial pulses (pulse rate: 20 pulses/s) was constructed using the “pulse-train generator” function of Avisoft. A single pulse was an initial broadband spike of ~ 10 ms followed by a 100 Hz oscillation [sound pulses of Mediterranean gobies are mostly oscillations at ~ 100 –200 Hz (Lugli *et al.*, 1995, 1997)] (see, the upcoming Fig. 6). The white noise sequence was bandpassed from 0.1 to 2 kHz. The pulse train was bandpassed from 0.1 to 0.5 kHz to mimic the low-frequency range of a typical goby pulse-train sound. Both filtered white noise and pulse train were then equalized (-4.5 dB/octave) to compensate for the high-frequency bias of the speaker’s amplitude response. The lower frequency limit of probe signals was set at 100 Hz (laboratory measurements, all types of signals), or 80 Hz (field measurements, probe tones only), because the response of the buzzer was poor at lower frequencies. Probe signals were amplified via a stereo amplifier [REVAC, 101 integrated classic stereo amplifier (REVAC©, Turin, Italy)] connected to a specially adapted output transformer (model PU-024) with fixed gain (28 dB). The level of sound stimulation was set to produce total band pressure levels [random noise: 119–134 dB root mean square (rms) re: $1 \mu\text{Pa}$] or peak

sound pressure levels (pulse trains: 109–124 dB rms re: $1 \mu\text{Pa}$; pure tones: 114–124 dB rms re: $1 \mu\text{Pa}$), measured at 3 cm from the source, within the range of goby sound levels measured at the same distance [e.g., 113–123 dB sound pressure level re: $1 \mu\text{Pa}$ (Lugli *et al.*, 1995)].

D. Experimental procedure

Individual shelters were placed in the middle of the tank above a small depression of the substrate (i.e., a pit) obtained by digging away a small amount (shells: 10–15 cm³; stones: 40–50 cm³) of sand (or gravel) with a finger, mimicking the hollow dug by the fish. Due to the small size of shelters used in the present study (e.g., the shell of *Cerastoderma* and *Mytilus*), care was taken to ensure the pit was deep enough to avoid the direct mechanical contact between the underside of the shelter and the transducer. Shelters commonly used by calling fish in the field (e.g., bivalve shells, small stones) typically have one opening. The opening in bivalve shells was obtained by placing the shell at a slightly oblique angle to the substrate leaving a small aperture (Fig. 2). The opening in flat stones was obtained by creating a small depression on the substrate between the pit and the outside.

Acoustic measurements were made with the projector placed in the pit (flat-side down) slightly buried into the substrate (see the following for exceptions). For the larger shelters (e.g., stones) the projector was placed at 3–4 cm from

the opening. Probe signals were collected using a small-size hydrophone (Brüel & Kjær, type 8103; Nærum, Denmark) held in place just above the substrate by means of a large photographic tripod placed on the floor. The tripod was equipped with a stainless-steel threaded vertical rod (\varnothing : 10 mm) attached to the lower end of the adjustable vertical tube of the tripod. The cable close to the hydrophone was secured to the lower end of the rod with adhesive tape, while the plug end was connected to a low-noise pre-amplifier (Brüel & Kjær, type 2626). The three legs of the tripod were set on blocks of vibration-absorbing material to minimize background vibrations from the floor. Measurements were made with the hydrophone held in place vertically, 2 cm in front of the shelter opening. This arrangement of source and receiver simulated a sheltered male courting a female at, or facing, the nest opening, a behavioral context characterized by high levels of sound emission by the territorial male goby (Torricelli *et al.*, 1986; Lugli *et al.*, 1995). Further measurements were conducted in sub-samples of shelters by changing the position of the source-receiver relative position (described in the following).

All measurements recorded the probe signal with (S^+ record) and without (S^- record) the shelter on the substrate, the record sequence being established on a random basis. The two recording periods of each acoustic test were separated for a few seconds to allow removal (record order: $S^+ - S^-$) or placing (record order $S^- - S^+$) the shelter above the pit. In both cases, care was taken to not alter the coupling between the buzzer and the substrate. All shelters were tested individually only once using white noise as replicated tests on the same shelter yielded similar results (Lugli unpublished; see also the upcoming Fig. 5 for examples of similar responses shown by artificial shelters differing only for the number of openings). Three stones, three shells, and three artificial shelters (small-size concrete block, one-end open terracotta flower pot, concrete cylinder) were further stimulated using the ten-cycle tone bursts and artificial pulse trains as probe stimuli in addition to white noise.

To explore possible variations of the shelter frequency response with receiver location, additional recordings were made in a sub-sample of nine shelters (six shells, two stones, small squared concrete block) by positioning the hydrophone 1 cm above or 1 cm lateral from the shelter (the side of the shelter being randomly chosen). To explore variations of the shelter frequency response with source location, measurements were carried out in three shelters (two stones, small squared concrete block) with the hydrophone positioned inside the shelter hollow. For these measurements the hydrophone was placed in the hollow horizontally, ~ 1 cm to the side of the pit location, the cable buried in the sand as it exited from the nest opening (note: shells were too small to permit this type of measurement). The shelter was stimulated by placing the sound source at three different locations along an ideal straight line on the substrate, i.e., in the pit, at the shelter opening, and outside the hollow 3 cm in front of the opening. The three measurements were repeated with the hydrophone held in place vertically in front of the opening as described previously.

E. Field experiments

Tone stimulation experiments were made on ten flat stones (mean weight and range: 3.3 kg, 1.1–6.2 kg) found at quiet sites of stream Stirone, i.e., places with modest water current far from sources of elevated noise levels (e.g., small waterfalls, Lugli and Fine, 2003). Water depth was below 50 cm and the bottom was mainly coarse sand, fine gravel, and pebbles (Lugli *et al.*, 1992). Stones used for the experiments were selected among those of the type used by gobies as shelters and nest sites (i.e., large, flat stones with a hollow underneath). Acoustic signals were recorded using a small-size hydrophone (GLN 9190; Gulton Industries, Metuchen, NJ; \varnothing : 45 mm; sensitivity: -200 dB re: $1 \text{ V}/\mu\text{Pa}$; frequency response flat ± 1 dB from 10 to 2000 Hz) connected to a DAT recorder (CASIO model DA-7; CASIO Computer Co. LTD, Tokyo, Japan). The buzzer used for laboratory measurements was placed on the substrate inside the hollow at ~ 3 cm from the hollow opening, while the hydrophone was positioned on the substrate facing the opening at ~ 3 cm from it. Then, a sequence of pure tones in $1/3$ octave steps in the range 80 Hz–1 kHz (i.e., 80, 100, 125, ..., 1000 Hz) was generated with a portable analog signal generator (MINIRATOR MR1; NEUTRIK AG, Shaan, Liechtenstein) connected to the output transformer in turn connected to the sound source. The level of sound stimulation was adjusted before each test to produce peak levels of tones within the range of the stream goby sound levels measured at the same distance in the field (Lugli *et al.*, 1995). The acoustic test consisted of measuring the tone sequence in the presence of the stone above the pit and after the stone was removed.

F. Signal analysis

All measurements were acquired with the PC (sampling rate: 44 100 Hz) using the real-time spectrogram function of Avisoft and stored as wave files for later analysis. Fast Fourier transforms (FFT) of the whole probe signal were computed using Avisoft (FFT length: 1024 Hz, frame size: 100%, Hamming window). The frequency response of the shelter was estimated by computing the pressure amplitude difference (AD, dB) between S^+ and S^- conditions. Broad-band noise signals were analyzed within 8 Hz wide bands in the range 0.1–2 kHz (filtered white noise), or in the range 0.1–0.5 kHz (pulse train). Thus, a positive value of AD for a tone signal or a frequency band of the noise signal would mean amplitude gain by the shelter, whereas a negative value would mean amplitude loss. Phase information was ignored.

Enhancement of the low frequency background noise by the shelter represents a potentially confounding factor for the estimation of the frequency response to noise stimulation, as this added energy from the background noise would appear only in the FFT_{S^+} . If an enhancement of the background noise frequencies was observed (this occurred only during a few acoustical tests carried out with the hydrophone inside the hollow) a 2–3 s segment of background noise from S^+ record was mixed to the background noise of the S^- record within a segment including the probe signal, using the “cut and paste” and the “mix” commands of Avisoft. The

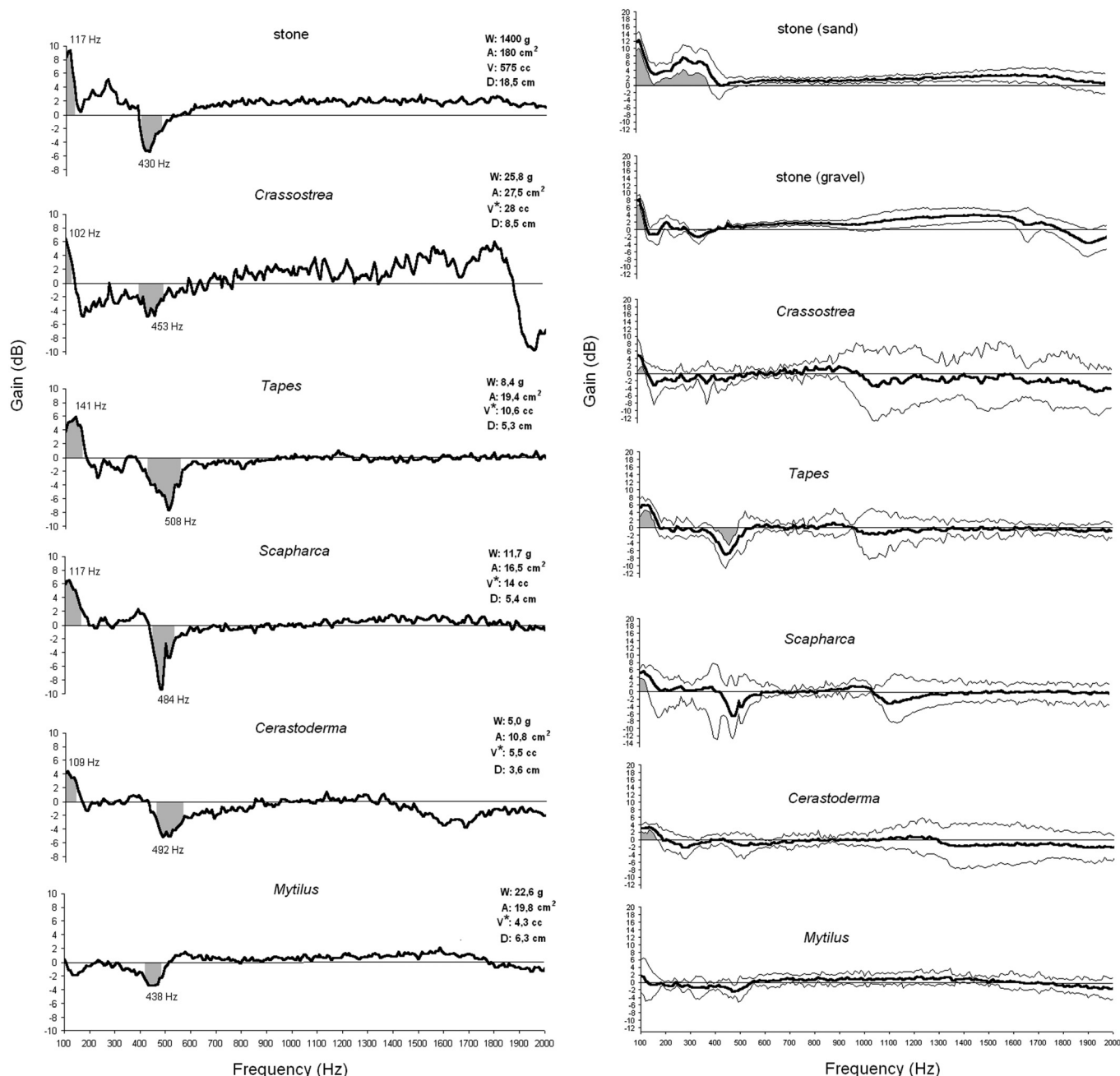


FIG. 3. Left plots: Frequency response of one stone and five different bivalve shells (one for each type of bivalve species), taken as an example. Shaded areas mark the most relevant gains and losses of the given shelter. The frequency value (F_{peak}) of maximum gain in the lower frequency range of each response function is shown, along with the weight and dimensional parameters of the shelter [W = weight, A = basal area, V = volume (stones), V^* = volume of the shell cavity, and D = longest axis, see the methods described in Sec. II for further explanation]. Right plots: Mean frequency response of stones ($n = 10$) and the five types of bivalve shell ($n = 5/\text{species}$). The upper and lower limits (thin lines) of the 95% confidence interval of the mean value (thick line) are shown. Shaded areas mark frequency regions with statistically significant gains and losses.

segment of the S^- record containing the probe signal and mixed background noise was then used for the calculation of the frequency response of the shelter.

G. Data analysis and statistics

Peaks of gain and losses were noted. The mean frequency response of natural shelters to filtered white noise (laboratory) or pure tone (field) stimulation was computed by averaging the values of AD (dB) within each frequency band ($n = 10$, stones; $n = 5/\text{bivalve species}$, shells) or for

each tone ($n = 10$, field stones). The 95% confidence interval for the mean AD of each band (or tone) was determined using the corresponding standard error of the t -distribution for paired comparisons (Sokal and Rohlf, 1981). Mean values were compared across shelters using non-parametric analysis of variance (Siegel and Castellan, 1988). An heuristic model for the gain properties of natural shelters tested in laboratory was offered by examining the relationship between the amplitude (G_{peak}) and frequency value (F_{peak}) of first peak of gain of the shelter (usually the highest AD value of the frequency response of the shelter, see

TABLE II. Mean + range of peak frequency (F peak, Hz) and amplitude (G peak, dB) at the point of low-frequency maximum gain of the frequency response curve of the shelter (stones on sand and gravel, five types of bivalve shell on sand substrate).

Shelter type	F peak (Hz)	G peak (dB) ^a	N
Stones (sand)	109.2 (102–117)	12.6 (8.7–18.3)	5 (10)
Stones (gravel)	106.9 (102–109)	8.4 (6.3–11.4)	6 (10)
<i>Crassostrea</i>	109.6 (102–133)	5.7 (3.1–7.5)	5 (5)
<i>Tapes</i>	123.6 (102–141)	6.8 (5.3–8.2)	5 (5)
<i>Scapharca</i>	117.0 (109–117)	5.7 (4.1–6.6)	5 (5)
<i>Cerastoderma</i>	128.2 (109–141)	3.7 (2.9–4.4)	3 (5)
<i>Mytilus</i>	104.8 (102–109)	1.9 (–1.5–3.2)	2 (5)

^aThe number of shelters for which G peak was also the highest gain within the measured frequency range (0.1–2 kHz) is also reported over the total number of replicates (in parentheses).

the results presented in Sec. III) and shelter weight. The analysis was conducted separately for the stone (on sand substrate, $n = 10$), clam shell (*Scapharca*, *Cerastoderma*, *Tapes*; $n = 15$), and oyster shell (*Crassostrea*) according to similarity of shape of the shelter (Fig. 1) (*Mytilus* shell were not examined because of lack of amplitude gain, see the results described in Sec. III). Statistical significance of these relationships was determined using the Kendall nonparametric correlation test (Siegel and Castellan, 1988) for the stone and clam shell, but not for the oyster shell (due to the low number of replicates). The gain properties of artificial shelters were only examined qualitatively. The frequency response of laboratory shelters to tones and pulse-train stimulation was compared to that obtained using filtered white noise by computing the dB difference of AD values respectively between the tone and the frequency band of the noise spectrum including the tone (tone vs noise) and for each

frequency band in the range 100–500 Hz (pulse train vs noise). In both cases, a positive value of the difference would mean a gain, whereas a negative value would mean a loss, in comparison to white noise stimulation.

III. RESULTS

A. The frequency response of shelter to noise stimulation

1. Stones and shells

All types of natural shelters but not the *Mytilus* shell showed consistent amplitude gains below 200 Hz (Fig. 3, left plots). Gain peaked below 150 Hz in all shelters (Table II). Mean peak frequency (mean F peak) did not differ significantly among the different types of shelter tested on sand (Kruskal-Wallis test, $KW = 8.86$, ns; *Mytilus* shells not included in the analysis because of the lack of amplitude gain, Fig. 3, bottom plots). There was no significant relationship between the value of F peak and weight of stone ($T = -0.404$, $n = 15$, ns) and clam shell ($T = -0.284$, $n = 15$, ns). However, stones tested on gravel had lower mean value of F peak than stones tested on sand (Table II). The magnitude of the gain peak (G peak) averaged 12 and 8 dB for stones tested, respectively, on sand and gravel substrate, and from 2 to 6 dB for shells (Table II). The mean value of G peak differed significantly among the different types of shelter tested on sand (Kruskal-Wallis test, $KW = 22.0$, $P = 0.0002$; *Mytilus* shells not included). The value of G peak increased with weight of stone, clam shell, and oyster shell (Fig. 4). The relationship was statistically significant for the stone ($T = 0.511$, $P = 0.04$, $n = 15$) and clam shell ($T = 0.619$, $P = 0.001$, $n = 15$). The frequency response of stones tested on sand showed a significantly broader secondary

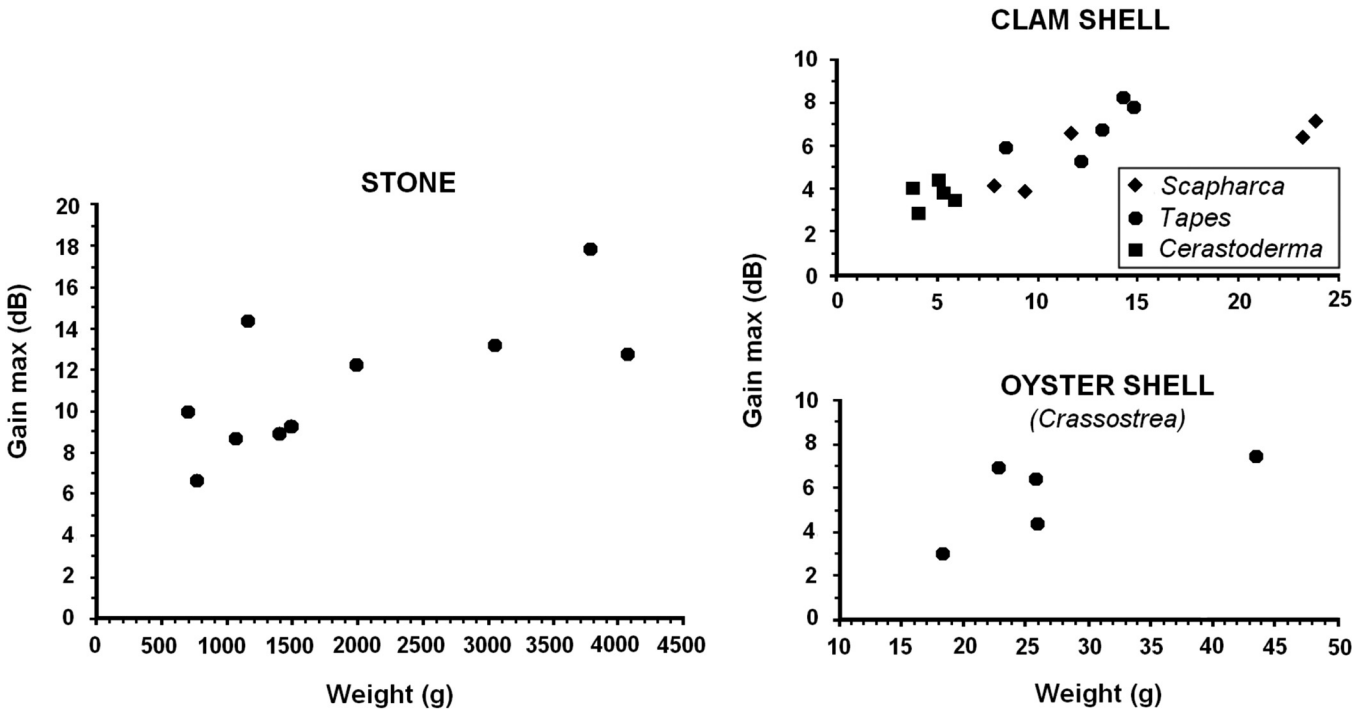


FIG. 4. The relationship between amplitude of the low-frequency peak of gain (G peak) and shelter weight shown separately for the stone (sand substrate), clam shell, and oyster shell.

peak at around 300 Hz (Fig. 3, top-right plot) which was not observed on gravel. Occasional amplitude losses in the frequency range 400–500 Hz were observed on the frequency response curve of single shelters (Fig. 3, left plots), but not on the average frequency response curve obtained using all replicates available for a given type of shelter (Fig. 3, right plots). The only exception was represented by the *Tapes* shell (Fig. 3, bottom plots), this type of shell showing statistically significant losses at frequencies ~ 400 Hz in all replicates.

2. Artificial shelters

Terracotta flower pots with one and both ends opened showed remarkable amplitude gains at frequencies below 200 Hz, the gain peaking at 117 Hz in the one-end open

shelter (+12 dB) and 132 Hz in the two-ends open one (+14.5 dB) (Fig. 5). Both shelters featured another peak at 398 Hz (+12 dB). The three concrete blocks showed remarkable amplitude gains below 200 Hz, the gain peaking just above 100 Hz, its amplitude varying from 10 to 12 dB. The concrete cylinder showed two broad amplitude gain peaks at 227 Hz (+12 dB) and ~ 600 Hz (+6 dB). All plastic shelters showed minimal amplitude gains (or losses) within the tested frequency range.

B. Effects of type of probe stimulus

1. Pulse-train stimulation

The three shells and three artificial shelters tested showed similar frequency response to pulse train and filtered

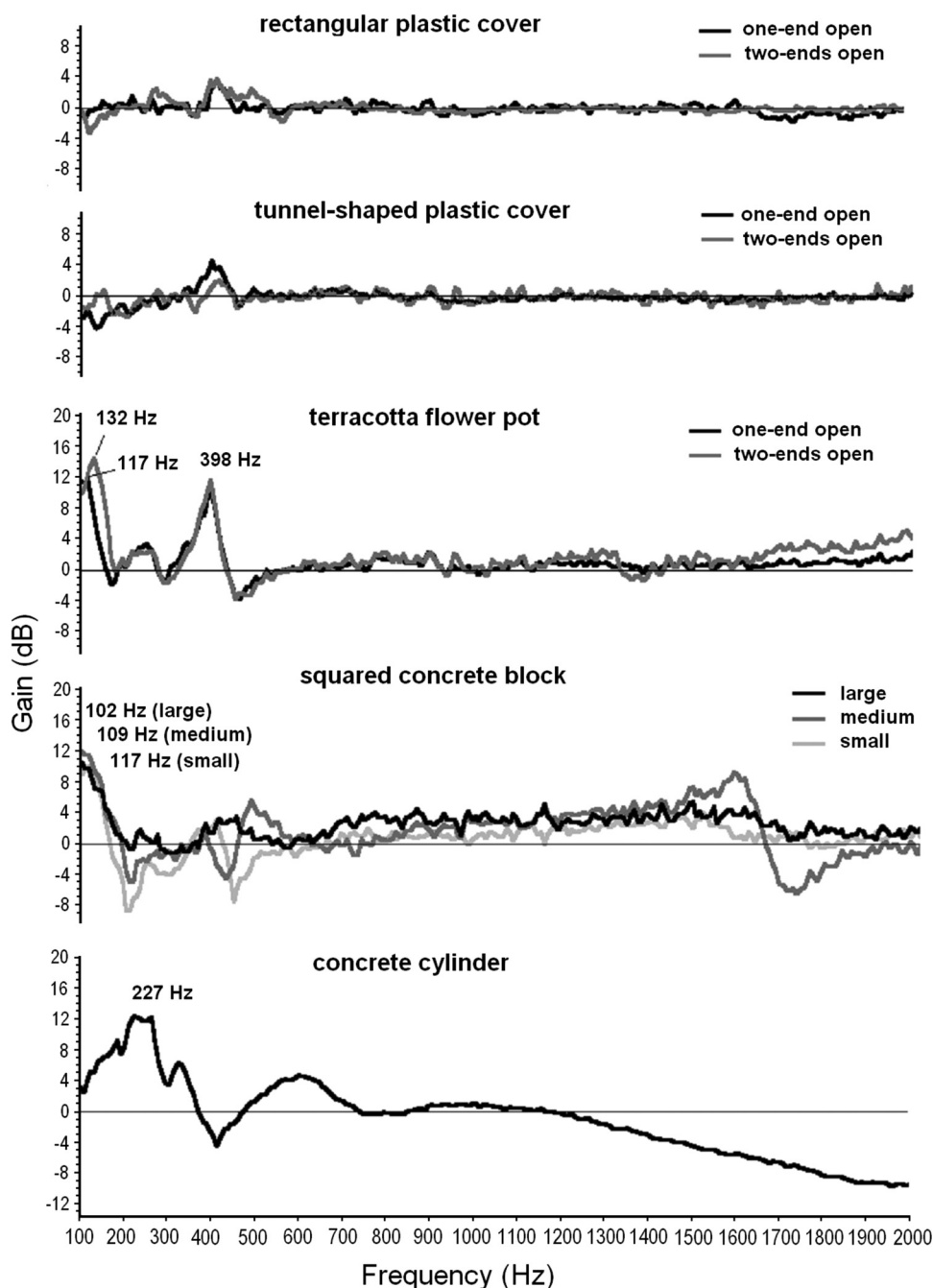


FIG. 5. Individual frequency response curves of artificial shelters. The frequency value of maximum gain in the lower frequency range of each individual response function is shown.

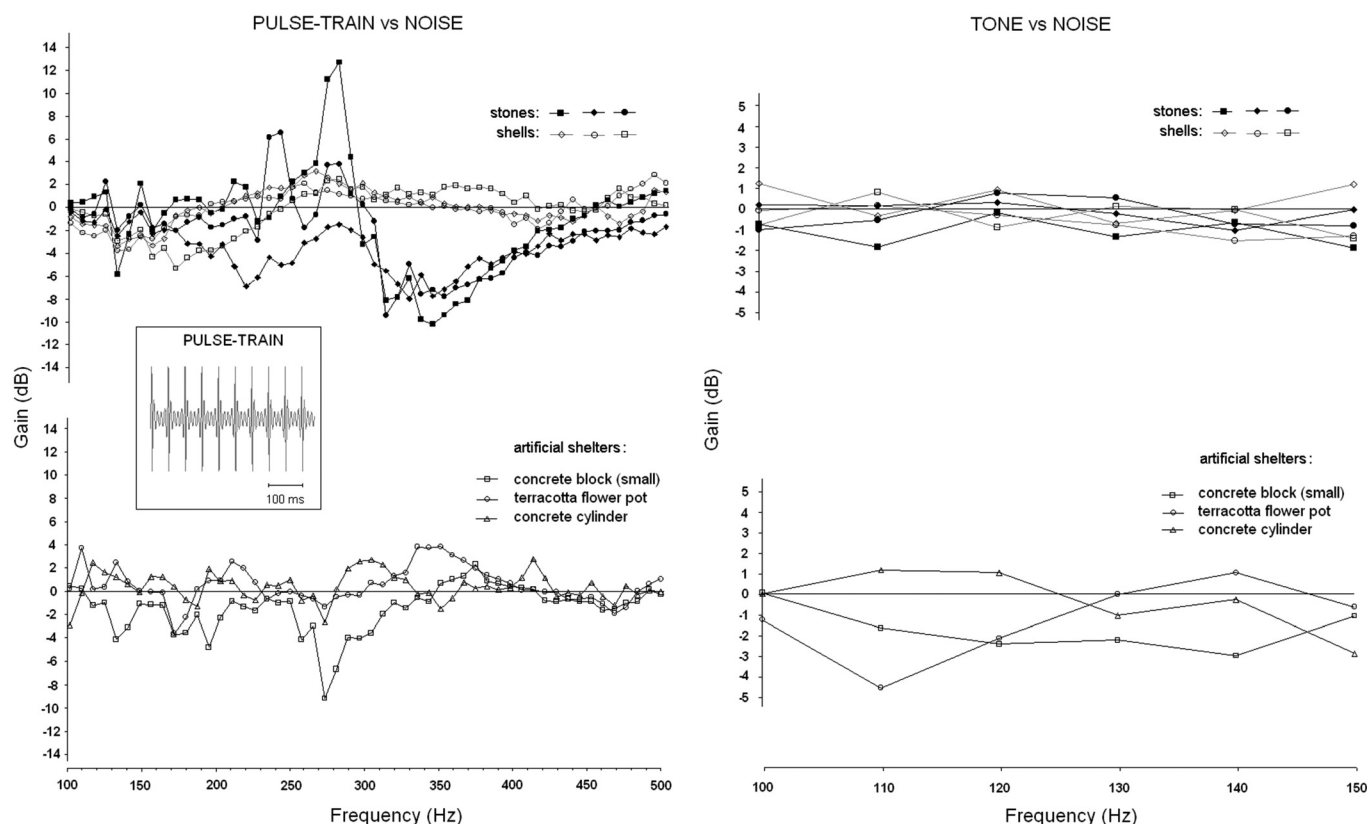


FIG. 6. Differences in the response of three stones, three shells (top plots), and three artificial shelters (bottom plots) to artificial pulse-train (left plots) and pure tone (right plots) stimulations, viewed in comparison to stimulation with filtered white noise. Left plots: Amplitude difference (dB) between the AD values of the pulse train and that of the filtered white noise within the same frequency band in the range 100–500 Hz, shown for the same shelters. Inset: Waveform of a 0.5 s segment of the artificial pulse train used for acoustical stimulation tests. Right plots: Amplitude difference (dB) between the value of AD of each tone frequency and that of the frequency band of the white noise spectrum including the tone, shown for each tested shelter.

white noise, the dB differences between the two probe stimuli generally resting in the range ± 3 dB in the band 100–500 Hz (Fig. 6, left plots). The three stones showed more marked decibel differences (Fig. 6, left plots). Notice in particular, the large (>4 dB, absolute value) negative decibel differences in the frequency range 300–400 Hz shown by all stones, indicating a lower amplitude gain by the stone in response to the pulse train.

2. Pure tone stimulation

All shelters showed a similar frequency response to tones and filtered white noise, the dB differences between the two probe stimuli for corresponding frequencies resting in all (stones and shells) or most (artificial shelters) cases in the ± 2 dB range (Fig. 6, right plots). Waveform examination of low-frequency pure tone bursts in the S^+ and S^- records showed in all shelters the occurrence of sound amplification at all tested frequencies (Fig. 7). Gain was greater in stones and artificial shelters, and these shelters show maximal gain and occurrence of resonance-like responses when the cavity was driven by 100 and/or 110 Hz tones.

C. Effect of source and receiver relative position

There was no amplitude gain when the buzzer drove the shelter laterally to the hollow opening, or just above the top of the shelter. Moving the buzzer from the inside to the

outside of the hollow of a stone and the small-size concrete block resulted in an almost complete loss of gain in both shelters when the probe signal was recorded by the hydrophone placed in front of the opening (Fig. 8, left plots), but not when the probe was recorded by the hydrophone placed inside the hollow (Fig. 8, right plots).

D. Frequency response of field stones to pure tones

Field stones showed significant amplitude gains only for tones in the range 80–200 Hz (Fig. 9, shaded area). The magnitude of mean gain increased with decreasing tone frequency, the maximum gain (+10 dB) being observed for the 80 Hz tone, i.e., below the lower frequency extreme of the noise stimuli used in the laboratory.

IV. DISCUSSION OF RESULTS

A. Fish shelters as low-frequency pressure amplification systems

The acoustical properties of cavities used by animals for sound communication have been thoroughly investigated in a few terrestrial species (e.g., insects: Bailey *et al.*, 2001; frogs: Penna, 2004), and never explored in aquatic organisms. This is the first study examining the gain properties of natural and artificial shelters commonly used by fishes for sound production and mating in the field and laboratory. The investigation was conducted using flat stones and shells from five different

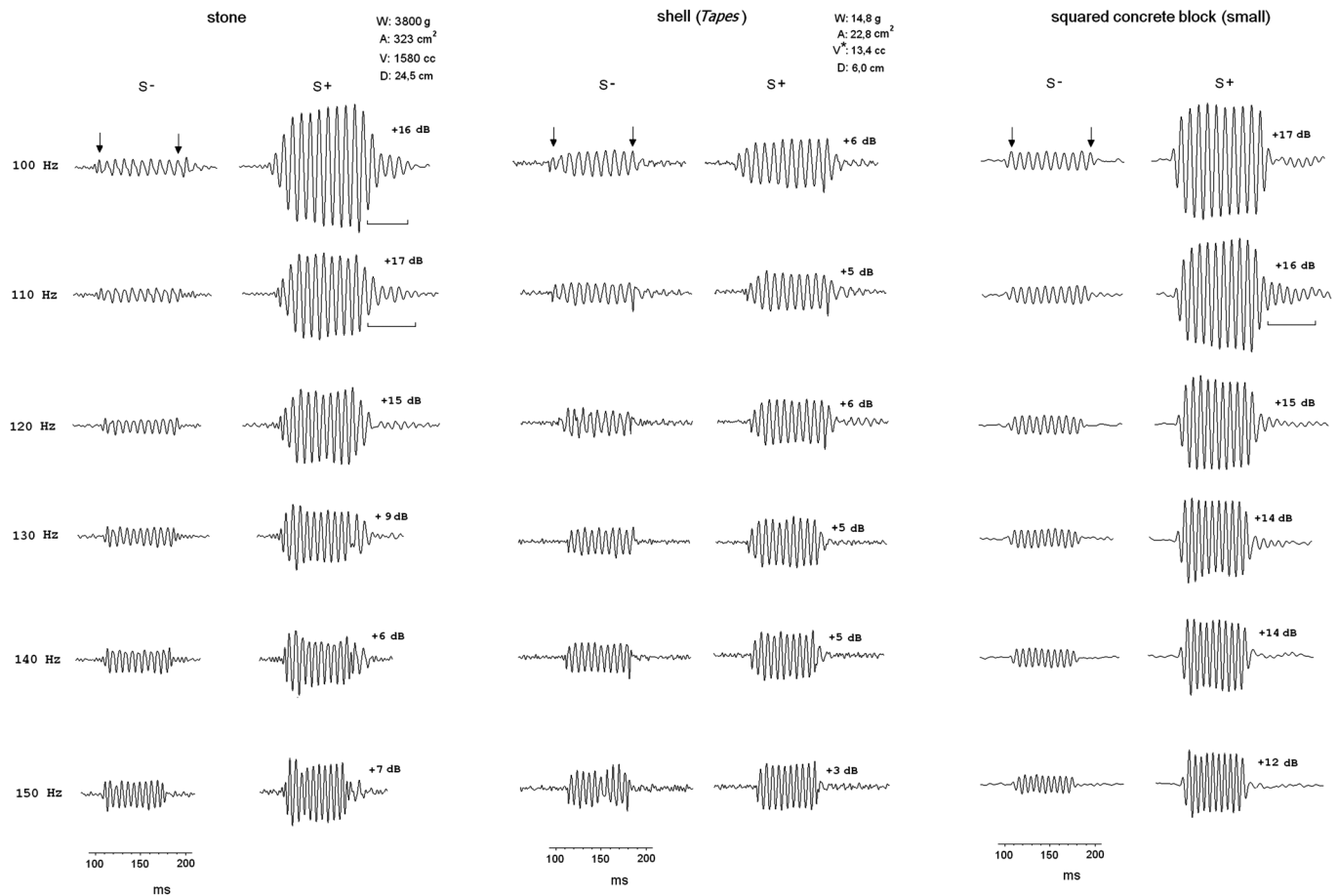


FIG. 7. Oscillograms of the six ten-cycle tone bursts recorded during S^- and S^+ conditions of the acoustic test performed on three representative shelters. The amplitude gain of the shelter at each tone frequency is reported on the oscillogram of the tone recorded during the S^+ condition. Arrows mark the beginning and end points of the tone burst transmitted during the S^- condition (no shelter above the buzzer). Note the resonance-like phenomenon, observed at the tone frequency with highest amplitude gain of the stone and concrete block, characterized by the build up and exponential decay of amplitude, respectively, at the beginning and end (horizontal bar below the oscillogram) of the tone burst when transmitted inside the hollow (S^+ condition).

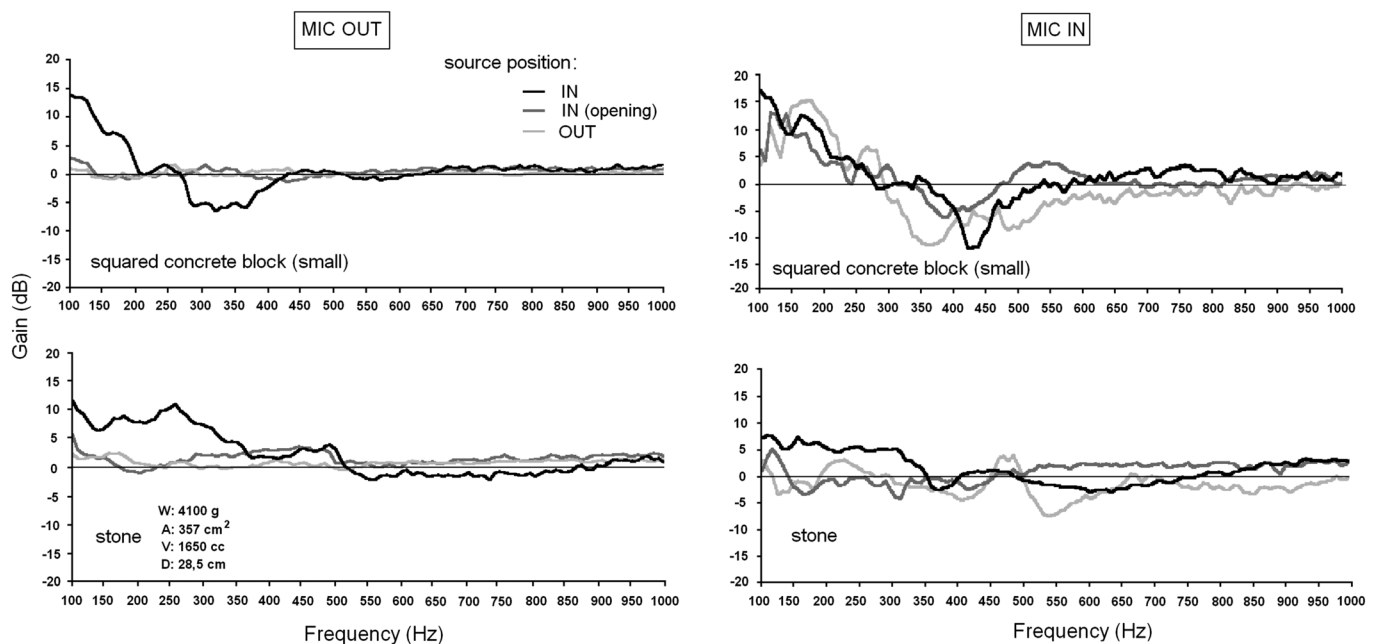


FIG. 8. Frequency response of the small-size concrete block (top plots) and one stone (bottom plots), taken as an example, at different locations of the sound source (IN = in the pit, IN-opening = at the shelter opening, OUT = outside the hollow, 3 cm in front of the opening, see the methods described in Sec. II for further explanation) and the receiver (MIC OUT = hydrophone in front of the opening, MIC IN = hydrophone in the pit, sideways to the buzzer location).

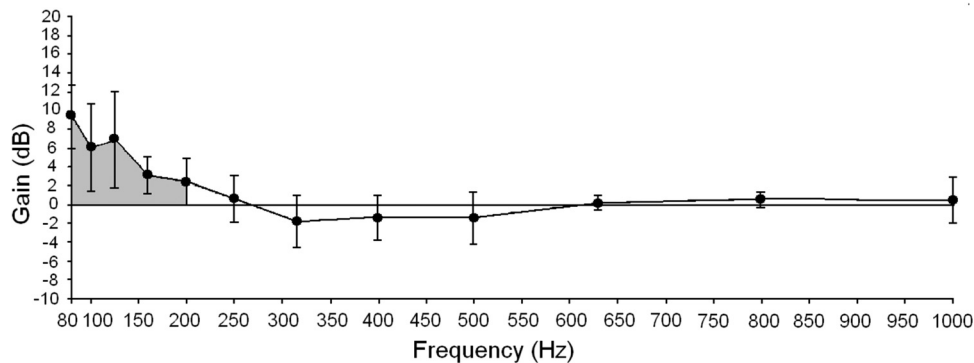


FIG. 9. Mean values (+95% confidence interval of the mean) of the shelter frequency response to tonal stimulation, determined for ten stones in the stream. The shaded area marks the tested frequencies with statistically significant gains (see the methods described in Sec. II for further explanation).

bivalve species as examples of natural shelters used by the territorial male of several species of Mediterranean gobies as nest sites in the field (Lugli *et al.*, 1995; Lugli and Torricelli, 1999). Results of the acoustical stimulation of the shelter hollow with white noise (100–2000 Hz) showed that both stones and shells, when placed on sand (all shelters) or gravel (stones only) substrate within a test tank, amplify sound frequencies below 200 Hz, the amplitude gain (from few decibels up to 18 dB) peaking always below 150 Hz. Further, the value of the peak frequency (i.e., the frequency of maximum gain) averaged over the replicates for each type of shelter does not differ significantly among different shelters. For example, the mean amplitude gain of stones and *Crassostrea* shells peaked in both cases at 109 Hz. This is a remarkable finding considering the huge size difference between the two types of shelter. However, stones had always higher amplitude gains than shells. For instance, the lower value of maximum gain determined for the stone (8.7 dB, stone tested on sand) was higher than the highest value of maximum gain determined for the cavity under a bivalve shell (8.2 dB). These conclusions are unlikely to be affected by the type of probe stimulus used as the acoustic stimulation of three stones and three shells with artificial pulse trains (100–500 Hz) and pure tones (100–150 Hz) produced results (i.e., amplitude gains) entirely comparable to those observed using noise stimulation. The only major discrepancy was observed in the frequency response of stones, all showing higher amplitude gains (up to +10 dB) in the frequency range 300–400 Hz when the hollow was driven by the pulse train. Acoustical tests were also conducted on flat stones in the stream using pure tones (range 80–1000 Hz) broadcasted from the buzzer placed in the pit below the stone. Results were similar to those obtained for stones in the laboratory, i.e., a stone with a hollow underneath significantly amplifies tone frequencies below 200 Hz, the maximum mean gain (10 dB) being observed at the lowest tone frequency tested (80 Hz). The latter result indicates that gain peak at around 100 Hz observed in a number of shelters tested in the laboratory might indeed have been reached at a lower frequency value, had these shelters been tested in the frequency band 50–100 Hz.

B. Shelter hollow as a resonant cavity?

The lack of major differences in the response of both natural and artificial shelters to different probe signals (from

single tones to broadband noise) indicates that a submerged shelter of small size likely behaves as a linear system in first approximation (Bradbury and Vehrencamp, 1998). This is of importance to the perspective of the maintenance of the spectral information content of the sound because it means that the amplitude gain by the shelter at a given sound frequency would not be affected by the frequency occurring alone, for instance as tonal sound, or together with many others, being part of a more complex sound (e.g., broadband pulse-train sound). The higher amplitude gains of stones may be due to resonance, as observed in two stones following pure tone stimulation at the frequency of maximum gain. The reasons of the resonance are not clear, however. Theoretical and empirical (this study) evidence indicate that the hollow below a stone (or any submerged object of small size) cannot be considered a simple resonant cavity. Any resonant system (e.g., the Helmholtz resonator) excited by a impulse noise would vibrate maximally at a characteristic frequency (the resonant frequency) whose value varies inversely with size of the resonator (Dowling and Ffowcs William, 1983). For instance, among burrowing frogs the resonant frequency is inversely correlated with burrow length (Penna, 2004). Clearly, this is not the situation of the acoustics of the hollow below stones and shells as these shelters amplified at similar frequencies. Further, there was no significant relationship between value of the peak frequency and weight of the stone and clam shell. Barimo and Fine (1998) provided both theoretical and empirical evidence that the large clay terracotta shelters used by male toadfish for calling could not behave as organ-pipes because the resonant frequency would be too high (Dowling and Ffowcs William, 1983). The very small size of shelters used in this study makes the interpretation of such shelters as organ-pipes even more unrealistic. Theory of sound propagation underwater (Albers, 1965) predicts small underwater objects do not produce a significant scattering (Rayleigh scattering) of low frequency sound waves, i.e., they are virtually transparent to sound (Rogers and Cox, 1988). Barimo and Fine (1998) reported a lack of interference on sound propagation by clay terracotta shelters housing the hydrophone (or the fish) inside them. In the present study, the gain properties of a stone and an artificial shelter (a concrete squared block) were quickly lost as long as the sound source was moved from inside to outside the shelter cavity, a finding consistent with the above-mentioned prediction.

C. Importance of the shelter-substrate coupling

Circumstantial evidence from this study indicates that the shelter–substrate coupling plays a key role in the amplification of the sound. For instance, amplitude gain disappears if the shelter–substrate coupling is dramatically decreased by, e.g., manually lifting the shelter 2–3 mm above the substrate or by placing a thin layer (5 mm) of sound-absorbing material (open-cell foam rubber) between the shelter and the substrate (Lugli, personal observations), or using artificial shelters (e.g., the PVC shelters used in this study, see the following) of density close to that of the water. A higher shelter–substrate coupling might be the reason why stones had higher amplitude gains than shells, or why a stone tested on sand had higher amplitude gains than when tested on gravel substrate. Further, the observed increase of gain peak value (*G* peak) with the weight of the stone and shell (clam shell, oyster shell) may be similarly interpreted, a heavier shelter likely providing a better coupling to the substrate. Thus, rather than a cavity with resonant properties, the shelter (with one or two open ends) coupled to the substrate might form a partially closed system absorbing part of the acoustic energy emitted by the small driver inside the cavity. Results of the measurements from different points around shelter indicate that the sound energy amplified by the shelter do not spread uniformly in all directions but is mainly channeled through the shelter opening where the acoustic impedance is lower, i.e., the shelter as source amplifier has directivity properties. In addition, the occurrence of constructive and destructive interferences of sound waves inside the cavity is likely, as shown by the presence of peak losses in the gain function of single shelters. However, analytical and/or numerical simulation of the pressure amplifications and acoustical interferences inside and around the shelter are outside the goal of this paper. Clearly, fish shelters appear complex pressure amplifying systems allowing a better transfer of low-frequency acoustic energy radiated inefficiently (Harris, 1964) by a small acoustic source (be it a fish or a small speaker) to the water.

D. Acoustical differences between natural and artificial shelters and their consequences for the study of fish acoustic communication

Compared to stones and shells, the frequency response of artificial shelters was variable, spanning from the marked low-frequency amplitude gain by tunnel-shaped concrete blocks and terracotta flower pots, similar to that of stones, to a lack of gain by plastic shelters. These differences might be partly due to the lower coupling of plastic shelters compared to concrete and terracotta shelters, the density of PVC ($\sim 1.26 \text{ g/cm}^3$) being only slightly higher than water density. In terms of quality of fish sound recording, a plastic shelter most likely leaves the frequency spectrum of the sound source unchanged. This would be a desirable property for a fish shelter if the scope of the study is obtaining a reliable spectral characterization of sounds emitted from the nest cavity. Plastic shelters have been widely used by the author in previous studies examining the acoustic behavior of the male goby (Lugli *et al.*, 1995; Lugli *et al.*, 1997). On the

other hand, the use of tiles, flower pots or concrete blocks as shelters/nest sites for the male is common in studies of fish sound production conducted in the laboratory (e.g., Ladich, 1989; Brantley and Bass, 1994; Lindström and Lugli, 2000; Amorim and Neves, 2007) and field (Barimo and Fine, 1998). Results of the present study showed that these shelters amplify sound frequencies in the range 100–500 Hz by up to 15 dB. For instance, results of acoustic stimulation tests on two small-size halves of a terracotta flower pots showed that their frequency response has two major amplitude gain peaks (maximum gain $> 10 \text{ dB}$) at ~ 100 and 400 Hz, respectively. Thus, the spectrum of a sound comprising these frequencies would be likely changed significantly by the presence of the shelter hollow housing the calling male. In the study of Barimo and Fine (1998) the terra cotta tiles used as shelters by the male toadfish were not reported to modify significantly the acoustic field and propagation of the species' call ("boat whistle"), a finding apparently in contrast with conclusions of the present study. However, it should be noted that the main energy of the toadfish call lies at the fundamental frequency between 200 and 300 Hz (e.g., Barimo and Fine, 1998), a frequency range where the two flower pots tested in the present study had little or no amplitude gain. Thus, results of acoustic tests of this study would be consistent with those reported in the study of Barimo and Fine.

E. Shelter gain properties and use of low-frequency sounds by cavity nesting fishes: Behavioral perspectives

Many soniferous teleosts using stones, shells, or other submerged objects as breeding sites emits sounds with dominant frequencies below 200 Hz (e.g., toadfishes, blennies, gobies, reviewed in Myrberg and Lugli, 2006), those for which amplitude gain by the shelter, be it a stone, shell, or artificial shelter, is greatest. For instance, the dominant frequencies at around 100 Hz of the sound emitted in the nest hollow by the male stream gobies, *P. bonelli* and *G. nigricans*, are clearly enhanced by 10–20 dB amplitude gain of the flat stone at these frequencies. In the very shallow waters of the stream a 15–20 dB increase in sound amplitude would propagate the *P. bonelli* sound only 20 cm further away from the source (a male calling inside the stone hollow) (Lugli and Fine, 2003), a small and yet significant increase of the active space of the sound considering the very-short communication range of this species. Tuning the sound to the frequencies enhanced by the shelter might benefit the emitter in other ways. For instance, among fishes it has been demonstrated that louder male vocalizations are preferred by gravid females (McKibben and Bass, 1998) and are predictor of dominance during fights (Ladich, 1998). Thus, besides the increase of communication distance, a male producing louder sounds through shelter pressure amplification would gain reproductive advantages both in terms of female choice and inter-specific competition.

V. CONCLUDING REMARKS

Acoustics of cavities, holes, and hollows under submerged objects is an important aspect of fish acoustic

communication that should be accounted for in future studies exploring the spectral characteristic of sounds produced by cavity nesting species and their importance for communication. On the basis of the present findings, the following few recommendations for such studies can be made: (i) if the scope of the investigation is the faithful characterization of the low-frequency spectrum of the species' acoustic signal, the use of light shelters (such as PVC or plastic tiles) should be preferred over those made of heavier materials (such as concrete blocks or terracotta flower pots and tiles); (ii) if the sound does not contain significant acoustic energy below 400–500 Hz one should not care about the type of shelter used as calling site by the emitter; (iii) investigators exploring orientation and mate attraction by acoustic means must be aware, before developing appropriate playback experiments, that sound pressure amplification by the shelter is most effective if the fish is listening from a place facing the opening(s) of the cavity; and (iv) when the sheltered fish acts as a receiver, the shelter behaves as if it were transparent to the sound generated by an external point source (i.e., the hollow is not likely to alter significantly the acoustic field of an incoming sound wave regardless of frequency). It must be stressed that conclusions of the present paper were drawn by measuring the pressure component of the sound wave. Therefore, some of the above conclusions, particularly those at points (ii) and (iv), might not be true for the hydrodynamic and flow stimuli (i.e., the particle displacement components) associated to the sound emission taking place inside the hollow.

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