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Acoustic communication in two freshwater gobies: Ambient noise and short-range propagation in shallow streams[a]

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Noise is an important theoretical constraint on the evolution of signal form and sensory performance. In order to determine environmental constraints on the communication of two freshwater gobies *Padogobius martensii* and *Gobius nigricans*, numerous noise spectra were measured from quiet areas and ones adjacent to waterfalls and rapids in two shallow stony streams. Propagation of goby sounds and waterfall noise was also measured. A quiet window around 100 Hz is present in many noise spectra from noisy locations. The window lies between two noise sources, a low-frequency one attributed to turbulence, and a high-frequency one (200–500 Hz) attributed to bubble noise from water breaking the surface. Ambient noise from a waterfall (frequencies below 1 kHz) attenuates as much as 30 dB between 1 and 2 m, after which values are variable without further attenuation (i.e., buried in the noise floor). Similarly, courtship sounds of *P. martensii* attenuate as much as 30 dB between 5 and 50 cm. Since gobies are known to court in noisy as well as quiet locations in these streams, their acoustic communication system (sounds and auditory system) must be able to cope with short-range propagation dictated by shallow depths and ambient noise in noisy locations. © *2003 Acoustical Society of America.* [DOI: 10.1121/1.1577561]

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I. INTRODUCTION

Sound attenuation (spreading loss and absorption), degradation, and ambient noise act as environmental constraints on acoustic communication (Wiley and Richards, 1982). For the emitter these factors are thought to be important for the evolution of animal vocalizations, and for the receiver, they affect the detection and recognition of sounds. Therefore, these factors are important for the design of the auditory system. Evidence for the effects of the environmental factors on acoustic signals and receptor systems has been provided for many terrestrial species, especially among birds and mammals (reviewed in Bradbury and Veherencamp, 1998).

Acoustic communication is also affected by the underwater environment. For instance, the short travel time of sound in water and the air–water and water–bottom boundaries account for the strongly frequency-dependent propagation and high degradation typical of underwater acoustic signals (e.g., Hawkins and Myrberg, 1983). These effects are pronounced in coastal waters in the sea and in shallow waters of rivers, lakes, and ponds where most sonic teleosts are found. Acoustic characteristics of noise in the deep sea are well known (Knudsen *et al.*, 1948; Wenz, 1962; reviewed in Urik, 1983), but little work has been devoted to shallow environments (Hawkins and Johnstone, 1978; Myrberg, 1980; Fine and Lenhardt, 1983; Forrest *et al.*, 1993; Mann and Lobel, 1997).

Teleosts have the most diverse sound-producing mechanisms, hearing abilities, and live in a wider array of environments than other vertebrate groups. However, because of low accessibility for experimental investigation and complex acoustics of the aquatic environment, the relationships between the environmental constraints and sound communication in fishes are less understood than in land vertebrates. Rogers and Cox (1988) suggested that high noise levels at low frequencies (<1 kHz) in many shallow-water environments should favor fishes that preferentially evolve sensitivity to high frequencies. Yet, many teleosts from shallow habitats produce sounds and have best hearing at frequencies well below 1 kHz (e.g., Fine *et al.*, 1977; Myrberg, 1981; Hawkins and Myrberg, 1983; Fay and Popper, 1999). The presence of physiological constraints (swimbladder resonance) or short-range communication are suggested explanations for the paradox (Fine and Lenhardt, 1983; Bradbury and Veherencamp, 1998).

Two gobies (*Padogobius martensii, Gobius nigricans*) live in streams and small stony rivers (Lugli *et al.*, 1992; Gandolfi and Tongiorgi, 1974) characterized by low water depths (<1 m) and high levels of low-frequency background noise from water turbulence and small waterfalls. These habitats offer an excellent opportunity to study the role of ambient noise and other environmental constraints on fish sound communication. In this paper we characterize ambient noise levels in various locations (quiet to noisy) in two such shallow streams (Stream Stirone, River Serchio). We also measure the propagation of noise downstream from a waterfall and the propagation of *P. martensii* sounds in a quiet
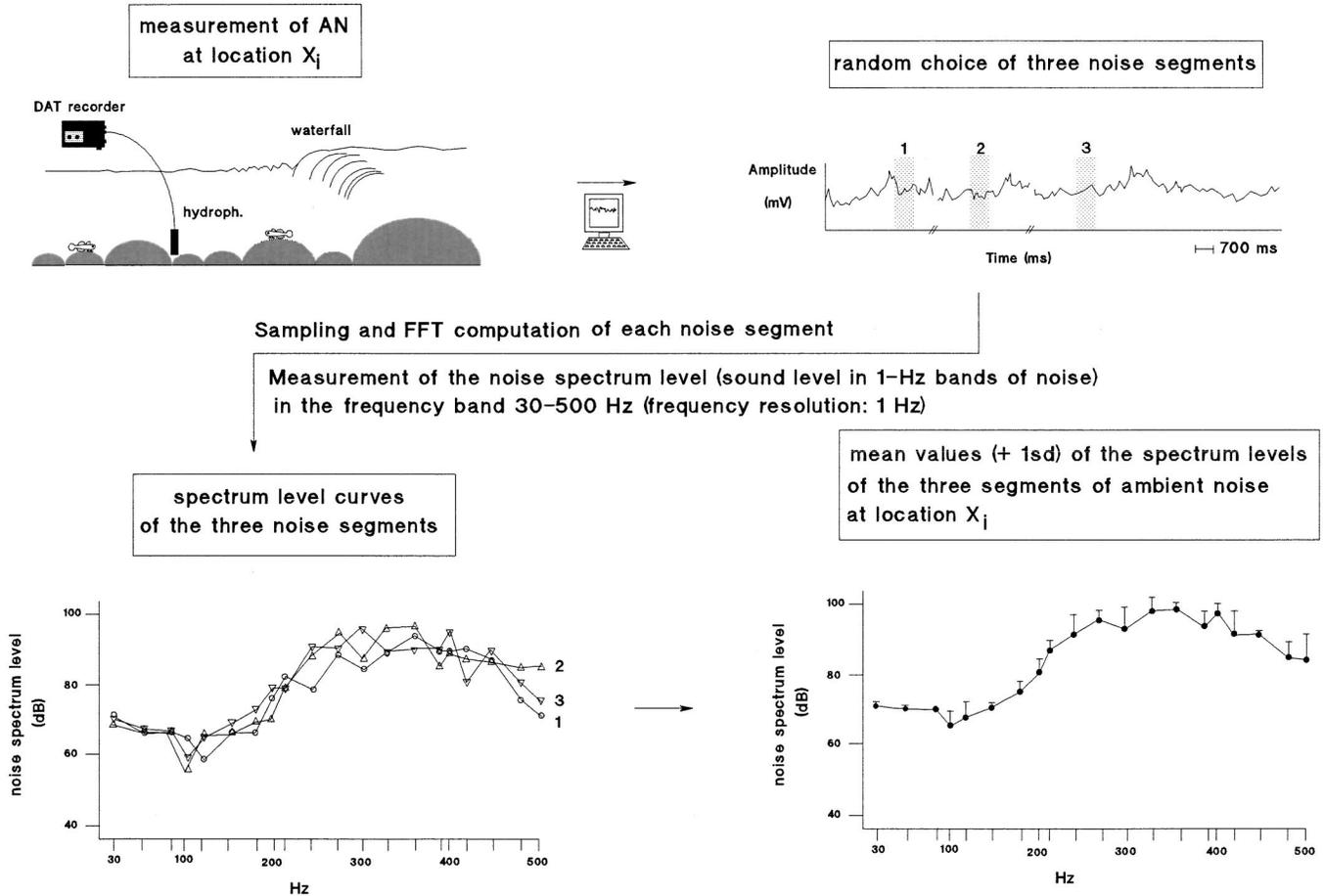
FIG. 1. Schematic diagram and main phases of the characterization of the ambient noise in the stream and in the laboratory. AN=ambient noise.

location of Stream Stirone. The results indicate severe constraints on acoustic communication both because of high noise levels in some subhabitats and short-range propagation of sound in shallow areas utilized by gobies for spawning. A window in the noise around 100 Hz coincides with the most sensitive hearing and the peak frequency of the sound spectrum in these fishes (Lugli *et al.*, 2003).

II. EXPERIMENTAL PROCEDURE

The study species come from two separate freshwater systems: *P. martensii* in Stream Stirone (a small hill stream located about 40 km west of Parma, Northern Italy), and *G. nigricans* in River Serchio (a small stony river located 2 km north of Lucca, Tuscany, Central Italy). The study site in Stream Stirone is 2.5 km long, with a width from 2 to 15 m, water depth usually <30 cm, and average gradient of 1.2 cm/m (Lugli *et al.*, 1992). The bottom consists mainly of flat stones and small areas of coarse gravel. Features of the stream vary greatly from place to place—due to changes in water current, depth, and bottom topography. The site in River Serchio is 14 km long, with a maximum width >50 m and a water depth up to 2 m. This river has a higher water discharge, a wider stream bed, and higher water depths than

Stream Stirone. The bottom consists of stones and coarse gravel, but the stones are clearly larger and more rounded than in Stream Stirone. Lugli *et al.* (1992) showed that the distribution of breeding individuals on the bottom is unaffected by hydrological parameters of the stream, such as water depth, current speed, or distance from the stream's banks.

A. Ambient noise measurements

Ambient noise (AN) was measured at various locations where nesting gobies were found (Fig. 1). Locations included quiet areas and sites within 4 m of small waterfalls, rapids, and other places where the water surface breaks because of the presence of a big stone producing an overfall downstream. Sites were not picked randomly but were chosen to favor sites likely to have elevated noise levels (Fig. 1).

AN was measured with a preamplified pressure-sensitive hydrophone (ITC 8073, sensitivity: −167 *re*: 1 V/μPa, frequency response: ±1.5 dB from 20 to 2000 Hz) placed on the bottom. The hydrophone was connected to a portable DAT recorder (Casio DA-7, sampling rate: 48 kHz). A single recording was made at each location for approximately 1 minute. AN measurements were made at 23 locations, of which 13 were from noisy areas, in Stream Stirone, and 16

locations, of which 10 where from noisy areas, in River Serchio.

Noise recordings were stored on a PC (sampling rate 5000 Hz), and analyzed using the AVISOFT software package for sound analysis. All recordings were low-pass filtered at 1 kHz to examine the low-frequency spectrum of the stream. For quantitative and statistical purposes, they were later bandpass filtered (30–500 Hz) to focus on frequencies important for goby acoustic communication. The AN spectrum was determined from three noise segments of approximately 700 ms that were randomly selected from each recording (Fig. 1). Segments were analyzed for noise spectrum level (the sound power in 1-Hz bands of noise, dB re: 1 $\mu Pa^2/Hz$) and total noise-pressure level in the 30–500-Hz band (i.e., the band-pressure level). The spectrum level was determined at intervals of 30 Hz (i.e., 30, 60, 90, 120 Hz, etc.), and also for the test frequencies 70, 100, 200, 400, and 500 Hz used for hearing threshold determinations in a companion study (Lugli *et al.*, 2003). The band-pressure level was calculated as the logarithmic root-mean-square pressure (SPL re: 1 μPa). The noise spectrum level and the band-pressure level were computed using the power spectrum and rms functions of AVISOFT, respectively. Decibel values of both noise parameters referenced to 1 V were converted into absolute measurements using the appropriate calibration factors for all components of the measuring system (i.e., hydrophone sensitivity, gain of the DAT recorder, gain of the sound card of the PC). Data from the three noise segments were used to compute the noise spectrum level curve as follows:

$$SLf = 20 \times \log[\Sigma_i(\exp10(SLf,i/20))/3], \quad dB$$

where SLf is the noise spectrum level at frequency "f", and SLf,i is the noise spectrum level at frequency "f" of the ith noise segment ($i = 1-3$). Similarly, the band-pressure level (BL) of the ambient noise was computed using the above formula, with SLf replaced by BL, and SLf,i replaced by BLi, i.e., the band-pressure level of the ith noise segment. The noise spectrum level measurements from each location were used to compute the average spectrum of the stream ambient noise at each frequency ($n = 21$) from 30–500 Hz. The mean spectrum level was calculated by averaging the values of SLf (dB) among a given group of locations (quiet and noisy). In addition, the mean spectrum was also calculated only among the group of five locations of the stream with the highest band-pressure levels. The purpose was twofold: to compare the AN close to the heaviest noise sources in the two streams, and to examine the relationship between AN at noisiest places of the stream and the hearing sensitivity of the fish (see Lugli *et al.*, 2003). Besides the mean level, the spectrum level standard deviation (i.e., the standard deviation of SLf) was calculated to estimate the environmental variability of spectrum levels at each frequency. Because only one noise measurement (i.e., only one replicate) was made at each location in the stream, the standard deviation of the mean spectrum levels is an unbiased measure of the environmental variability of the noise level at a given frequency.

B. Noise and sound propagation in Stream Stirone

In addition to single AN measurements at representative sites of the stream, multiple AN measurements were made at two sites of Stream Stirone to study the variability and propagation of AN close to small waterfalls. Variability was determined by recording AN at three locations in a pool below a waterfall (site 1). The three locations were chosen randomly within a small area, about 1 m from the water fall. AN propagation was measured both underwater and above the water surface (site 2) along a transect at 1, 2, 3, and 5 m from a waterfall with depths of 45, 20, 40, and 70 cm, respectively. The transect was positioned to the side of the main channel to minimize the effects of noise generated by rapidly moving water. The air microphone (a miniature condenser microphone with a sensitivity 15 mV/Pa and a frequency response flat in the range 0.01–2 kHz) was manually held about 40 cm above the water surface, with the sensitive element oriented towards the waterfall. The underwater and air recordings were made simultaneously on the left and right channels of the DAT recorder, respectively. As before, three 750-ms segments of the recordings were averaged to quantify spectrum level variability (see figure legends for further details). Spectrum levels (dB re: 1 $\mu Pa^2/Hz$ for underwater measurements, or 20 $\mu Pa^2/Hz$ for air measurements) were also computed from a 10-s noise sample (FFT length of 1024 samples, Hamming window and resolution of 3 Hz) at sites 1 and 2 to ascertain whether the differences between locations were real or an artifact of short-term temporal variations.

Propagation of *P. martensii* courtship sounds was also measured in the stream. Sound production was elicited by presenting three territorial males with a ripe, conspecific female inside a small plastic-mesh cage, placed in front of the nest entrance. The caged females elicited courtship sounds, which were monitored by orienting a small, directional Gulton Industries model GLN 9190 hydrophone (sensitivity: −200 dB re: 1 μPa, frequency response flat ± 1 dB from 10 to 2000 Hz) toward the male. The hydrophone signal was amplified by 40 dB with a Sensor Technology model SA02 preamplifier and recorded onto the DAT. The hydrophone was placed at approximately 5, 20, and 40 cm from the calling male (the exact distance depended upon positioning the hydrophone in relation to the complexity of the bottom), and we recorded multiple sounds for each male at each distance. After the recording, water temperature was measured with a digital thermometer, and the male was netted and measured for total length in millimeters. Sound-pressure level was calculated for the fundamental frequency of the sound as the logarithmic root-mean-square pressure (SPL re: 1 μPa) using the power spectrum function of AVISOFT (bandwidth: 10 Hz, Hamming window) and converted to absolute dB (re: 1 μPa) using the appropriate calibration factors for all components of the measuring system. Levels of at least five sounds of each male at each distance were averaged to determine transmission loss.
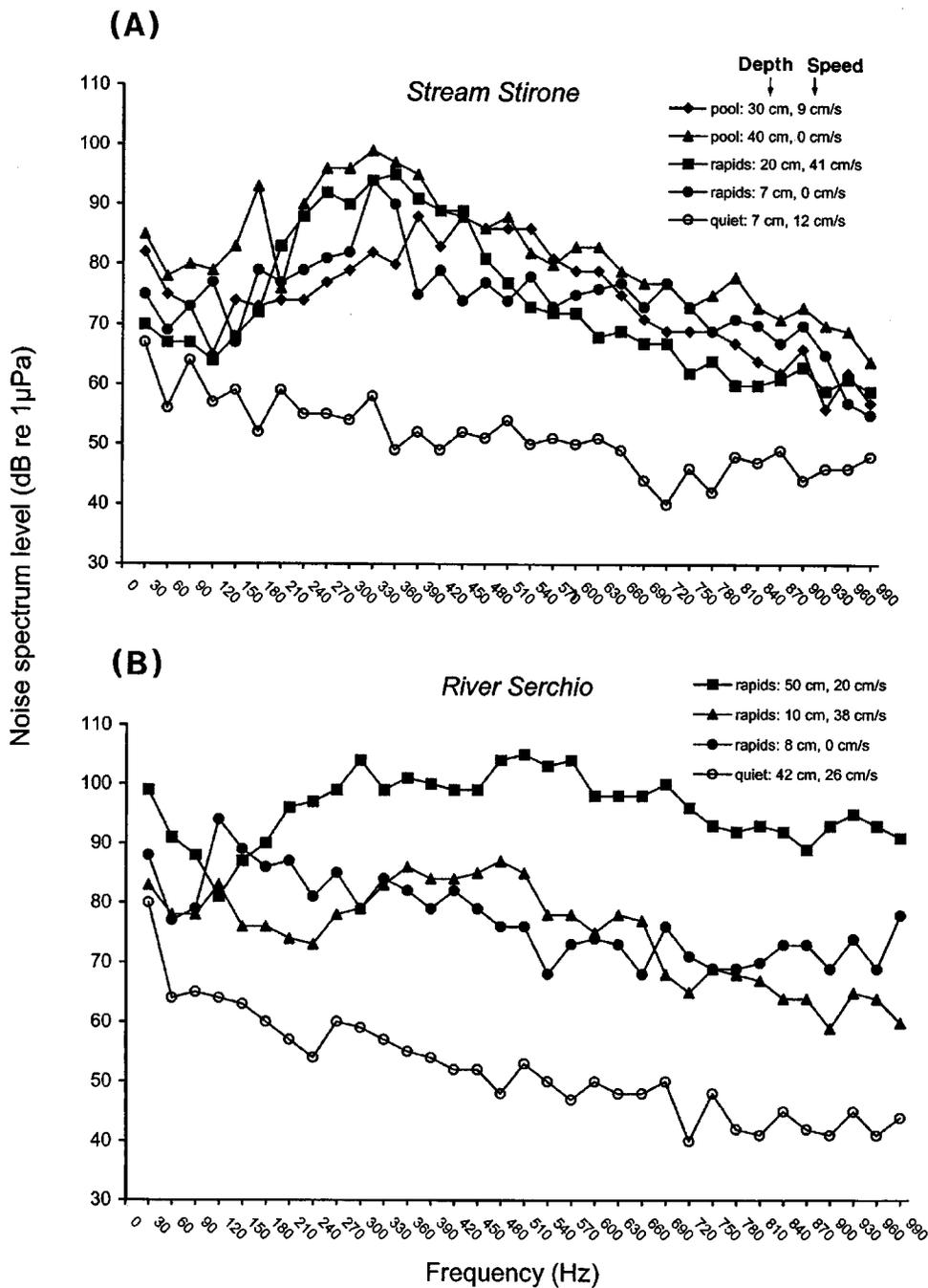
FIG. 2. Ambient noise spectra at four noisy locations and one quiet location from Stream Stirone (A), and at three noisy and one quiet location from River Serchio (B), along with the characteristics of the location (type of location: POOL = hydrophone on the bottom of a pool located below a small waterfall, RAPIDS = hydrophone close to small rapids; water depth, cm; water speed, cm/s). Note spectra of Stream Stirone were similar at noisy locations despite differences in type of location, depth, and water speed, whereas those of River Serchio exhibited greater variability in spectrum shape.

III. RESULTS

A. Stream ambient noise and comparison between streams

Ambient noise (AN) spectra in the frequency range 0.03–1 kHz from quiet locations of both streams have similar shapes and spectrum levels that are usually below 70 dB (*re*: 1 μPa) (Fig. 2). Noise levels are high at low frequencies and fall off with increasing frequency (see also Fig. 3). At noisy locations, however, levels increase at all frequencies, and a variety of spectrum shapes is observed, particularly from River Serchio (Fig. 2). The noise spectra from Stream Stirone are similar in shape, despite differences in the noise source (i.e., waterfall vs rapids), water depth, and current [Fig. 2(A)]. These spectra share a region between 60 and 150 Hz with decreased noise levels. Levels increase to a peak

between 300–450 Hz and then decrease by about 5 dB per 100 Hz to 1 kHz. Noisy spectra from River Serchio are more variable than those from Stream Stirone. For example, the curve with highest noise levels [squares, Fig. 2(B)] has a minimum at about 120 Hz, increases by 25 dB to about 500 Hz, and then decreases gradually to 1 kHz. Another curve (circles) has a low-frequency minimum at 60 Hz, a peak at 120 Hz, followed by a decrease to about 600 Hz. The greater variability of AN spectrum shape at River Serchio is statistically supported by converting spectrum level values between 30 and 500 Hz from noisy locations into ranks and comparing them with Kendall's concordance test (Siegel and Castellan, 1988). There is a significant concordance in spectrum shape among locations in Stream Stirone ($W = 0.696$, chi-square $= 79.3$, $P < 0.01$, df $= 20$) but not in River
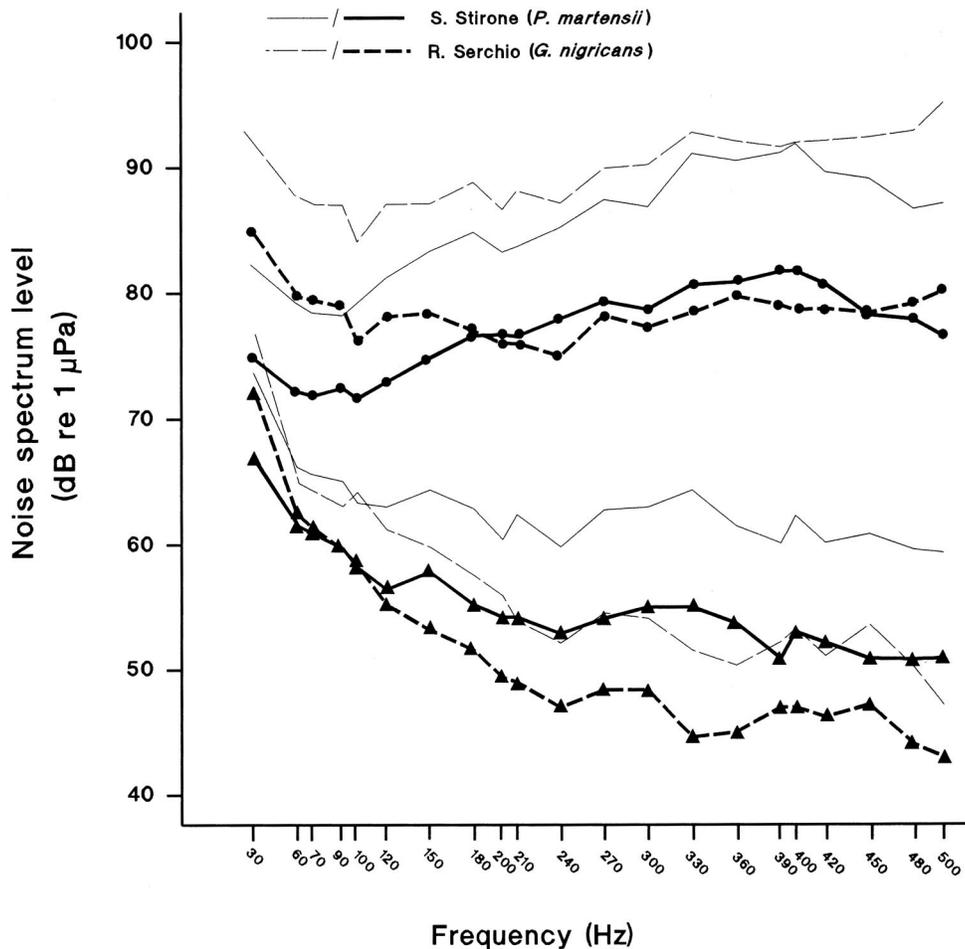
FIG. 3. Mean (thick lines) + 1 s.d. (thin lines) ambient noise spectrum levels at noisy (circles) and quiet (triangles) locations of Stream Stirone and River Serchio. The curve connecting points at 1 s.d. above the mean spectrum level (i.e., the s.d. curve) estimates the environmental variability of the noise levels above the mean level. Notice the flatness of the mean noise spectrum level curve from noisy areas of River Serchio, although a notch at 100 Hz is present in the s.d. curve (see also Fig. 5), and the lower spectrum levels at around 100 Hz (i.e., the quiet window) in the mean spectrum from noisy areas of Stream Stirone.

Serchio ($W = 0.127$, chi-square $= 24.0$, ns; df $= 20$). Levels at noisy locations are also different between streams. Although the total noise level from noisy locations in River Serchio ($n = 10$) and Stream Stirone ($n = 13$) does not differ (ns, Mann-Whitney U-test), mean spectrum levels below 100 Hz are 10–15 dB higher in the River Serchio (Fig. 4). The spectrum level differences between the streams decreases from 100 to 150 Hz, and values are similar at higher frequencies (Fig. 3). Note for Stream Stirone, the mean spectrum for noisy locations and particularly for the five noisiest locations (Fig. 4) exhibits a narrow region of lower AN levels around 100 Hz. By contrast, the shape of the mean spectrum for River Serchio is remarkably flat above 30 Hz, regardless of whether it is computed from the ten noisy locations or from the subset of five noisiest locations. This feature of the AN mean spectrum from River Serchio is consistent with the variety of spectrum shapes observed close to sources of AN in this stream. A remarkable feature of the AN at River Serchio is the presence of a ''notch'' at 100 Hz in the s.d. curve of the mean spectrum, particularly from noisiest locations (Fig. 4). The 100-Hz notch may also be a characteristic of individual AN spectra in this stream [see an example in Fig. 2(B)].

B. Short-range propagation and variability of waterfall noise in the Stream Stirone

Noise spectra close to the waterfall at site 1 [Fig. 5(A)] exhibit wide variation in both level and shape despite the short distance between the three selected locations. The frequencies with highest and lowest amplitudes differ among spectra. Note, however, the presence of relatively low noise levels at lower frequencies in two spectra, with minima at 90 and 180 Hz, respectively. Noise spectra determined from 10 s of sampling [Fig. 5(B)] have similar shapes to those in Fig. 5(A), indicating that the spatial differences observed are not due to short-term temporal variations in AN.

The underwater noise spectrum 1 m from the waterfall at site 2 (Fig. 6) has a quiet notch of 82 dB around 100 Hz and maxima around 250 Hz (105 dB) and 420 Hz (104 dB), followed by a gradual but variable decrease in noise level. The noise spectrum from a 10-s sample (Fig. 7, top graph, circles) is similar to the shorter samples (Fig. 6), except for a less deep notch at 100 Hz and a lower peak at 420 Hz. This shape of the AN spectrum is typical for the noisy locations in Stream Stirone (see Fig. 2). Noise spectra from locations 2 or more meters from the waterfall (Figs. 6, 7) have lower spectrum levels at all frequencies and irregular shapes using both procedures for spectrum level calculation (i.e., average value of three 700-ms noise segments or determined from 10 s of sampling). Noise levels at individual frequencies do not vary with distance from the waterfall, except for occasional frequencies (e.g., 30 Hz, 480 Hz, Fig. 6), or narrow frequency ranges (e.g., below 80 Hz, 350–480 Hz, Fig. 7, top graph). Therefore, most of the noise energy from the waterfall attenuates rapidly in these shallow depths (water depth gener-
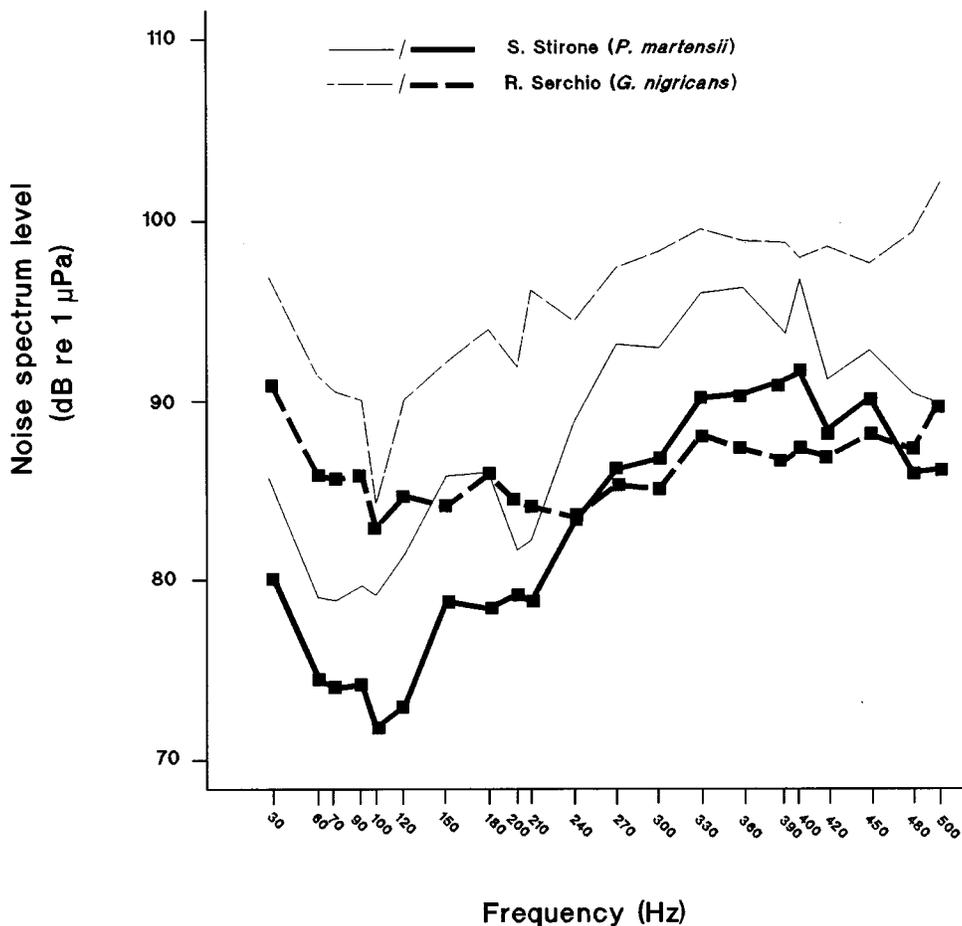
FIG. 4. Mean (thick lines) + 1 s.d. (thin lines) AN spectrum levels from the five noisiest locations of Stream Stirone and River Serchio. Notice the deeper notch at 100 Hz in the s.d. curve, contrasting with the relatively flat mean spectrum level curve, at River Serchio, and the more marked quiet window at Stream Stirone (compare with AN spectra reported in Fig. 3).

ally <50 cm). Note that at frequencies above 540 Hz (Fig. 6, 7), noise levels at the location 5 m from the waterfall tend to exceed those at locations 2 and 3 m from the waterfall. Water height is 70 cm at this location, and 540 Hz is the value of the cutoff frequency for this depth over a rigid bottom (Officier, 1958). Therefore, it is likely that increased noise at higher frequencies is generated by flowing water in the nearby channel. The AN spectrum above the water surface 1 m from the waterfall (Fig. 7, bottom graph) has little or no energy below 200 Hz and maxima around 500 Hz (29 dB), and thereby demonstrates no relationship with the underwater spectrum at the comparable distance (Figs. 6, 7, top graph). In addition, levels of the waterfall noise frequencies exhibit the expected increased attenuation with distance.

C. Propagation of *P. martensii* sounds in Stream Stirone

Sounds were recorded from nest sites in quiet, shallow places (depth<50 cm) over a stony bottom with low current speeds. The three males were 58-, 72-, and 79-mm TL, and water temperature varied from 19.8 °C to 23.8 °C across recordings. Transmission loss is large in all cases (Fig. 8), with attenuation of 15–20 dB from 5 to 20 cm (all males) and by 30 dB from 8 to 45 cm (one male). No sound is heard with the hydrophone placed 60 cm or more from the nest. Presuming a loss from cylindrical spreading (3-dB/distance doubled), a distance from 5 to 20 cm would account for 6 dB

of loss (two doublings). Therefore, 9 to 14 dB of the 15–20-dB loss would be due to absorption within 15 cm, which is equivalent to a loss of 60–90 dB/m.

IV. DISCUSSION OF RESULTS

A. The stream ambient noise

An extensive literature exists on ambient noise in the ocean (Knudsen *et al.*, 1948; Wenz, 1962; Zakarauskas, 1986) and its sources (reviewed in Urik, 1983). Generalized AN spectra of deep water and water over the continental shelf (depth<200 m) have relatively high noise levels at low frequencies that decrease with increasing frequency (Wenz, 1962). Wide daily and seasonal variations occur at individual locations due to changing weather conditions and types of noise sources. Variability of noise levels is highest in shallow, or very shallow environments, where water depth becomes a critical factor for sound propagation (see below), and wind and wave motion become increasingly important (Urik, 1983). When shipping or biological sources of noise are absent, AN in estuaries is strongly dependent upon wave action, fluctuating widely in relation to prevailing weather conditions. AN levels at low frequencies may be as low as 20–30 dB (pressure spectrum level, dB *re*: 1 μPa) in these very shallow-water environments under calm conditions (Fine and Lenhardt, 1983).

The abundance of literature on AN in the sea contrasts with the paucity of studies in freshwater environments.
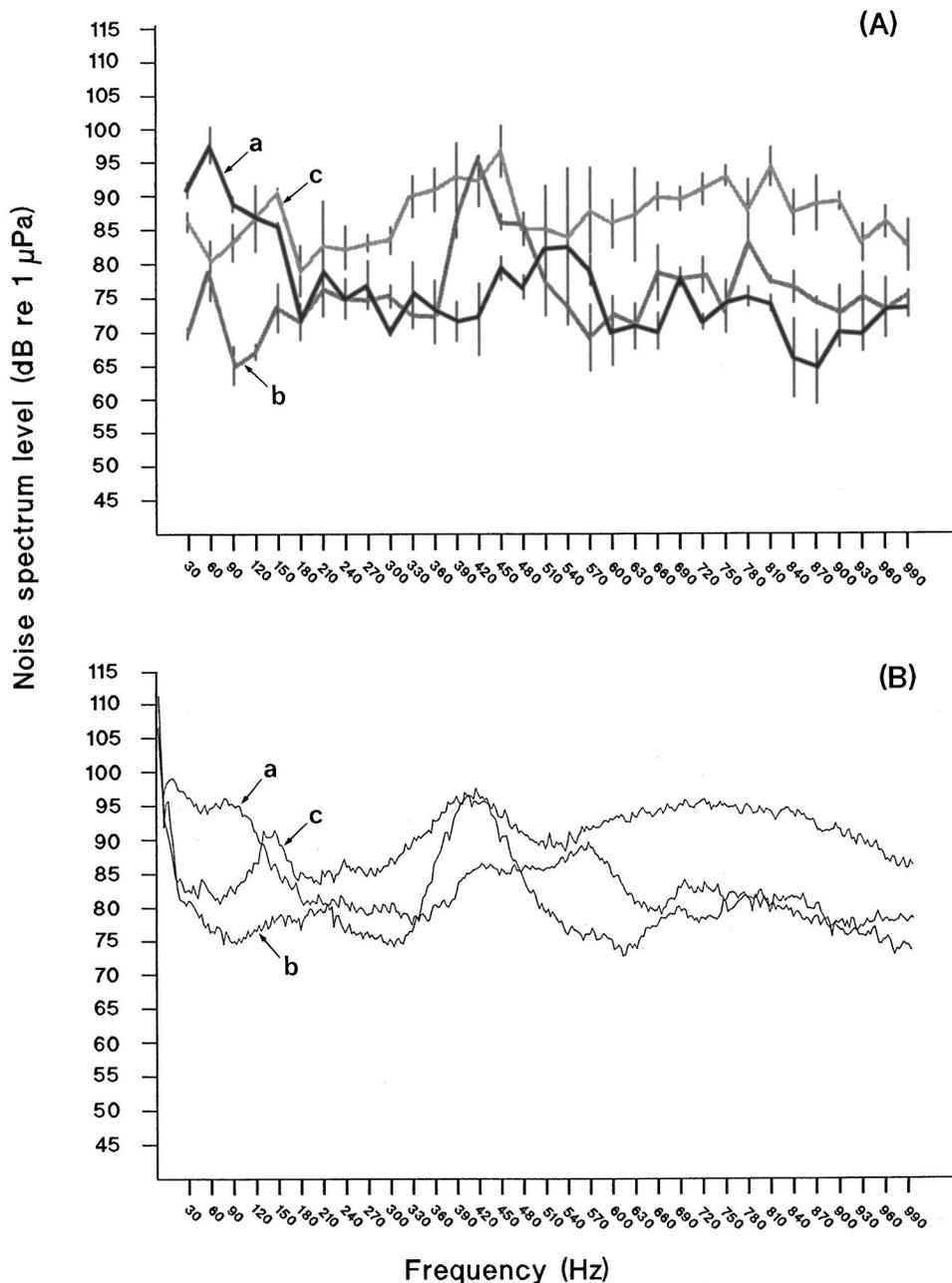
FIG. 5. Variability of AN spectrum in a pool below a small waterfall of the Stream Stirone (site 1). AN was measured at three locations (a, b, and c) chosen randomly within a range of 1.5 m. Water depth was 80, 5, and 15 cm at location a, b, and c, respectively. (A) means (±1 standard error) are SL*f* values computed by averaging spectrum level measurements from three 700-ms segments as indicated in Sec. II (see also Fig. 1). (B) the AN spectrum at the three locations computed using a 10-s noise segment taken from the same recordings.

Hawkins and Johnstone (1978) found 5–10-dB higher noise levels in the River Dee than in the sea (Loch Torridon) at frequencies of 30–100 Hz, whereas above 150 Hz, and at sea state 3, noise levels were comparable. Highest noise levels measured in the river were around 75 dB *re*: 1 μPa, although Hawkins and Johnstone (1978) predicted even higher levels close to noise sources such as a waterfall.

In the present study, AN spectra were obtained at both quiet and noisy places in two habitats (River Serchio and the small Stream Stirone), which differ in hydrological parameters (stream bed width and average water depth) and bottom characteristics (size and shape of stones on the bottom). However, considering the overlap of AN levels in the streams (total and spectrum noise levels expressed as sound pressure), and the small amount of energy present above 1 kHz, the present measurements are likely representative of rock-lined shallow streams. Regardless of water current, the streams are remarkably quiet in places where the water surface is unbroken (noise spectrum levels from 40 to 60 dB *re*: 1 μPa). Such places are fairly common in the two streams because of the modest slope of the stream bed (Lugli *et al.*, 1992, for Stream Stirone). When the water surface breaks, trapping air underwater, background noise increases significantly at all frequencies, with highest increments in the 200–500-Hz band. Noisiest places in the stream (i.e., total SPL in the frequency band 30–500 Hz: 110–130 dB *re*: 1 μPa) occur near small rapids or in pools below a small waterfall. The spectrum levels at such places may differ up to 35 dB between different frequencies in the 0.03–1-kHz band of a spectrum, and they often exceed levels measured in shallow ocean at higher sea states or during heavy shipping by 10–15 dB. Furthermore, the AN spectrum may vary remarkably in both shape and level among nearby locations (<1.5 m) close to a waterfall. Large variations in AN levels between nearby
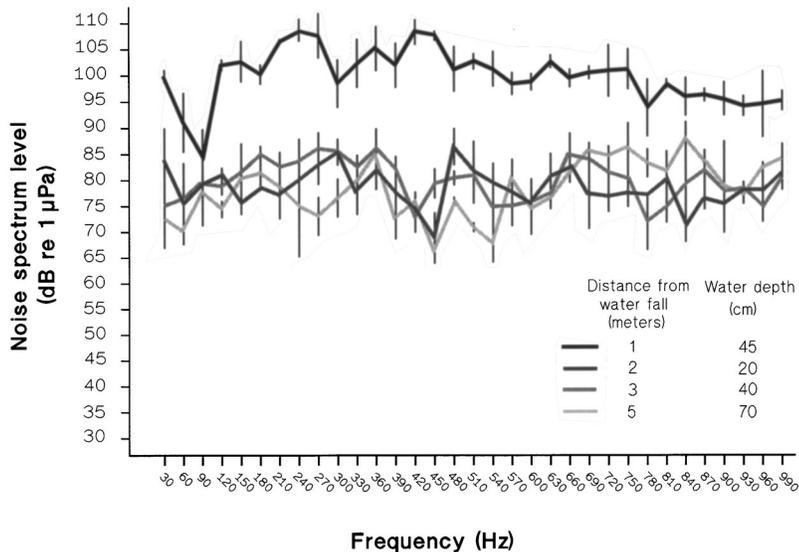
FIG. 6. Variation of AN spectrum with distance from a waterfall in Stream Stirone (site 2). AN was measured at four locations along a transect line downstream from 1–5 m from the waterfall. The bottom of the study site was mainly pebbles and stones and varied from 20–70 cm in depth among the four locations. Means and standard errors of the underwater AN spectrum computed from three 700-ms segments as indicated in Sec. II.

locations are expected because lower frequencies do not propagate at shallow depths and decay exponentially with distance from the source, i.e., the frequency cutoff phenomenon (Officier, 1958; see below).

Our measurements of AN propagation in Stream Stirone indicate that most energy of the low-frequency noise generated underwater by a waterfall is lost within only 2 m of the fall, whereas the airborne noise from the same waterfall propagates above the water surface several meters away from the source. Furthermore, regardless of the distance (i.e., 1, 2, 3, or 5 m) from the waterfall, there is little resemblance between the waterborn and airborne noise spectra at the same location, indicating that little of the acoustic energy from the waterfall noise in air is transmitted to the water. Low transmission is expected because of the difference in acoustic impedance between air and water and because of the large angles (near 90°, in this case) between the noise source and the receiver, i.e., Snell's law (Urik, 1983).

A previously undescribed feature of stream AN is a quiet window around 100 Hz in many noisy locations (particularly in Stream Stirone). The window is about 130 Hz wide in Stream Stirone (Figs. 3, 4), and it is more sharply tuned at 100 Hz, i.e., resembling a notch, in River Serchio (Fig. 4).

The 100-Hz "notch" in the AN spectrum occurs between two sources of water noise, which we attribute to water turbulence at the low end, and waterfalls and rapids, the equivalent of wave action in the ocean at the high end (Urik, 1983). Water turbulence is the likely source of AN (i.e., turbulence noise) at frequencies below 100 Hz since underwater currents in the sea generate turbulence noise in the 1–100-Hz band (Wenz, 1962; Urik, 1983). In the stream, propagation of low frequencies is further constrained by the low water depths (Urik, 1983). Therefore, low-frequency noise originating from water turbulence is likely to be a significant component of stream AN at places near or inside a turbulence zone. Two findings of the present study support this
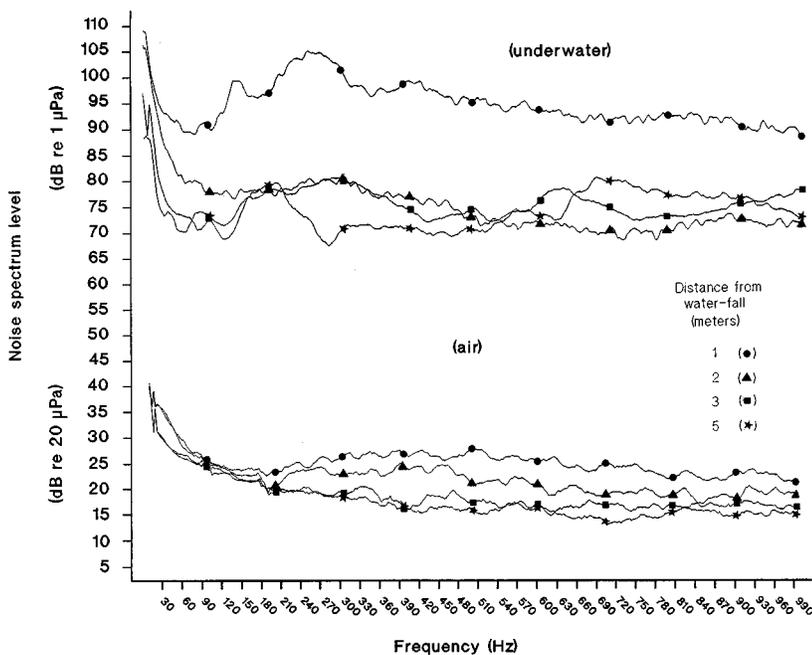

FIG. 7. Top graph: the underwater spectrum at the four locations of Fig. 6 computed using a 10-s noise segment taken from the same recordings. Bottom graph: the spectrum of the waterfall noise propagating above the water surface computed using a 10-s noise segment taken from recordings with the air microphone at the four locations.
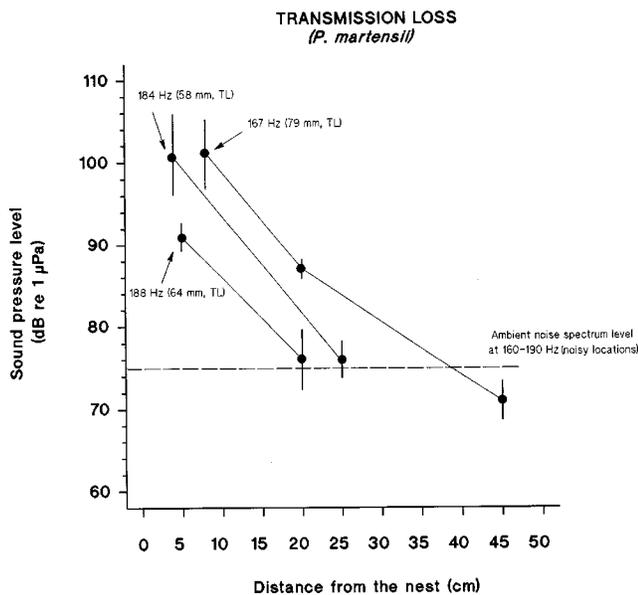
TRANSMISSION LOSS
(P. martensii)

FIG. 8. Transmission loss with distance (cm) for the fundamental frequency of sounds emitted by three male *P. martensii* courting a conspecific, ripe female in the field (Stream Stirone). Sounds were emitted by the male at the nest entrance. Mean pressure levels (dB *re*: 1 μPa) of the fundamental frequency (at around 180 Hz) were computed from five sounds at each distance. Differences in fundamental frequency between males are explained by water temperature (Torricelli *et al.*, 1990). In addition to the sound levels, the mean ambient noise spectrum level at 180 Hz from the noisy locations of Stream Stirone (see Fig. 3) is reported for comparison.

hypothesis. First, measurements of propagation in Stream Stirone indicated that AN levels at frequencies below 100 Hz decrease with distance from the waterfall (see Figs. 6, 7), a result consistent with decreasing water turbulence at greater distances. Second, River Serchio has a higher water discharge and, presumably, higher pressure changes associated with water turbulence than Stream Stirone, which is consistent with higher low-frequency noise levels measured in River Serchio (see Fig. 3).

Small waterfalls and rapids are likely sources of stream AN at frequencies above 100 Hz. Prosperetti (1985) and Carey (1985) suggested that entrainment of clouds of air bubbles below the surface during wave action may be a significant source of energy of AN below 1 kHz in the sea. Laboratory investigations indicated main energy of collective bubble cloud oscillations resting in the 200–600-Hz band (Yoon *et al.*, 1991). The stream environment is characterized by abundant water splashes and formation of air bubbles underwater, with most of the energy close to waterfalls and rapids falling in the 200–500-Hz band. Presumably, water splashes and air bubbles are important interrelated sources of low-frequency ambient noise in the stream, as are wind-dependent bubble and spray noise in the ocean (Franz, 1959; Wenz, 1962; Prosperetti, 1988).

The combined effects of turbulence noise and bubble noise, as inferred from studies on sources of oceanic ambient noise and observations of the present study, would leave a narrow region (a "notch") of relatively low noise levels around 100 Hz, a feature common to the mean spectrum from noisy locations of both streams.

B. Sound propagation in the stream

Acoustics of very shallow water (estuaries, rivers, and ponds) is more complex than of deeper waters because of the proximity of the surface and the bottom (Rogers and Cox, 1988). Additionally, water depth strongly constrains low-frequency communication in shallow water because no frequency corresponding to a wavelength longer than approximately four times the water depth will propagate underwater, i.e., the frequency cutoff phenomenon over a rigid bottom (Officier, 1958; Rogers and Cox, 1988). For example, frequencies below 750 Hz will not propagate in water with a depth of 50 cm or less, and *P. martensii* and *G. nigricans* emit sounds with main frequencies in the 80–200-Hz band (Lugli *et al.*, 1995, 1996b, and Lugli *et al.*, 2003). These frequencies are well below the cutoff frequencies of the stream (0.8–7 kHz for water depths from 5 to 50 cm) over a rigid bottom (Officer, 1958). Our field measurements of courtship sound transmission in *P. martensii* indicate an attenuation of 15–20 dB over 20 cm at depths <50 cm. Due to the low amplitude of these sounds (90–120 dB at 5–10 cm, Lugli *et al.*, 1995; Lugli *et al.*, 2003), calls are lost in noise 50–60 cm from the source, even under quiet conditions. Attenuation is far higher than previously measured for fish sounds, and is similar to values of aquatic insects singing at frequencies >2 kHz in 21-cm-deep freshwater (Aiken, 1982).

The effects of the high transmission loss of the sound in the stream, the low sound amplitude and auditory sensitivity of *P. martensii* and *G. nigricans* (see Lugli *et al.*, 2003) combine to restrict acoustic communication in these species to only a few decimeters from the calling male. Playback sounds broadcast to *P. martensii* in laboratory tanks may attract individuals (aggressively aroused males or ripe females) as far as 40 cm away from the speaker (Lugli *et al.*, 1996a; Lugli, 1997), and they are probably not heard at distances greater than 50 cm (Lugli, 1997, personal observation). However, since the average distance between neighboring male *P. martensii* in the stream is also around 60 cm (Lugli *et al.*, 1992), and females are interspersed among male territories, there is probably no need for long-distance acoustic communication in this species.

Short-range communication in territorial shallow-water fishes (freshwater, estuaries, coastal waters) has been reported by other authors (Tavolga, 1958; Gerald, 1971; Fine, 1981; Fine and Lenhardt, 1983; Mann and Lobel, 1997) although propagation occurred over several meters. Attenuation was not as extreme as in the goby streams because some of the sound energy was above the cutoff frequencies in these environments. Furthermore, softer sand and mud bottoms, unlike the stones in the current study, appear to permit some degree of propagation, i.e., they don't appear to function as a rigid boundary.

Studies on acoustic communication in terrestrial environments have shown that animals have coped with environmental constraints on sound transmission by evolving sound features that maximize long-range communication (Waser and Waser, 1977; Brenowitz, 1982; Wiley and Richards, 1982; Ryan and Brenowitz, 1985; Klump, 1996). The importance of the environment on acoustic communication and

sound features among fishes is far less clear (Fine and Lenhardt, 1983; Roger and Cox, 1988; Forrest *et al.*, 1993; Bradbury and Veherencamp, 1998). This study establishes that depth and AN level are the major constraints on acoustic communication range in the stream gobies. A companion paper (Lugli *et al.*, 2003) further demonstrates that these factors appear to represent strong selective forces on the evolution of sound frequencies produced by these fishes and their hearing sensitivity.

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