Chapter 6
Habitat Acoustics and the Low-Frequency Communication of Shallow Water Fishes

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Abstract Many teleosts known to produce sounds during territorial and breeding activities live in coastal, transitional, or freshwater habitats characterised by shallow, or very shallow, water. The variability of ambient noise levels and the complexity of sound propagation conditions make acoustic communication in such environments problematic, especially at lower frequencies. Yet, use of low frequencies for communication (sound signals and hearing) is common among these species (e.g. toadfishes, gobies, blennies, darters, sculpins). This chapter examines the relationships between environmental factors and the sound emitted by shallow water teleosts, focusing in particular on the role of the calling site and ambient noise for the sound frequencies employed for communication. Two ecological factors, nest site acoustics and noise windows, appear to favour the use of low-frequency sounds by teleosts living in shallow noisy habitats by providing higher signal-to-noise (S/N) ratios for communication. The final part of the chapter examines the variety of fish audiograms and emphasises the importance of ambient noise as a possible main environmental factor shaping the auditory sensitivity, especially among shallow water fishes. A theoretical argumentation is provided to explain how this would be accomplished.

6.1 Overview

Habitat acoustics concerns the study of the acoustic characteristics of the environment that affect the production, transmission, and reception (detection and recognition) of the sound emitted by a species in a given habitat. The way the acoustical environment affects the three stages of the acoustic communication process is examined to determine the type of environmental constraints and infer long-term (evolutionary) effects on sound and receptor systems. For instance, sound

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attenuation (spreading loss and absorption), degradation, and ambient noise may act as environmental constraints on acoustic communication (Wiley and Richards 1982). These factors are thought to be important for the evolution of long-distance vocalisations (the ‘Acoustic Adaptation Hypothesis’ of bird songs, Morton 1975, reviewed in Boncoraglio and Saino 2007), and may affect the detection and recognition of sounds. Evidence for the effects of environmental factors on acoustic signals and receptor systems has been provided for many terrestrial species, especially among birds and mammals (Bradbury and Vehrencamp 1998). For example, ambient noise (including mad-made noise) has been suggested to be a major constraint on the evolution of frequencies used in acoustic communication among birds and primates (e.g. Wiley and Richards 1982; Waser and Brown 1986; Slabbekoorn and Peet 2003; reviewed in Brumm and Slabbekoorn 2005; Brumm and Zollinger 2013).

Teleosts have the most diverse sound-producing mechanisms and hearing abilities, and live in a wider array of environments than other vertebrate groups. Yet, the relationships between the environmental constraints and sound communication are less understood than in land vertebrates. Three major reasons are the low accessibility for experimental investigation (for both technical and practical reasons; Myrberg 1996), the secretive, context-specific nature of fish sound production often characterised by low emission amplitudes (with some relevant exceptions, e.g., the midshipman humming sound; Bass 1990), and the acoustical complexity of the aquatic environment (Rogers and Cox 1988). Furthermore, although the sound-producing capability of certain fish species has long been recognised since the time of Aristotle, up until a few decades ago it was still questioned whether sound emission had any real functional significance for fish life. Consequently, the study of fish acoustic communication and the environmental pressures acting on it has lagged well behind that of land vertebrates.

In an influential paper on the physics of underwater sound propagation and detection by aquatic animals, Roger and Cox (1988) showed that general features of the fish sound production and hearing cannot be predicted by considerations simply based on the physical characteristics of the environment. For instance, sound pressure is much higher in water compared to air (about 60 times; Albers 1965) for a given value of the sound intensity. Therefore, the sensitivity to acoustic sound pressure typical of land vertebrates should also be a property of the fish ear. In fact, most fishes can detect only the particle displacement components associated with the sound wave (Kalmijn 1988; Roger and Cox 1988). Also, underwater ambient noise is highest at lower frequencies (Albers 1965). Thus, fishes should communicate acoustically using preferentially high frequencies. Another environmental constraint on the use of low frequencies for fish communication is represented by water depth because low frequencies cannot propagate in shallow waters (see below). Yet, available evidence indicates that many teleosts from the most diverse habitats, and especially those living in shallow environments (e.g. coastal areas, rivers, ponds), employ very-low–frequency sounds for territorial and mating purposes (e.g. Ladich 1989; Myrberg and Lugli 2006). Most knowledge of fish acoustic communication comes indeed from studies on the vocal behaviour of these shallow-water species (Fine et al. 1977; Ladich and Myrberg 2006; Myrberg and Lugli 2006). Because of its relevance for fish bioacoustics, the issue of low-frequency acoustic communication and possible relationships with habitat acoustics is thoroughly examined in the chapter. Before focussing on these topics, however, a few notes on acoustical features of the water medium and underwater sound transmission are necessary.

6.2 A Glimpse of Underwater Environment Acoustical Features Constraining Sound Propagation

The physics of sound propagation and the basic principles governing the interaction of sound with the physical environment are the same in air and in water (Albers 1965). However, the high density and low compressibility of water compared to air have important consequences regarding transmission of sound and acoustic information in aquatic environments. For instance, compared to air, a propagating sound wave travels faster (about five times) and with little absorption underwater. This bears two contrasting consequences for acoustic communication by aquatic animals. The sender of the sound may potentially extend the range of signal active space to distances not covered by sounds travelling in terrestrial environments (baleen whales are able to communicate acoustically over hundreds or even thousands of miles using low-frequency vocalisations). On the other side, the listener is easily, and often, exposed to a variety of noises generated by close and distant abiotic and biotic sources. Thus, an individual attending a sound relevant for fitness or survival is often faced with the problem of extracting the relevant information of the signal embedded in noise of changing and unpredictable form. When the sound is transmitted close to reflecting boundaries (i.e. air–water, water–bottom interfaces) further problems arise because direct and reflected paths of the sound may add or subtract, yielding fluctuations in the received sound level and introducing reverberations (Hawkins and Myrberg 1983; Spiesberger and Fristrup 1990). Thus, the effects of multipath propagation of the sound are prominent close to reflective surfaces (e.g. a sandy or rocky bottom) or in shallow habitats (coastal areas, small rivers, backwaters, ponds etc.), where most soniferous teleosts breed and interact acoustically (Hawkins and Myrberg 1983). For instance, the measurement of propagation of damselfish courtship sounds (*Dascyllus albisella*, Pomacentridae) conducted in a shallow reef environment revealed major alterations of spectral and temporal sound parameters at only a few metres from the source (Mann and Lobel 1997). Multipath propagation and signal degradation are not the only constraints on sound communication in shallow water. When the water depth is approximately one fourth the wavelength of the sound, the environment acts as a high-pass filter by allowing propagation only of frequencies above the critical frequency, that is, the frequency cutoff phenomenon (Officier 1958; Rogers and Cox 1988; Chap. 3, this volume). The value of the cutoff is also affected by bottom composition, being lower for hard substrates such as rocky or stony bottoms (Rogers and Cox 1988). Therefore, in shallow environments sound propagation becomes increasingly complex and strongly frequency and site dependent.

6.3 The Puzzling Paradox of Low-Frequency Communication of Shallow-Water Fishes

Soniferous fishes inhabit a variety of environments, from deep and open waters of oceans and lakes to very shallow streams and creeks, and emit sounds under different behavioural contexts (territory defense, mate attraction, distress, or anti-predator reactions, etc.) and circumstances (alone in the nest or in aggregation, during schooling or chorusing, at dusk, etc.). However, a large number of species, including many of those spending most of their lifetime in deeper waters (e.g. the midshipman, *Porichthys notatus*), emit sounds mainly during reproductive activities taking place at breeding sites located near, or on, the bottom at shallow depths. Some of these species (e.g. majority of cyprinids) are substratum egg-scatterers and do not defend nest sites or care for eggs. Others, like many cichlids, lay demersal eggs on prepared surfaces that one or both parents defend. Still others spawn inside nest cavities (a hollow under a hard submerged object, a hole between rocks, etc.) and care for eggs. Examples of the latter group are numerous and include members of several teleost families, such as gobies, toadfishes, blennids, cottids, and darters, comprising mainly bottom-dwelling species. Nest sites of these species are often found in very shallow waters (depths of 1–2 m or less), for example, small rivers, streams, ponds, or coastal waters of lakes and sea, with complex bottom topography (presence of stones, boulders, changing slope conditions, etc.), and variable substrate composition. These environments are often characterised by high levels of low-frequency background noise (below) and/or short-range transmission of low-frequency sounds due to the frequency cutoff. Therefore, the finding that teleosts from shallow habitats produce sounds and have best hearing at frequencies well below 0.5 kHz is somewhat paradoxical (e.g. Fine et al. 1977; Myrberg 1981; Hawkins and Myrberg 1983; Fay and Popper 1999; Fig. 6.3; see review Ladich and Fay 2013). The presence of physiological constraints or short-range communication constitutes suggested explanations for the paradox (Fine and Lenhardt 1983; Bradbury and Vehrencamp 1998; Lugli and Fine 2003, 2007). The acoustic communication of the stream goby represents a case in point. Two small gobies, *Padogobius bonelli* (formerly, *P. martensii)* and *Gobius nigricans*, living in very shallow streams, respectively, in northern and central Italy, emit sounds with main frequencies in the 80–200 Hz band (Lugli et al. 1995, 1996b, 2003). These frequencies are well below the cutoff frequencies of the stream (0.8 kHz for water depth of 50 cm, over a rigid bottom; Officer 1958). Indeed, sound transmission measurements in the stream showed the level of the courtship sound of *P. bonelli* (Lugli and Fine 2007) attenuated by 15–20 dB over 20 cm (at a depth of 50 cm).

The effects of the high transmission loss in the field, the low sound amplitude (90–120 dB at 5–10 cm; Lugli et al. 1995, 2003), and low auditory sensitivity of *P. bonelli* and *G. nigricans* (see below) combine to restrict acoustic communication in these species to only a few decimetres from the emitter. Nonetheless, playback sounds of *P. bonelli,* when broadcast in small laboratory tanks, are capable of attracting conspecific receivers (aroused males and ripe females) as far as 40 cm away from the speaker (Lugli et al. 1996a, 2004). Results of a field study showed distance between nests of *P. bonelli* in the stream averaged about 60 cm (Lugli et al. 1992), and females were often found interspersed among male territories. Furthermore, laboratory observations showed most sounds are emitted by the territorial male goby close to the intended receiver (a ripe female or a rival male) after the latter has been visually or chemically detected (Torricelli et al. 1986; Lugli et al. 1996a, 2004). Thus, there is probably no need for long-distance acoustic communication in these species. Acoustic communication over short distances is not unique to gobies. Many other teleosts (cichlids, damselfishes, sculpins, gouramies, blennies, other gobies) emit vocalisations only after a nearby conspecific has been detected. Propagation distances of these sounds may vary from decimetres to few metres, but are unlikely to exceed 9–10 m (reviewed in Ladich and Bass 2003; Mann 2006) even under the most favourable environmental conditions (presence of low ambient noise levels, main sound frequencies above the cutoff; Crawford et al. 1997; Mann and Lobel 1997). Curiously, low-frequency vocalisations are also used by a few teleost species whose males call from the nest site to attract distant prospective mates. Two well-known examples of such sounds are the ‘hum’ call (main energy at around 100 Hz), produced by the male midshipman (*P. notatus*), and the boatwhistle call (main energy from 100 to 200 Hz), produced by the male toadfish (*Opsanus tau*, *O. beta*). These vocalisations are emitted from nests located in 1–5 m deep water (e.g. Bass 1990) or less (Fine and Lenhardt 1983). At such shallow depths, low frequencies may be near or below the cutoff, and the sound may decay quickly with distance (Fine and Lenhardt 1983). On the other hand, high-frequency sounds may be used by species that communicate in shallow water over distances of only 5–10 cm, for example, the sounds of croaking gouramies showing main energy between 1 and 2 kHz (Ladich 2007). From these few examples it would seem that environmental constraints on sound propagation operating in shallow habitats (e.g. water depth) cannot account for the widespread use of low frequencies among teleosts living in such environments.

Short-range propagation of teleost sounds does not necessarily imply that pressures from the environment are not important for other functions of the species’ acoustic communication system. In animal communication, signal efficacy is a useful measure of the success of a signal, that is, how strongly the signal affects the receiver’s behavior (Endler 2000). Signal amplitude is an important feature affecting all components of efficacy (i.e. efficiency and effectiveness). For instance, louder sounds not only propagate farther but may provide fitness benefits to the emitter also during close-range interactions. Studies on terrestrial species have shown that louder male vocalisations may be preferred by females (Castellano et al. 2008; Ritschard et al. 2010), and promote more effective territory defence. Among fishes, sound amplitude has been found to be tightly related to body size (e.g. Takemura 1984; Myrberg et al. 1993; Ladich 1998). Larger individuals are better able to acquire and defend resources important to females (e.g. Torricelli et al. 1988), including protection of eggs and embryos (Parmigiani et al. 1988). Indeed, it has been demonstrated that louder male vocalisations are preferred by gravid females (McKibben and Bass 1998) and are predictors of dominance during fights (Ladich 1998). However, a loud sound might be heard low by a receiver exposed to high levels of masking noise or with a frequency sensitivity mismatched to the spectrum of the sound. Thus, frequency composition of the sound may crucially influence the value of the signal-to-noise (S/N) ratio of communication. Consequently, sound spectrum is an important acoustic trait which may evolve in response to pressures from the environment other than, and independently of, those constraining propagation.

Two environmental factors may help to explain why low-frequency sound communication is so common among shallow-water fishes, namely sound amplification by the nest site and the environmental pressures from the ambient noise. Both factors appear to favour the use of particular frequency bands for sound production and reception, so as to increase the S/N ratio of communication. These are examined in detail below.

6.4 Nest and Spawning Sites Acoustics and Relationships with Low-Frequency Sound Communication

Among soniferous teleosts that spawn inside cavities below a hard submerged object, sounds are mostly produced by the male in the nest. Usually these species (toadfishes, gobies, blennies, etc.) are not very selective about the type of shelter used as a nest in the field. For instance, the male oyster toadfish *O. tau* may use stones, oyster shells, or artificial covers (including tin cans or pieces of cement; Michael L Fine, personal communication) as suitable nests. Therefore, among investigators studying the acoustical behaviour of these species in the laboratory or in the field, it is a common practice to provide males with artificial nest sites, such as terracotta tiles, halves of flowerpots, or plastic pipes. These enclosures have one or two openings and, therefore, may be considered semi-open systems analogous to organ pipes with one or two open ends. As such they could affect the amplitude and frequency spectrum of the sound produced inside them. However, until recently no study was conducted to explore the acoustic properties of natural and artificial nest cavities and their effect on the sound spectrum.

One of the first attempts to investigate the phenomenon was the study of Barimo and Fine (1998) on the propagation pattern of the oyster toadfish sound. They examined the radiation pattern in the field of the sound emitted by the male calling inside a terracotta tile open at both ends. They found an elongated and bilaterally symmetrical sound field around the fish and related the directional response of the system to the hearth-shaped swim bladder. A possible interference of the nest on the radiation pattern of the sound was excluded both on the basis of theoretical predictions, by equating the tile to a waveguide possibly amplifying the sound ahead of the two openings, and by noting the sound amplitude and spectrum of two sounds (a toadfish grunt and a croaker sound), emitted at 1 m by a free-swimming fish in a pen, was unaffected by the presence of tile above the receiver. Theoretically (Albers 1965; Bradbury and Vehrencamp 1998), this is an expected result because the small size of the shelter cannot produce significant scattering of the long wavelengths of these sounds (the shelter is virtually transparent to the sound).

In another study Parmentier et al. (2006) investigated the acoustic behaviour of two carapids that emit sounds (main frequencies comprised between 0.25 and 1.6 kHz) inside invertebrate hosts (sea cucumbers and sea stars) and were able to show that attenuation by the soft tissues of the sea cucumber was negligible at frequencies of the carapids' sound. The experiment consisted of feeding pure tones (200–1,000 Hz) into a transmitting hydrophone placed inside the cloacal cavity of the sea cucumber (*Holothuria stellati*) and examining whether the probe stimuli, collected by a receiving hydrophone placed at 25 cm from it, differed from the same stimulus transmitted after the cucumber was removed. What the authors essentially did was the computation of the frequency response of the system (Bradbury and Vehrencamp 1998) represented by the sea cucumber cavity and surrounding tegument. Results showed the amplitude of sounds recorded inside and outside the sea cucumber essentially overlapped (amplitude differences in the two conditions <0.5 dB).

Recently Lugli (2012) employed a similar method to investigate whether shelters commonly used by male gobies as calling and nest sites in the field (i.e. flat stones, bivalve shells) and in the laboratory (small terracotta flower pots, tunnel-shaped concrete blocks, plastic shelters, etc.) would affect the sound (main frequencies below 250 Hz, Fig. 6.3). Contrary to the lack of an effect reported in the two previous studies for the terracotta tile and the sea cucumber, Lugli (2012, 2013) found that the 'goby shelters' may exhibit remarkable 'amplification properties' towards these sounds. Because the phenomenon also may be potentially relevant to other fish species using cavities or enclosures for their low-frequency communication and for spawning findings of these studies are examined in some detail.

Anecdotal laboratory observations showed sounds emitted by a male freshwater goby (*P. bonelli*) inside the hollow under a stone sometimes appeared louder than those emitted by the male just outside it, suggesting that the stone cavity might have been responsible for the observed sound amplification. The phenomenon was explored by measuring the transfer function (frequency response) of the shelter within a laboratory tank under a variety of experimental conditions (described below), and using different types of probe stimuli (white noise, pure tones, artificial pulse trains) and shelters, from natural (stones, bivalve shells) to artificial (plastic covers, concrete blocks, halves of terracotta flower pots). Initially, shelters were stimulated by placing the sound source inside the cavity and the hydrophone just outside, an arrangement of the source and the receiver mimicking the situation of male fish emitting the sound from the cavity towards a nearby female (or rival male) in front of the nest. Results of the acoustical stimulation of the shelter hollow with white noise (the main driving stimulus used) showed that stones and shells, when placed on sand (all shelters) or gravel (stones) substrate, amplify sound frequencies below 200 Hz, the amplitude gain (from few dB up to 20 dB, or more) always peaking below 150 Hz (Fig. 6.1). Acoustical tests were also conducted on flat stones in the stream (Lugli 2012) and bivalve shells in the lagoon (Lugli unpublished data, Fig. 6.2) using pure tones as driving stimuli, with results similar to those obtained in the laboratory.

Compared to the natural shelters, the frequency response of artificial shelters was more variable, spanning from the marked low-frequency amplitude gain by, for example, terracotta flowerpots or concrete blocks, similar to that of stones (example in Fig. 6.1), to lack of gain by light plastic tiles, the latter leaving the frequency spectrum of the sound source unchanged (a useful property if characterisation of sound spectral quality is the focus of the investigation). The use of tiles and flowerpots as nest covers is common in studies on 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). Because low frequencies may be amplified substantially by the shelter, published spectra and frequency characteristics of sounds recorded from males from the nest cavity are likely to be biased towards lower frequencies.

A remarkable finding of the acoustical tests of shelters was that peak frequency (i.e. the frequency of maximum gain) did not differ significantly among shelters differing, often considerably, in shape or size. So, for example, the mean amplitude gain of stone and the small oyster shell (*Crassostrea gigas*) peaked in both cases at around 100 Hz (examples in Fig. 6.1). However, stones and heavier artificial shelters had higher gain values than shells or light plastic shelters. Interestingly, amplitude gain could be increased by putting a load above the shelter, or eliminated completely by experimentally decoupling the shelter from the substrate (e.g. by manually lifting the shelter a few millimetres above the substrate, Lugli 2012). Similarly, if sand is manually piled on top of the shelter, gain is enhanced further at lower frequencies (Lugli 2013; Fig. 6.2). This may be one reason why the sand goby males so eagerly dig and pile sand on the nest cover (typically, a small bivalve shell or a small stone). Male sand gobies (gen. *Pomatoschistus*, *Knipowitschia*) generally emit sounds only during the mating activities inside the nest cavity (Lugli and Torricelli 1999; Lindström and Lugli 2000). These vocalisations are low-frequency pulse trains with dominant frequencies in the range 80–200 Hz (e.g. Lugli et al. 1997; Malavasi et al. 2008), that is, the frequencies amplified by the nest (Fig. 6.3). Lugli (2013) showed an artificial sand pile on top of the shell may further amplify the sound up to 8–10 dB within the same frequency range. Notably, the sand pile enhanced these frequencies also in shelters without amplification properties (plastic tiles, *Mytilus* shells, Lugli 2013). Results of a correlative study of natural nest builds in the sand goby *Pomatoschistus minutus* showed amplification was higher in shelters constructed using larger amounts of sand. Producing louder sounds may confer advantages to the emitter in terms of enhanced male

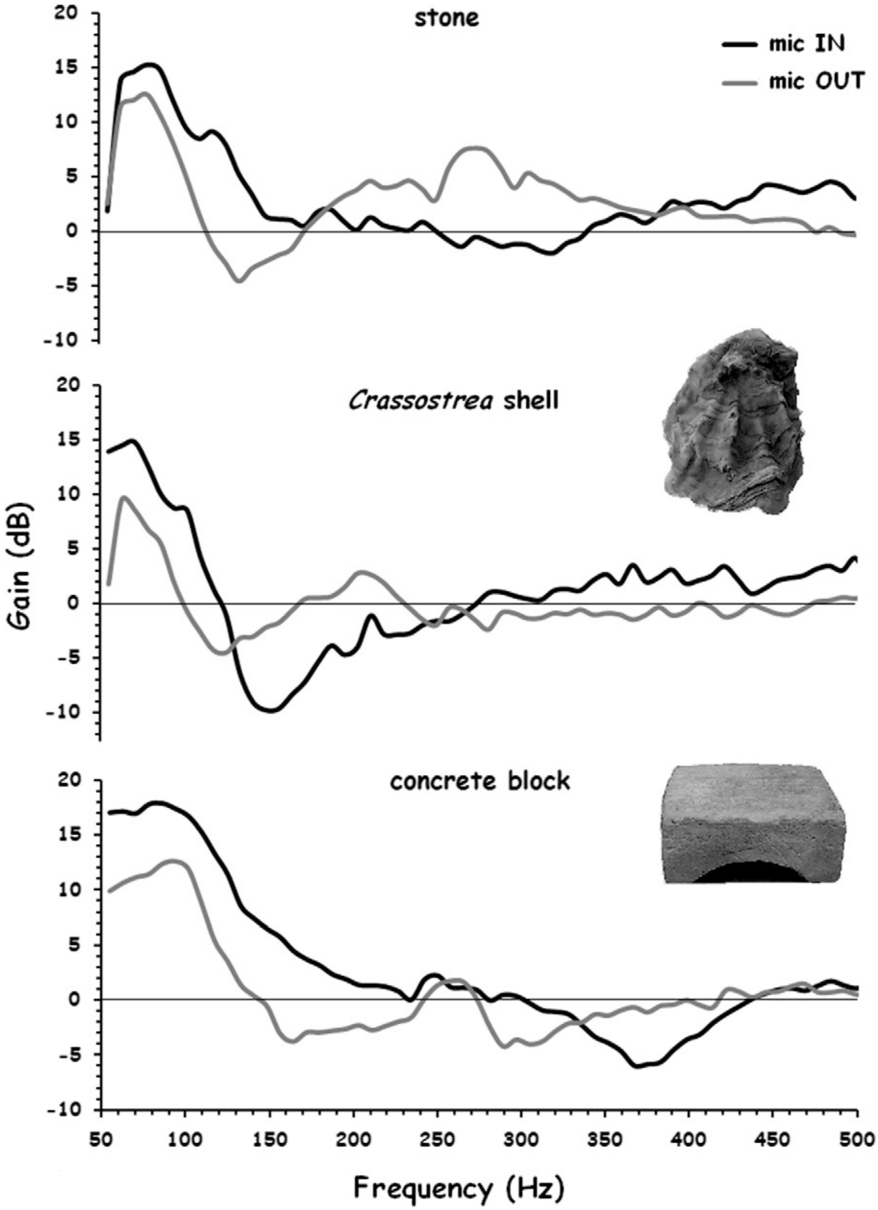

Fig. 6.1 Frequency response of a stream stone (weight: 1,400 g, basal surface: 180 cm^2), lagoon oyster shell, *Crassostrea gigas* (weight: 47.1 g, basal surface: 63 cm^2) and a small *concrete block* (weight: 290 g, see Lugli 2012 for dimensions) having a tunnel-shaped cavity, tested in laboratory twice: by positioning the hydrophone horizontally inside the cavity (mic IN) and, then, in the upright position at about 3 cm in front of the opening (mic OUT; see Lugli 2012 for experimental conditions and methods). Shelters not drawn to scale

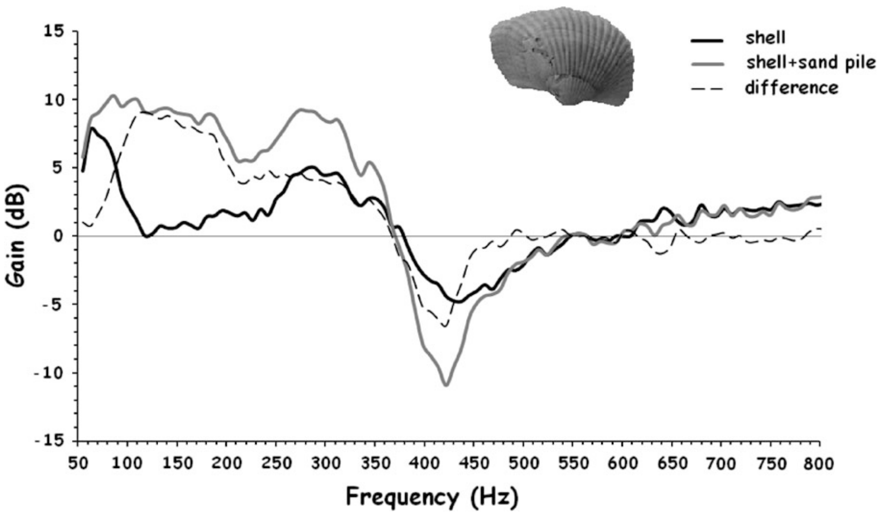

Fig. 6.2 Frequency response of a clam shell (*Scapharca inaequivalvis*, weight: 26.3 g, basal surface: 20.4 cm^2) tested in laboratory before (*black line*) and after (*grey line*) the shell was covered with an artificial sand pile. The difference between the two functions is the effect of the sand pile alone (*dashed line*; see Lugli 2013 for details)

attractiveness (McKibben and Bass 1998) and/or higher chances of attracting potential mates to the nest site due to larger active space of the sound signal. This suggests that sand piling by sand gobies might be an adaptation to increase sound amplitude and, hence, male attractiveness/reproductive success. It should be noted that gain properties of fish shelters were determined using sound frequencies below the cutoff recorded near the source (Lugli 2012). Thus, it is presently unknown whether the observed low-frequency sound enhancement by the nest is effective at greater distances and/or under conditions of sound propagation.

The use of stones or other hard underwater objects as a nest site is common to many cavity-nesting species from diverse fish families (Fig. 6.3). Therefore, the acoustical properties of the nest might have promoted low-frequency communication among these species. The presence of a close relationship between sound frequencies and gain properties of the nest may be observed by comparing the range of main frequencies of breeding sounds produced by these species (Table 6.1 in Myrberg and Lugli 2006) with the frequencies enhanced by the nest cavity (Lugli 2012; Fig. 6.3). Among the different fish taxa that use stones as a calling site the range of dominant frequencies of the sound matches, or fits, within the range of those enhanced by the stone. A similar relationship occurs between sounds of brackish sand gobies and the frequencies amplified by their nests (small bivalve shells with the sand pile, Lugli 2012, 2013). Notice among gobiids, the only two species known to spawn inside nests made of soft material (reeds, *Knipowitschia puctatissima*; burrows in the mud, *Zosterisessor ophiocephalus*), courtship sounds are produced at frequencies above those enhanced by a stone or shell

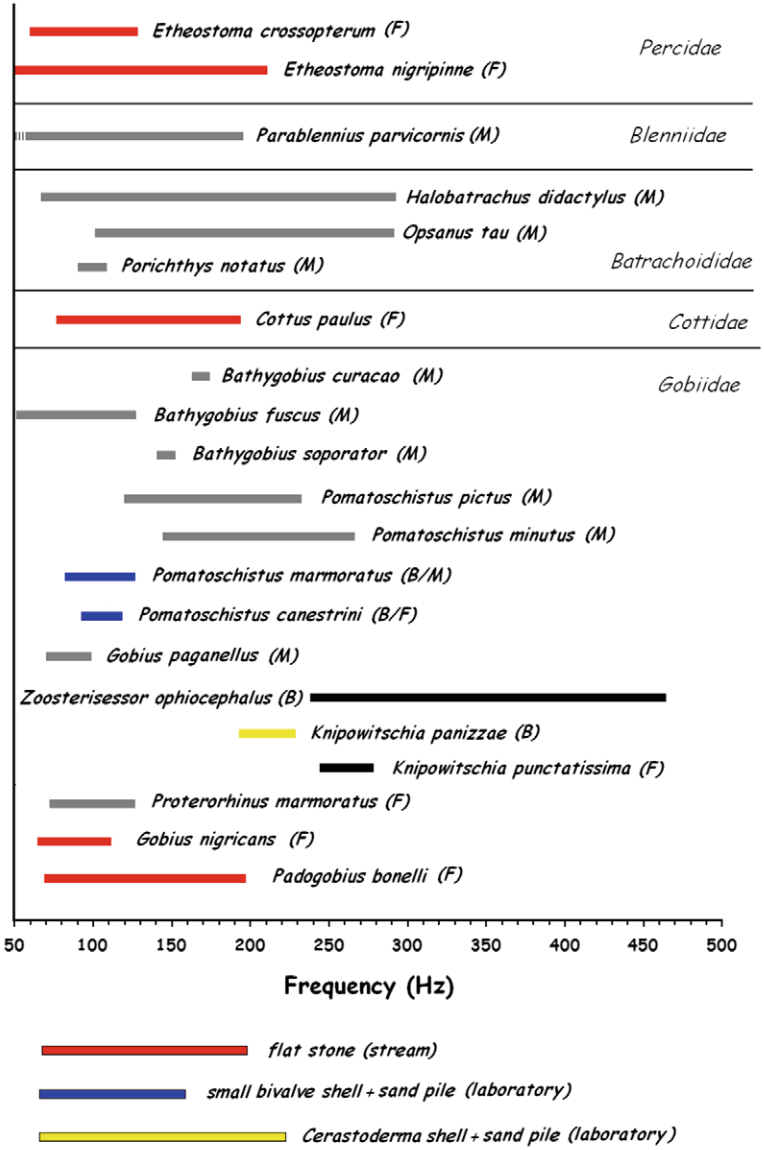

Fig. 6.3 The range of dominant frequencies (*horizontal bars*) of the courtship sounds emitted by cavity-nesting, egg-caring species from different habitats (*F* freshwater, *B* brackish lagoon, *M* coastal, marine; data from Myrberg and Lugli 2006; Lugli 2010; Amorim and Neves 2007; de Jong et al. 2007; Kierl and Johnston 2010). In all species but two (*Z. ophiocephalus*, *K. punctatissima*; *black bars*) the nest is a cavity below a hard object on the *bottom* (usually a stone or shell). For all species reported in the scheme, sound production occurs both inside and outside the nest cavity. The range of frequencies enhanced by the stream stone and lagoon bivalve shells is reported below the frequency axis for a comparison (the frequency ranges of species using these type of shelters are marked with coloured bars, whereas those of species potentially exploiting stone amplification are marked grey; data from Lugli 2012, 2013). Among gobiids, the high-frequency sounds of *Gobiosoma bosci* have been omitted from the scheme (see text)

[Note: in some cases—for instance, species producing broadband sound pulses in the nest, e.g. the sand gobies—the presence of the shelter might have biased the sound spectrum towards lower frequencies. This possibility is to be excluded for most of the goby species listed in the table (including all the sand gobies) because their sounds have always been recorded in the laboratory from males under light plastic shelters without amplification properties (Malavasi et al. 2008; Lugli 2012)].

What about the many vocal species not spawning inside cavities? A quick survey of their breeding sounds reveals these teleosts (e.g. cichlids, damselfishes, gurnards and searobins, croakers and drums, catfishes, croaking gouramis; see Table 6.1 in Myrberg and Lugli 2006; Ramcharitar et al. 2006) emit sounds with dominant frequencies usually extending well above 200 Hz. For instance, sound production among cichlids has been documented in more than 12 species belonging to different genera and differing for reproductive style (from substrate-spawning to mouth brooding) and habitat. Yet, main sound frequencies are above 300 Hz (up to few kHz), with the presence of significant acoustic energy below 200 Hz being observed in a few sounds (mainly agonistic) from a limited number of species (e.g. *Herotilapia multispinosa*, Brown and Marshall 1978).

In sum, this cursory analysis shows that species calling from cavities under cover (stones, shells) on the substrate emit low-frequency sounds with dominant frequencies below 200 Hz (the frequency range amplified by these shelters), whereas noncavity-spawning species tend to emit sounds at higher frequencies. There are, of course, exceptions to this ‘rule’, within each ‘category’. The male naked goby (*Gobiosoma bosci*) uses oyster shells as a nest site and courts ripe females by producing ‘clicking’ sounds with main energy around 2 and 4 kHz, a case of high-frequency communication unique among gobiids (Mok 1981). However, many *G. bosci* sounds in the original recordings contained a great deal of low-frequency energy heavily corrupted by background noise. Considering that all goby species whose hearing has been investigated up to now are maximally sensitive to sound frequencies below 0.5 kHz (see Ladich and Fay 2013), a study of the hearing abilities and a redescription of sounds by the naked goby would be desirable. An intriguing example of noncavity-spawning species producing low-frequency sounds is represented by the group of cyprinids living in small streams and creeks (genera *Cyprinella*, *Codoma*). These fishes are, with a few exceptions (e.g. the cavity-nesting minnow, *Codoma ornata*, Johnstone and Vives 2003), crevice-spawners, non-guarding species; yet, the territorial male emits very-low–frequency sounds (main energy below 100 Hz, typically from 40 to 80 Hz) associated with mating and territory defence (Phillips and Johnston 2009). In this case one explanation may be these species would fit the sound energy within the quiet window at around 100 Hz in the stream ambient noise (see below). However, sound emission among these species often occurs in proximity to the spawning site (a crevice in a rock, a space between stones, which rarely form a flat surface in the field). Acoustical tests conducted in the laboratory (Lugli unpublished data) showed a depression between two rocks or semi-open cavities may indeed exhibit amplitude enhancement of low frequencies when acoustic stimuli are broadcast from a speaker placed close to, or inside, these ‘crevices’. Further studies on the acoustics of the spawning environment of these species are clearly needed and results might reveal interesting and unexpected relationships with the sound.

In conclusion, cavity-spawning teleosts seem to have exploited the acoustic properties of the nest for increasing the amplitude of their sounds and, hence, the S/N ratio of acoustic communication, at least over short distances from the source. Thus, the acoustic environment of the nest site might play an important role in the evolution of low-frequency communication among these species. Because these fishes usually inhabit noisy environments, another potential environmental pressure for the low-frequency acoustic communication is represented by the habitat ambient noise. The constraining role of ambient noise on low-frequency communication is examined below.

6.5 Characteristics and Variability of Ambient Noise in Shallow Environments: Importance of Noise Windows for Sound Communication

There is an abundant literature on main sources and characteristics of ambient noise (including man-made noise) in the ocean and shallow marine environments. The topic has been reviewed by many authors (e.g. Wenz 1962; Urick 1983; Dahl et al. 2007). However, the vast majority of soniferous teleosts live and/or reproduce in very shallow marine and freshwater habitats (water depth of a few metres or below; see above), for which noise literature has only recently begun to accumulate. Furthermore, unlike land species, bioacoustical studies on vocalising fishes have seldom included a detailed characterisation of the habitat ambient noise, a necessary step towards the understanding of the role of ambient noise as a constraint for fish acoustic communication. Characterisation of the ambient noise at specific locations inhabited by fish species communicating acoustically has been recently done for very shallow, noisy environments (e.g. stony streams, near-shore marine areas, brackish lagoons, water depth <1 m; Lugli and Fine 2003; Wysocki et al. 2007; Lugli 2010; Speares et al. 2011). These habitats are probably the most unfavourable ones for acoustical communication to take place, being characterised by high noise levels (mainly from sources of bubble noise) and no sound propagation at frequencies below the cutoff (see above). Yet, a number of species from different teleost families have adapted and communicate acoustically in such environments.

Lugli and Fine (2003) measured several noise spectra at both quiet and noisy places of two Italian streams (the Stream Stirone and River Serchio), each inhabited by a different stream goby species (*P. bonelli* and *G. nigricans*, respectively). The streams were remarkably quiet in places where the water surface was unbroken (spectrum levels from 40 to 60 dB re: 1 μPa in the frequency range 0.1–1 kHz). However, at places where the water surface breaks, trapping air underwater, background noise increases significantly at all frequencies, with the highest increments in the 200–500 Hz band (Figs. 6.4 and 6.5). The spectrum levels at the

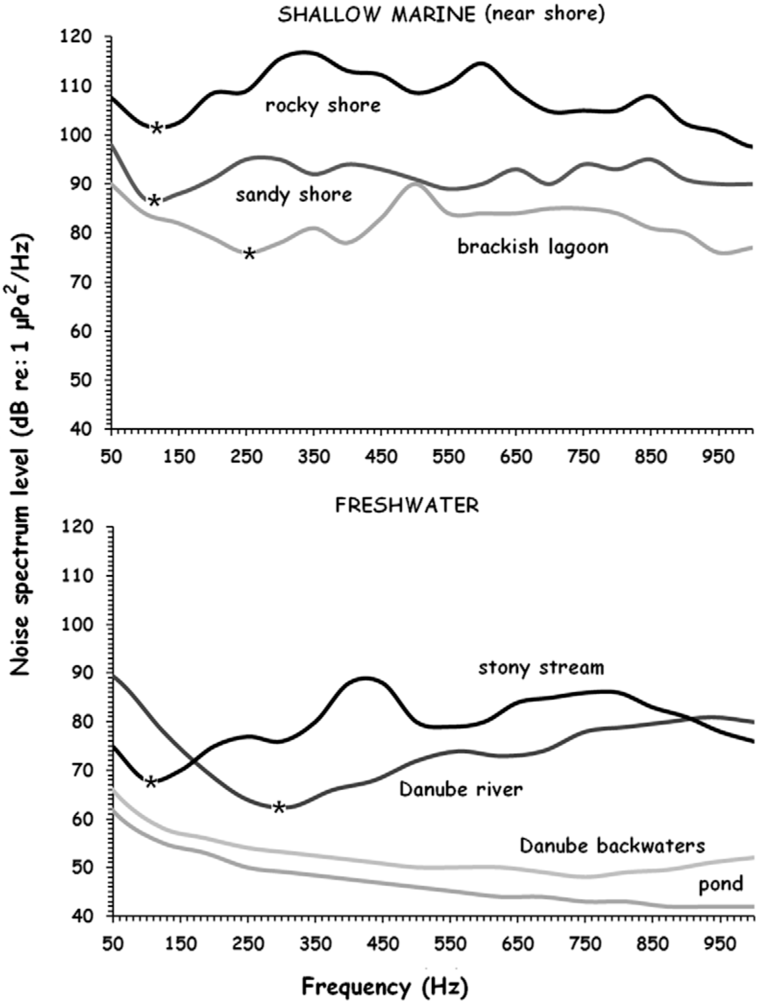

Fig. 6.4 Individual low-frequency ambient noise pressure spectra representative of the noise conditions found in very shallow marine (*upper plot*) and freshwater (*lower plot*) habitats inhabited by soniferous fishes (from Lugli and Fine 2003; Lugli 2007; Wysocki et al. 2007). Notice the presence of a frequency region with lower noise levels (termed '*noise window*' by Lugli and Fine 2003) in the noise spectrum of noisy marine and freshwater habitats (an *asterisk marks the center of the* '*window*'), and the lack of it in the two quiet freshwater habitats

noisiest places (i.e. near cascades, small rapids, pools below a small waterfall) differed up to 35 dB between different frequencies in the 0.03–1 kHz band of a spectrum, the maximum noise levels often being comparable to, or even exceeding, levels measured in the shallow ocean at higher sea states or during heavy shipping (i.e. 80–90 dB). Furthermore, the noise spectrum could vary remarkably in both shape and level among nearby locations (Fig. 6.5). Large short-range variations in

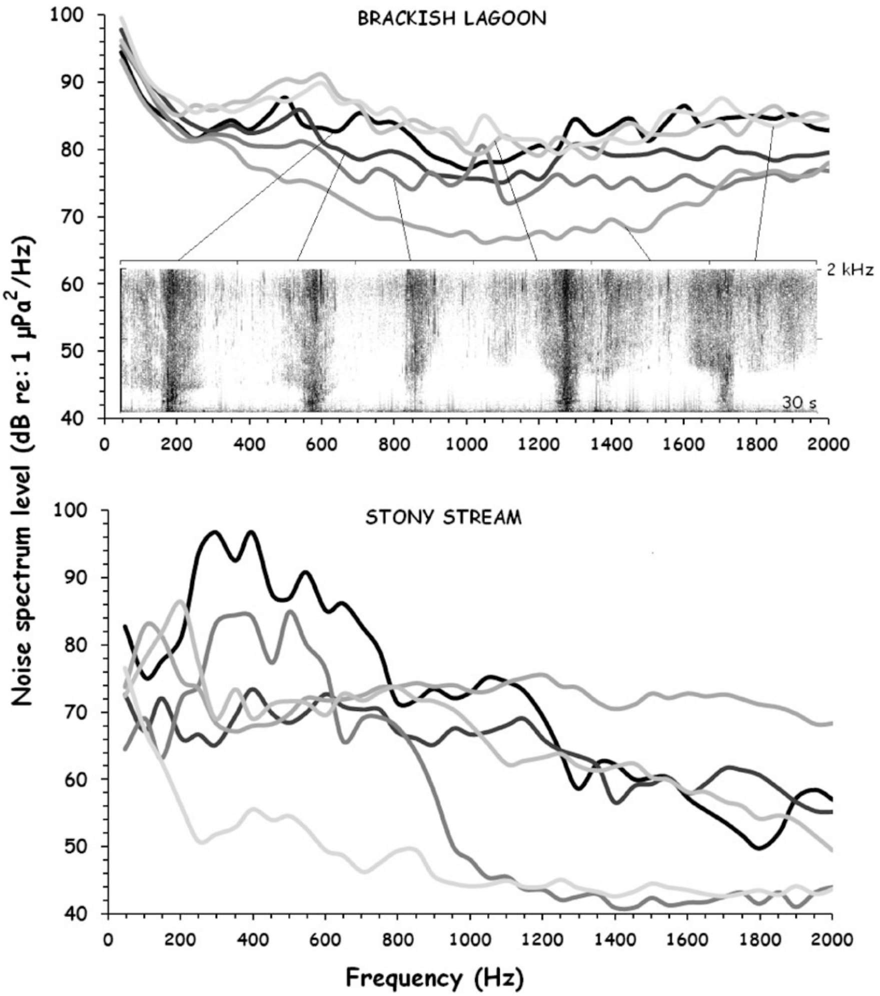

Fig. 6.5 Examples of variability of ambient noise spectrum in a lagoon (*upper plot*) and stream (*lower plot*) inhabited by soniferous gobies. *Upper plot* Temporal variability of noise spectrum determined for each subsequent 5-s segment of a 30-s continuous underwater noise recording at a fixed location of the lagoon (Sacca del Canarin, river Po delta, Northern Italy, water depth ~50 cm). Ambient noise consisted mainly of bursts of bubble noise produced by travelling breaking waves (*spectrogram below*) passing nearby the measurement location (see Lugli 2010 for further information). *Lower plot* Variability of stream ambient noise spectrum between nearby recording locations (*Stream Stirone*). Most locations were close to sources of underwater bubble noise (see Lugli and Fine 2003, 2007 for further information)

ambient noise levels and spectrum are expected in such very shallow and complex habitats with many noise sources and exponential decay of low-frequency noise energy due to frequency cutoff (Akamatsu et al. 2002; Lugli and Fine 2003). A notable feature of stream ambient noise was the presence of a relatively quiet

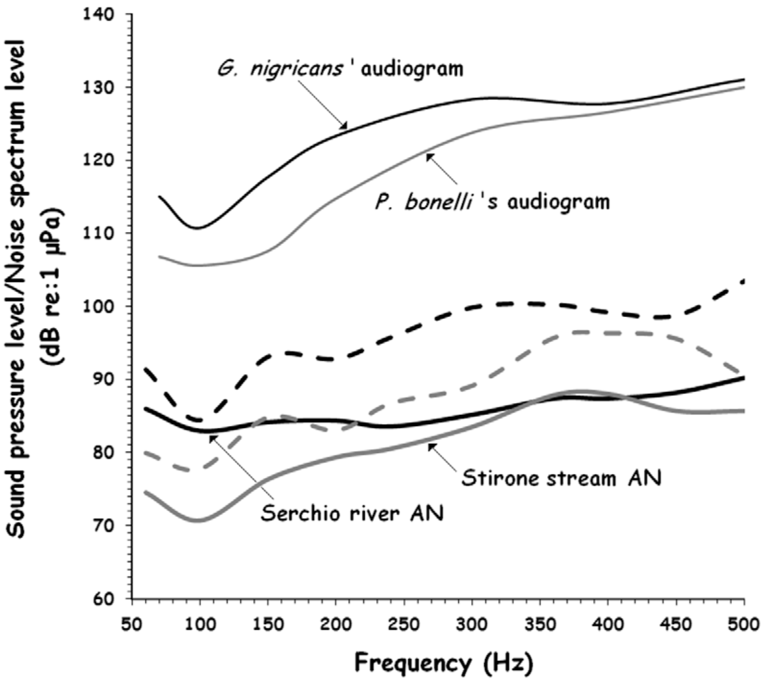

Fig. 6.6 The pressure audiogram of two allopatric stream goby species (*thin lines*) and average (*continuous thick line*) +1 SD (*dotted line*) ambient noise pressure spectrum from noisy locations of the corresponding stream (*P. bonelli* and Stream Stirone: *grey lines*; *G. nigricans* and River Serchio: *black lines*). Note the low-frequency noise window around 100 Hz in Stream Stirone and the standard deviation curves of the ambient noise of both streams matching the audiogram's profile. The matching improves using data from the noisiest locations of the stream (see text for further explanations). The data suggest that hearing is influenced by common selective pressures from the environment

window around 100 Hz in many noisy locations (particularly in Stream Stirone). The window, about 130 Hz wide in Stream Stirone, was more sharply tuned at 100 Hz, that is, resembling a notch, in River Serchio (Fig. 6.6). This quieter noise spectral region is exploited by the two gobies for communication: the main sound frequencies matched the window/notch frequencies (Lugli 2010; compare also Fig. 6.6 with Fig. 6.3); furthermore, the goby hearing sensitivity also peaked at 100 Hz (Fig. 6.6). It should be noted that the window band overlaps the range of frequencies enhanced by the stone. Thus, in the stream goby both ambient noise and nest/calling site appear to act synergistically to increase the S/N ratio of acoustic communication (see discussion below).

A subsequent study (Lugli 2010) examined the spectral features of ambient noise in freshwater, brackish, and shallow marine habitats inhabited by other vocal gobies and often characterised by elevated noise levels. The habitats investigated, among others, were two brackish lagoons, a near-shore sandy bottom, and a rocky shore.

In these habitats the main noise source was the bubble noise generated by breaking ripples and wave splashes. Overall, noise levels were higher (80–110 dB, re: 1 μPa) than those measured in the stream. However, because of the repetitive and unpredictable nature of waves, noise levels showed high short-time variability associated with the presence of a wave-breaking event at or near the recording position (Fig. 6.5). Bubble noise energy concentrated mostly in the 0.03–4 kHz band and peaked usually below 500 Hz. Like the stream bubble noise, the noise spectrum of breaking ripples and wave splashes featured a low-frequency ‘quiet window’ in all habitats surveyed. The window, about 100–150 Hz wide, was tuned at 100 Hz in the coastal habitats surveyed, and at 200 Hz in the lagoon. The spectral features of the window were then correlated with the range of dominant frequencies of sounds used by gobies reproducing in these environments. Results showed the dominant frequencies of sounds of the two marine gobies (*Gobius paganellus*, *G. cobitis*) showed the best fit within the quiet window at around 100 Hz in the noise spectrum of marine areas, whereas those of four brackish gobies (*K. panizzae*, *P. marmoratus*, *P. canestrinii* and *Z. ophiocephalus*), better fitted the quiet window at around 200 Hz in the noise spectrum of the lagoon (Fig. 6.7).

It should be noted that these studies (Lugli and Fine 2003; Lugli 2010) were conducted using acoustic pressure as the measurement unit. However, gobies, as are many other teleosts with ‘poor’ hearing that communicate at close distance (i.e. in the near field), are primarily or exclusively particle-motion–sensitive species. In the near field, acoustic pressure and particle velocity do not have a constant relationship but vary with the characteristics of sound source and propagation distance in complex, site-dependent ways (Kalmijn 1988). Thus, the measurement of the sound and ambient noise in terms of particle velocity is therefore required. This has been done for the stream ambient noise and *P. bonelli* sounds (Lugli and Fine 2007) using a pressure (*p*)-velocity (*u*) sensor in the stream. Results showed the noise spectrum was similar for *p* and *u* (including the quiet window at noisy locations). The energy distribution of the sound was quite similar for *p* and *u* spectra. Most important, the sound/ambient noise window match occurred for both *p* and *u*, the matching being shifted 50 Hz higher for *u*. Overall, results of this study validated conclusions about sound communication derived by measuring only acoustic pressure.

Spectral features of ambient noise and their relationships with fish sounds have also been examined in other species. Speares et al. (2011) examined ambient noise characteristics of two separate North American creeks inhabited by sound-producing fishes belonging to the genus *Etheostoma* (darters, family Percidae). In these streams noise levels were high (up to 100 dB), below 100 Hz, and decreased with frequency more quickly in quieter places (pools and runs) than in fast-flowing riffles, where underwater bubbles formed from the breaking of the water surface. As with the Italian streams, the noise spectrum at the noisiest places of one stream (the riffles of Cypress Creek) featured a low-frequency band, between 150 Hz and 330 Hz, with quieter noise levels. The dominant frequency of the aggressive vocalisations of the species inhabiting these riffles (*E. flabellare*) fell within the quiet window. The second species investigated (*E. crossopterum*) produced vocalisations

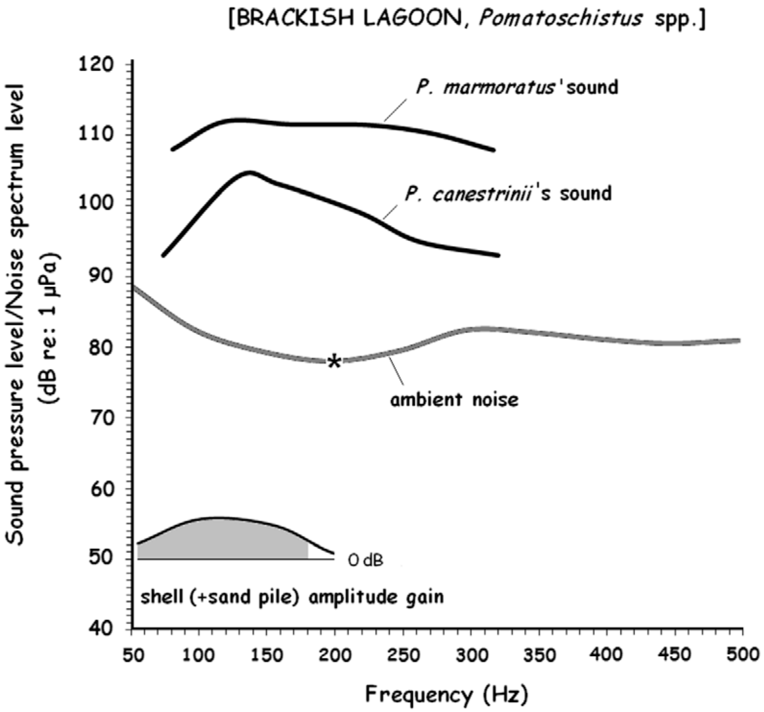

Fig. 6.7 The mean sound spectrum of two brackish sand gobies (the Marmoreal goby, *Pomatoschistus marmoratus*, and Canestrini goby, *P. canestrinii*, *dark lines*) and the 50–500 Hz mean (*pale line*) spectrum of the breaking wave noise in the lagoon (data from Lugli 2013). The asterisk marks the center frequency of the quiet window in the low-frequency ambient noise spectrum (approx. 100–270 Hz). Superimposed on the plot is the mean amplitude gain (dB) from the bivalve shell with a sand pile above, the typical nest site of these species (Lugli 2013). Axes have the same units of the main plot except that dB units on the *Y*-axis are relative to the 0 dB gain line

with lower average frequency and wider frequency range, more suitable for communication in the much quieter environment of the pool (spectrum levels at frequencies above 100 Hz well below 70 dB) with a not clear quiet noise window. The authors concluded that both species produce vocalisation with dominant frequencies working within the acoustic constraints of their respective microhabitats. Because both species call and spawn below stones (Speares et al. 2011) it remains to be seen whether and to what extent their sounds are also amplified by the nest cavity.

A much wider quiet noise window was described in the background noise of African floodplains inhabited by the weakly electric fish *Pollimyrus isidori* (family: Mormyridae; Crawford et al. 1997). The window (from 0.2 to 3 kHz) was supposed to result from low-frequency noise due to water motion and other unidentified sources, and from a high-frequency noise produced by aquatic insects stridulating underwater. A significant amount of energy of the courtship sounds (moans, grunts) of *P. isidori* falls within this noise window (Crawford et al. 1997).

The presence of quiet noise windows has been reported for other freshwater habitats. Wysocki et al. (2007) determined the underwater noise spectrum of 12 aquatic environments in Austria, from noisy fast-running streams to quiet ponds and river backwaters. Although the study did not capture the ambient noise variability of each habitat, nonetheless results showed large variations of noise level and spectrum between different environments consistent with the different water flow regimes. The spectrum levels of stagnant habitats (lakes, backwaters, ponds) were higher at frequencies below 100 Hz and decreased with increasing frequency, resting generally below 60 dB in the frequency band 0.1–5 kHz (Fig. 6.4). The noise spectra of running water habitats, on the other hand, showed higher noise levels at lower frequencies, a rapid decline of the spectrum levels to a minimum, followed by an increase again towards a peak (around 80 dB) or a plateau (at around 100 dB, Danube river at Orth), thus defining an area of lower spectral levels (i.e. a ‘noise window’) at frequencies from 170 to 450 Hz (Fig. 6.4). The spectral energy above the window was believed to originate from noise produced by transport of sediment and cavitation. The authors also noted noisy habitats exhibited large differences in the noise spectrum, whereas stagnant habitats had a similar noise profile, an observation supported by the results of investigations of stream ambient noise discussed above. However, they did not specifically relate the presence of these windows to sounds produced by teleosts inhabiting these environments.

In sum, the occurrence of low-frequency regions with lower noise levels (termed ‘noise windows’; Lugli and Fine 2003) is a recurrent feature of noise spectra in shallow-water habitats with intermittent or continuous sources of elevated noise levels. The number of teleosts living in such noisy shallow environments is numerous, and studies exploring the relationships between their sounds and ambient noise characteristics could reveal further cases of sound/ambient noise matching. A cursory examination of these relationships was attempted by Lugli (2010) using published data on sounds produced by other teleosts breeding in small streams, creeks, and very shallow marine habitats similar to those examined above. The species surveyed belonged to families as diverse as cottids, batrachoidids (*Porichthys*, *Opsanus*), and cyprinids (genus: *Cyprinella*). The range of the main frequencies of sound produced by these species was superimposed on a generic noise spectrum of a breaking wave and a stream waterfall, two main sources of elevated background noise of these environments both featuring the quiet window around 100 Hz. In all species the main frequencies of the sound fitted within the quiet window, including two stream cyprinids, a teleost family well known for including many species living in quiet environments (e.g. backwaters, ponds) and characterised by well-developed hearing and typical sound frequencies well above 100–200 Hz (reviewed in Amorim 2006). Thus, these data indicate that the sound/ambient noise match may be widespread among marine and freshwater species breeding in shallow noisy environments.

A match between call energy and ambient noise has also been described in marine mammals (baleen whales) communicating in shallow coastal habitats (Bass and Clark 2003), and in many land vertebrates (birds, primates, frogs; Brenowitz 1982; Ryan and Brenowitz 1985; Waser and Brown 1986; Brumm and Zollinger 2013). Ambient noise therefore may act as a main constraint upon frequencies used for acoustic communication in both marine and terrestrial species.

6.6 Fish Low-Frequency Communication Explained by Habitat Acoustics?

Attempts to explain the widespread use of low-frequency sounds by teleosts in terms of adaptation to environmental factors have already been made in the past. Bass and Clark (2003) interpreted low-frequency signalling by developing a set of complementary explanations linking environmental to behavioural and structural factors. Thus, for instance, the constraining effect of water depth on sound transmission was taken as an example of an ecological factor favouring the use of low frequencies for short-range communication in shallow waters. The short propagation distance of frequencies below the cutoff might avoid degradation of sound signals caused by multipath propagation and limit interception by competitors or predators. There is no compelling evidence in support of this behavioural–ecological explanation, however. For example, stream gobies (*P. bonelli*, *G. nigricans*) do not have aquatic predators (with the possible exception of the collared snake, *Natrix natrix,* whose hearing capabilities are unknown) and sound interception by competitors occurs despite the very short propagation distance (few decimetres) of their low-frequency sounds (Lugli 1997). Bass and Clark (2003) indicated as an example of an ecological–structural mechanism favouring low-frequency acoustic signalling, the maintenance of the inner ear's most fundamental function of low-frequency particle motion detector in the near field in many extant species, as hypothesised by Kalmijn (1988). Inasmuch as the lateral line detects the local hydrodynamic flow in the very near field, the inner ear might have evolved originally to extend the detection range and frequency sensitivity of the lateral line to the remaining part of the near field. The strength of the local flow and extension of the near field are greater for sounds with longer wavelengths (Kalmijn 1988). Thus, fishes are expected to use preferentially low-frequency vocalisations for near-field acoustic communication. Another explanation for low-frequency acoustic communication relates to the physiology of sound production. Many fishes produce sounds by contraction of sonic muscles (often attached to the swim bladder) whose contraction rate translates into the sound's fundamental frequency. The maximum sustainable repetition rate of these muscles (up to 300 Hz among batrachoidids; Skoglund 1961) would set an upper limit to the main frequency of the sound, a behavioural–structural explanation for the occurrence of low-frequency communication among these species (Bass 1998). However, there are many ways by which a fish can extend the frequency range of the sound originated by muscular contraction (e.g. Ladich and Bass 2011).

In the two previous sections we have shown that two ecological factors, nest site acoustics and occurrence of noise windows, may favour the use of low-frequency sounds by teleosts living in shallow noisy habitats by providing higher S/N ratios for communication. For example, the main frequencies of sound of the male stream goby, *P. bonelli*, fit within the 10-dB–deep noise window at around 100 Hz of the stream noise and, curiously, are also those maximally amplified by the stone hollow (around 12 dB, on average, for a 100 Hz tone, Lugli 2012). The joint contribution of these two environmental factors might increase the S/N ratio of the 100 Hz pitched sound signal emitted by the male *P. bonelli* inside the nest site substantially (from 10 to 20 dB, when compared to a higher pitched sound). A similar fortunate circumstance occurs among sand gobies of the genus *Pomatoschistus*, where the frequencies enhanced by the nest (a shell with sand pile) happen to be within the noise window of the lagoon ambient noise. As expected, the sound spectrum of these species fits within the broad noise window of the lagoon ambient noise, but the peak frequency of the sound matches the frequency of maximum gain of the nest (Fig. 6.7). Thus, it would seem that both ambient noise and nest acoustics jointly operate to increase the S/N ratio of goby acoustic communication in the presence of elevated noise levels. Like gobies, many other teleosts (e.g. toadfishes, sculpins, darters, blennies) live in shallow noisy habitats and communicate acoustically over short, or very short distances. In addition, in many of these species the male calls from cavities under stones or other submerged objects used as a nest site. Thus, the widespread use of low frequencies for communication among these fishes may be promoted by one or both of the above acoustical features of the habitat.

However, in order to be effective, acoustic communication requires that the sound must be detected and clearly recognised by intended listeners (e.g. a potential mate). Both detection and recognition depend on the S/N ratio. Thus, the next section explores the importance of ambient noise on hearing sensitivity.

6.7 Environmental Pressures Operating on Receiver Auditory Sensitivity

An unresolved mystery of fish acoustic communication is the great variability of hearing sensitivities found among different, in some cases also closely related, species (e.g. Fay and Megela-Simmons 1999; Ladich 2014). The variety of fish auditory sensitivities (Fig. 6.8) is much higher than that found among other vertebrate groups, where the audiogram form usually shows only minor changes among related species. To a large extent, these differences are related to the way the sound is processed by the inner ear of the fish. The fish ear responds to acoustic particle motion associated with the incoming sound wave passing through the acoustically transparent fish tissues. Hair cells of the inner ear function as low-frequency, particle motion detectors (Kalmijn 1988). In terms of hearing sensitivity fishes can be classified into two main categories: the hearing specialists, like the goldfish, show high sensitivity, extended hearing range towards higher frequencies (up to several kHz), and higher frequency discrimination; on the contrary, the hearing nonspecialists (also referred to as 'generalists'; e.g. the perch), have poor hearing sensitivity, a narrow hearing range restricted to lower frequencies (100–300 Hz), and poor frequency discrimination (e.g. Ladich and Popper 2004; Fig. 6.8). Species belonging to the first group (e.g. cyprinids, mormyrids, anabantoids), have developed accessory hearing structures (like the Weberian ossicle chain of otophysans) connecting the inner ear with the swim bladder, or other pressure-to-displacement conversion mechanisms (e.g. auditory bullae of mormyrids), enabling them to detect the acoustic pressure from distant sound sources and the associated far-field acoustical information. Auditory specialists are mainly found in quiet freshwater habitats (lakes, ponds, large slow-flowing rivers). Those of the second group (e.g. toadfishes, blennids, gobies, darters) can only detect the particle motion components of the near field generated by a close sound source (a task also accomplished by auditory specialists). Auditory nonspecialists are typically found in noisy freshwater habitats (streams, creeks, small rivers) and in shallow marine environments (coastal areas, lagoons). Between these two broad categories there is a third group of species showing intermediate hearing sensitivity. These fishes appear to be sensitive to sound pressure but lack morphological adaptations for hearing enhancement (e.g. damselfishes). The above distinctions do not have to be considered too rigidly as one category may grade into the other (Smith et al. 2004; Ladich 2014). Interestingly, remarkable differences in sensitivity also exist between closely related members of the same family, both with and without hearing specialisations (e.g. Ladich and Yan 1998; Schulz-Mirbach et al. 2013).

Until recently, the causes of variability of fish audiograms has remained a matter of speculation and largely unexplained (reviewed in Ladich and Bass 2003). Factors unrelated to the natural environment, such as differences in the testing procedures, methods, or the acoustic units used to assess auditory sensitivity of a particular species (Hawkins and Myrberg 1983; Fay and Megela-Simmons 1999; Ladich 2014) may partly account for such variability. However, there are indications that the acoustical characteristics of the species' habitat may also play an important role. I have shown before that fishes live in environments differing greatly for sound propagation and ambient noise characteristics. The importance of the acoustic environment in the evolution of fish auditory sensitivity has been emphasised by few investigators (Hawkins and Myrberg 1983; Rogers and Cox 1988; Schellart and Popper 1992; Ladich 2014). Myrberg (1980) noted among fishes with good hearing abilities the auditory thresholds below the point of greatest sensitivity parallels those of the spectrum-level noise, the levels of the audiogram resting from 15 to 20 dB above the ambient noise curve (sea state 1). He also noted that adding only a few dB to the noise levels would affect sensitivity and impair hearing within the region of greatest sensitivity (400–600 Hz), and concluded that low-frequency auditory sensitivity among fish with good hearing appears to be governed by the

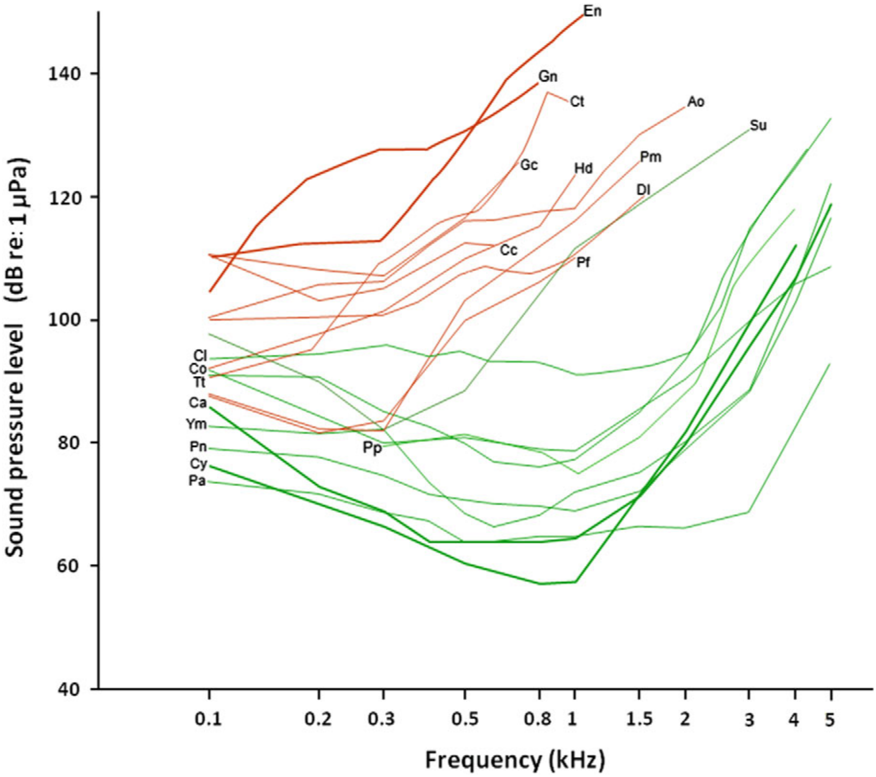

Fig. 6.8 Pressure audiograms for 20 representative auditory specialists (*green lines*) and nonspecialists (*dark red lines*) teleosts (*species initials in brackets, see below*) living in shallow or very shallow habitats. Audiograms of species living in very noisy (streams, creeks: *thick red lines*) or very quiet (ponds, stagnant waters; *thick green lines*) habitats are highlighted. All thresholds curves were obtained using AEP technique (Kenyon et al. 1998). Ao, *Astronotus ocellatus*; Ca, *Carassius auratus*; Cc, *Chromis chromis*; Cl, *Colisa lalia*; Co, *Corydoras aeneus*; Ct, *Cottus carolinae*; Cy, *Cyprinus carpio*; Dl, *Dicentrarchus labrax*; En, *Etheostoma neopterum;* Gn, *Gobius nigricans;* Gc, *Gobius cruentatus;* Hd, *Halobatrachus didactylus*; Pa, *Platydoras armatulus*; Pf, *Perca fluviatilis*; Pm, *Poecilia mexicana*; Pn, *Pygocentrus nattereri*; *Pp, Pimephales promelas*; Su, *Sciaena umbra*; Tt, *Trichogaster trichopterus*; Ym, *Yasuhikotakia modesta* (Modified from Ladich 2014; further references: Zeyl et al. in press, Ct, En; Ladich and Yan 1998, Cl; Lugli et al. 2003, Gn; Scholik and Yan 2001, Pp; Lovell 2003, Dl)

slope of the ambient noise. Hawkins and Myrberg (1983) argued that there is no advantage in having sensitive hearing when noise masks the auditory system, implicitly advocating the importance of ambient noise in the evolution of hearing sensitivity.

Investigators have considered the possible relationships of hearing abilities with vocal activity and spectral characteristics of species' sound, with contrasting results. For instance, in anabantoid fishes (*Trichopsis vittata*, *Colisa lalia*) there is a general agreement between the main energies of the high-pitched sounds and the best hearing sensitivity of the fish (Ladich and Yan 1998). However, best hearing and main sound energy are mismatched in several other teleost groups, regardless of the presence of hearing aids (Ladich 2000). Furthermore, within-family comparisons (e.g. among Cyprinids) showed nonvocal species (e.g. the goldfish) do not have poorer hearing than vocal ones (Ladich 2000). These results are consistent with the hypothesis that the hearing function is more primitive than sound production (Kalmijn 1988), implying that other factors are responsible for the evolution of hearing sensitivity.

A study of Lugli et al. (2003) supported the Hawkins and Myrberg (1983) insight on the importance of ambient noise for shaping the species' hearing sensitivity. They found in the two stream gobies, *G. nigricans* and *P. bonelli*, the main sound frequencies and the region of greatest sensitivity of the fish audiogram fitted within the low-frequency quiet region of the stream noise (i.e. the 100 Hz 'notch' of the *G. nigricans*' stream noise and the quiet window of *P. bonelli*'s stream noise, Fig. 6.6), a set of related adaptations enhancing the signal-to-noise of acoustic communication in line with principles of optimal communication in a noisy environment (e.g. Wiley and Richards 1982; Endler 1992). They also found that higher noise levels in the 100 Hz notch correctly predicted the lower sensitivity and the narrow range of best hearing of *G. nigricans* in comparison to those of *P. bonelli* (Fig. 6.6). Furthermore, in each species the absolute auditory sensitivity tracked the mean ambient noise spectrum level determined at noisy locations of the species' stream (Fig. 6.6). The presence of fine audiogram/noise matching in the two gobies addresses the importance of ambient noise in shaping the form of the stream goby's hearing sensitivity. Lugli (2002) noted the presence of similar audiograms in other hearing nonspecialist species living in noisy shallow water habitats (e.g. the European perch, *Perca fluviatilis,* reviewed in Popper and Fay 1973), and argued the habitat ambient noise may represent an important environmental constraint upon the evolution of fish hearing sensitivity in general. Subsequent investigations supported this view. Amoser and Ladich (2005) found that hearing thresholds of a hearing nonspecialist (the European perch, Percidae, audiogram in Fig. 6.8), were only slightly affected by the highest noise levels of noisy freshwater habitats (stream, small river), whereas those of a hearing specialist (the common carp, Cyprinidae, audiogram in Fig. 6.8) were masked also by the low noise levels of quiet standing waters (backwaters, lake, pond). They concluded that only the low noise levels of quiet habitats would facilitate the evolution of auditory specialisations that broadened the hearing sensitivity to higher frequencies (the only ones propagating above the cutoff frequency in shallow habitats), in order to detect the acoustic pressure from distant sound sources produced by relevant biotic (e.g. predators) and abiotic (waves, splashes) sources (Amoser and Ladich 2005). Recently, Ladich and Schulz-Mirbach (2013) reviewed the results of comparative studies on the effect of noise masking on hearing, and noted that major threshold shifts occurred only under noisy conditions among fishes with hearing specialisations. However, situations characterised by the presence of elevated noise levels are rare in quiet habitats (excluding the presence of anthropogenic noise), but common in noisy ones (examples in Fig. 6.4). As already pointed out by Lugli et al. (2003)

for the stream goby, there might not be a strong selective advantage for a species with limited hearing ability and low-frequency sensitivity to change the status quo if the fish is likely to encounter high levels of background noise, and other unfavourable acoustic conditions (e.g. multipath propagation) constraining long-distance communication in these environments. In this regard, the results of a recent study on amblyopsid cavefishes living in noisy subterranean streams are notable in that they showed that moving from quiet habitats to a noisy one may lead to decreased auditory sensitivity at frequencies where ambient noise is highest (Niemiller et al. 2013). This is a remarkable and unexpected finding considering these fishes are blind, because of the total darkness of the cave environment, and must rely on auditory function for orientation and communication. The picture that emerges from these observations indicates that the auditory sensitivity of fishes might indeed be well suited to cope with the prevailing ambient noise conditions of their habitats. This conclusion is further strengthened by examination of audiogram/ambient noise relationships in two unrelated vocal species (the red-mouthed goby *Gobius cruentatus,* and the damselfish *Chromis chromis*) breeding within the same marine shallow area (Picciulin et al. 2010). These species have a similar audiogram (Wysocki et al. 2009) and absolute hearing thresholds that appear to track the profile of the ambient noise of the breeding area (a coastal rocky reef, Fig. 6.9). The importance of ambient noise conditions in the evolution of hearing sensitivities in fishes (and less so acoustic communication) has also been emphasised by Ladich (2014), who labeled the issue as 'ecoacoustical constraints hypothesis'.

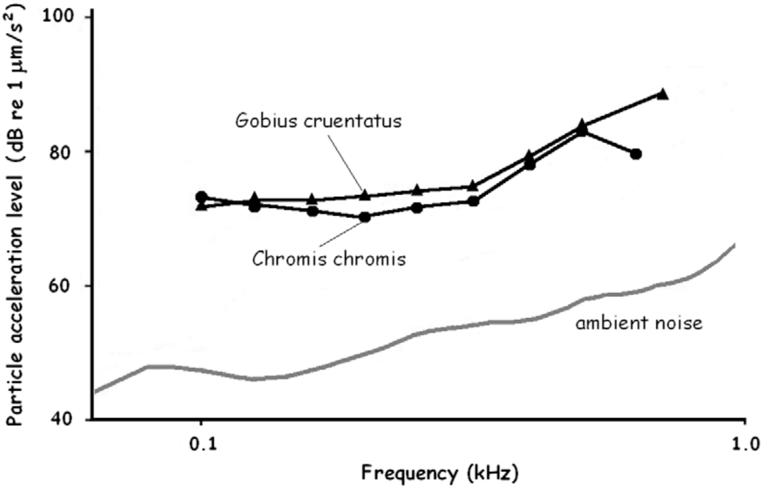

Fig. 6.9 The particle acceleration audiogram (AEP method) of *C. chromis* (Pomacentridae, *filled circles*) and *G. cruentatus* (Gobiidae) (*filled triangles*) shown together with particle acceleration level underwater ambient noise spectrum measured close to a coastal rocky reef (150 m long), within an area where both species live and reproduce (water depth: 3–7 m). All analyses are done in 1/3 octave bands (modified from Picciulin et al. 2010)

This hypothesis attempts to explain why numerous vocalising taxa such as toadfish, gobies, and sculpins possess poor hearing abilities and why nonvocalising species such as many cyprinids (goldfish, carps, etc.) evolved specialisations for the improvement of hearing such as auditory ossicles.

But why and how should the auditory sensitivity of a species be well matched to the habitat ambient noise? In particular, what are (if any) the costs for an individual fish by listening with a too-sensitive ear for the noise conditions encountered in the species' habitat? A potential advantage for a fish having thresholds above the prevailing ambient noise levels is the avoidance of sensory overstimulation and deleterious effects of elevated noise levels on the auditory system such as hair cell damage (Popper and Clarke 1976; Enger 1981; Hastings et al. 1996). Studies conducted on teleosts with good hearing have shown that longer exposure to moderately loud noises may produce sensory cell damage and lead to permanent loss of hearing (e.g. Hastings et al. 1996). Thus, a fish with a sensitive ear living in noisy environments would be frequently exposed to elevated noise levels which might have deleterious consequences for reproduction and survival, from alteration of normal behavioural activities and chronic stress, to permanent loss of hearing in the long run. This possibility has yet to be tested experimentally, however. Interestingly, Hopkins (1988) interpreted low sensitivity of electroreceptors in African freshwater electric fishes as an adaptation to avoid sensory overstimulation from the more or less continuous electrical noise of lightning storms.

However, the adverse effects of noise on auditory performances may be more subtle and occur at much lower levels than those required to damage the functionality of the inner ear. It is well known that noise can impair the perception of sound by masking auditory thresholds and cause temporary hearing loss (Yost 1994; Ladich 2013). Studies conducted among vertebrates over the last 20–30 years have clearly demonstrated the detrimental effects of noise masking on auditory performances of great adaptive value, such as the ability to assess correctly the overall intensity and spectral shape of the sound. The correct assessment of the intensity of multiple frequency components of the sound is fundamental for the reliable identification of the sound source, classification of acoustic events, or assessment of mate quality through comparison of sounds from different individuals (e.g. Bregman 1990; Wolleman and Wiley 2002). Because classification processes of acoustical stimuli by the receiver's auditory system must rely upon the perceived quality of the sound embedded in noise, one might expect a lowered ability to discriminate acoustic variants by a hearing-sensitive receiver when the masking background noise spectrum varies at, or between, locations at which sound detection occurs. We have seen (Fig. 6.5) that noise levels in shallow water environments, such as a stream waterfall, may vary unpredictably even at short temporal and/or spatial scales. Such fluctuations in level and spectrum of the noise give rise to complex masking patterns in a sensitive ear that may greatly alter the spectral appearance of the sound and, hence, affect the subjective perception of the sound quality, even at a close distance from the source. Animals have developed many peripheral and central adaptations to cope with the negative effects of noise masking on signal perception (e.g. peripheral auditory filtering, auditory templates and feature detectors, cross channel analysis, and comodulation masking release; reviewed in Brumm and Slabbekoorn 2005). However, there is no way a sound embedded in noise can be reconstructed by the hearing system into its original spectrum, a process known as noise spectral subtraction (Boll 1979). These observations suggest a potential advantage of having absolute sensitivity above the prevailing ambient noise conditions of the environment is to avoid, or minimise, the negative effects of noise masking on complex auditory performances (such as signal recognition). The cost to be paid, of course, would be a lowered capability of the hearing system to detect potentially relevant sound stimuli. Thus, a tradeoff between the detection and recognition or discrimination of sound signals might take place when communication occurs under variable masking conditions. Furthermore, the tradeoff between these two functions might operate to set the optimal hearing sensitivity within the constraints of the species' environment (ambient noise characteristics, sound transmission properties, etc.).

6.8 Concluding Remarks

This chapter focused on acoustic communication by shallow-water fishes and the environmental factors promoting the use of low frequencies by these species. The constraining role of ambient noise, and the amplitude gain of the nest favouring the use of low frequencies by many cavity-nesting species, have been emphasised. Ambient noise appears to function as a constraining factor not only for the use of appropriate low-frequency bands for acoustic communication but also for the development of an optimal hearing sensitivity within a particular underwater environment.

Not all soniferous fishes live in very shallow waters, however. For instance, gadoid fish (e.g. cod, haddock) emit low-frequency sounds close to the bottom at great depths (Hawkins and Rasmussen 1978). Similarly, not all shallow-water fishes communicate using low frequencies. Environmental factors promoting the use of high frequencies by these species (i.e. predator detection, propagation conditions) have also been discussed by other authors (e.g. Ladich and Bass 2003). In the present chapter, sound transmission properties of the underwater environment and their effects on acoustic communication in different habitats have been only briefly mentioned. Again, this topic is examined in more detail in other reviews (Fine and Parmentier, this volume, Bass and Clark 2003).

Frequency composition aside, there are many other sound features (e.g. duration, temporal structure, amplitude and frequency modulation, emission rate) that may potentially evolve in response to acoustical properties of the environment in order to convey acoustic information reliably to intended receivers. For example, many teleosts (e.g. some gobies, toadfishes) produce mating sounds characterised by slow frequency modulation, concentration of acoustic energy at a main (low) frequency, and high repetition rates. These characteristics are typical of bird and mammal vocalisations that must propagate with little distortion through an environment characterised by reverberations and irregular amplitude fluctuations (Wiley and Richards 1982). Unfortunately, there is a paucity of experimental and comparative studies addressing the effect of acoustical environment on these sound traits amongst teleosts.

A number of studies have addressed the issue of short-term effects of both ambient and man-made noise on fish behaviour and hearing. Current evidence indicates that both types of noise may potentially impair fish sound detection and hearing, thereby hampering information-gathering processes important for acoustic communication (and orientation; reviewed in Ladich 2013). However, the long-term effects of increased noise levels on acoustic behaviour, perceptual abilities (including auditory scene analysis), and survival of fishes in their natural environments are largely unknown. For instance, although fishes show avoidance reactions in response to loud underwater noises (e.g. Picciulin et al. 2010), there are with one exception (Holt and Johnston 2014) no fish studies showing the presence of adaptive responses to increased noise levels, such as increased signal output, frequency shift, and the like, as observed in birds or mammals.

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