

Chapter 4

Effects of Noise on Sound Detection and Acoustic Communication in Fishes

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Abstract The ambient noise in aquatic habitats is characterized by a large variety of noise levels and spectral profiles due to various abiotic and biotic factors such as running water, wind, tides, and vocalizing animals. Fish hearing sensitivity declines when exposed to high noise levels or in the presence of masking noise, in particular, in taxa possessing hearing enhancements. Most vocal fishes communicate over short distances (<0.5 m), probably because of low sound levels produced, low sound frequencies and the ambient noise conditions. Some species exploit ‘quiet windows’ of low spectral noise levels for acoustic communication. Human-made noise such as ship noise masks the hearing abilities of fishes and hinders acoustic communication. Whether fishes are able to cope with anthropogenic noise by increasing sound amplitude, shifting dominant frequencies of sounds, or by other mechanisms remains unknown.

4.1 Introduction

Fishes rely on their auditory sense for collecting acoustic information of biotic or abiotic origin (acoustic orientation). In order to fulfill this task, fishes possess inner ears consisting of three semicircular canals and three otolithic end organs, the utricle, saccule, and lagena. In contrast to tetrapods, they lack external or middle ears and, to our knowledge, sensory structures solely devoted to hearing (Ladich 2010). Most fishes apparently utilize the saccule for sound perception. Interestingly, while all fishes are sensitive to particle motion at low frequencies, at least one-third of all species have developed accessory morphological structures, termed ‘hearing specializations’ to detect sound pressure and extend their hearing abilities

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to lower sound levels and higher frequencies (Ladich and Popper 2004; Braun and Grande 2008). Popper and Fay (2011) propose to assign species onto a continuum of pressure detection mechanisms. At one end of the scale are fish with no air-filled structures such as shark and sculpins that only detect particle motion, on the other end are fish with hearing specializations such as swim bladders with an extensive use of sound pressure such as carps and catfishes. Fishes lacking hearing specializations have previously been termed 'hearing non-specialists or generalists' those possessing such structures were called 'hearing specialists'. The importance of hearing improvements is illustrated by the fact that one of the most successful bony fish groups, namely otophysines (carps, catfishes, tetras, and knifefishes, 8,000 species), are characterized by accessory hearing structures (Weberian ossicles) connecting the inner ear (greek: otos) to the swim bladder (physa).

The acoustic sense is a prerequisite for sound communication. Fishes evolved a unique diversity of sound-generating mechanisms among vertebrates. The main group of sound-producing mechanisms (sonic organs) is based on swim bladders. These can be vibrated by intrinsic drumming muscles located in the wall of the swim bladder (toadfishes, searobins), or by extrinsic drumming muscles originating on structures such as the skull or vertebral processes. Pectoral sound-producing mechanisms include vibration of the pectoral girdle (sculpins), rubbing of the enhanced pectoral spine in a groove of the shoulder girdle (catfishes), and plucking of enhanced fin tendons (croaking gouramis, genus *Trichopsis*). In addition, sounds can be produced by other mechanisms such as teeth grating (clownfish) but in many cases the exact process is still unknown (for reviews see Ladich and Fine 2006; Ladich and Bass 2011).

Sound production and acoustic communication usually do not take place in sound-proof chambers but in habitats with a certain amount of natural ambient and possibly anthropogenic noise. Thus, any acoustic process such as sound detection, sound transmission, and communication will be limited by noise and fishes as well as other animal that use sounds to communicate have to cope with this situation. Noise in the communication system may lead to errors by receivers in various contexts such as foraging, predator avoidance, agonistic, and reproductive behavior and these errors can have fundamental consequences for the optimal behavior of both receivers and signalers (see Chap. 2). The effects of underwater noise on fishes have been studied from quite different points of view. Most studies focussed on the effects of noise on inner ears and hearing, a few on sound production and transmission in the environment, and almost none on communication. The influence of anthropogenic noise on fishes in general has been reviewed recently (Popper 2003; Popper and Hastings 2009a, b; Slabbekoorn et al. 2010).

Studies on the effects of noise on hearing may be subdivided into three categories depending on the noise types involved: those applying artificial noise such as white (Gaussian) noise, ambient noise, and anthropogenic noise. Artificial sounds such as white noise are used to understand basic auditory capacities, e.g., the temporary hearing loss as a function of noise level and time of noise exposure, and the degree of masking in relationship to the noise level. Natural ambient noise consists of biotic (animal and plant sounds) and abiotic components (e.g., running

waters, surf, rain) and is an integral part of each fish's life. On the other hand, anthropogenic sound primarily derives from ships and boats, from construction sites (pile driving), from geological surveys (airs guns), from military operations (LFA sonar), and fishing operations (sonar, bottom trawls).

This chapter first examines the effects of different kinds of noise on sound detection, then focuses on the potential influence of ambient noise on transmission of fish vocalizations, and finally concentrates on studies investigating the influence of ambient and anthropogenic noise on the detectability of communication sounds. Noise-related changes on behavior, on morphology or on fish kept in aquaculture are not treated specifically. Note that all the areas outlined are characterized by a major lack of field experiments. Accordingly, we need to know more about acoustic communication distances of fishes in the field to estimate negative effects of human-made noise on communication (see [Chap. 14](#)). Our knowledge on the effects of noise on acoustic orientation and communication in fishes and the responses of fishes is quite limited ([Ladich 2008](#)) and often based on assumptions derived from other animal taxa ([Slabbekoorn et al. 2010](#)).

4.2 Effects of White Noise on Hearing

4.2.1 Noise Exposure

Several studies have investigated the potential effects of high levels of white noise on sound detection in fishes. Animals were usually exposed to white (Gaussian) noise for several hours (or days) at different noise levels in order to study the decline as well as the recovery of hearing sensitivities. Typically, exposure to high noise levels resulted in a temporal shift in thresholds (TTS) for a particular time period depending on the absolute auditory sensitivity of the species, the exposure time, and the exposure level. Due to a lack of appropriate miniature particle motion sensors for lab purposes hearing thresholds in noise exposure and masking studies have been described in sound pressure units independently of the ability of species to detect sound pressure.

Scholik and Yan ([2001, 2002a](#)) exposed fathead minnows *Pimephales promelas* (family Cyprinidae) and bluegill sunfish *Lepomis macrochirus* (family Centrarchidae) for 24 h to white noise at 142 or 148 dB re 1 μ Pa. They observed a significant decline in hearing thresholds in the best hearing range by about 10–18 dB in the minnow but not in the sunfish. Recovery to baseline thresholds took more than two weeks in the minnow. Amoser and Ladich ([2003](#)) exposed goldfish *Carassius auratus* (family Cyprinidae) and the Amazonian catfish *Pimelodus pictus* (family Pimelodidae) to white noise at 158 dB for 12 and 24 h and found a threshold shift of up to 26 dB in the goldfish and up to 32 dB in the catfish. The recovery took much longer in the catfish than in the goldfish (>14 vs. 3 d). The higher TTS and longer recovery time in the catfish was explained by its higher

baseline auditory sensitivity. Smith et al. (2003, 2004) exposed goldfish to white noise levels of 160–170 dB between 10 min and 21 d and found that recovery took up to 2 weeks when exposed for 3 weeks. In contrast to goldfish, the cichlid *Oreochromis niloticus* showed little or no hearing loss. The observation that sunfish and cichlid are not affected by noise at considerable levels can be explained by the fact that they lack hearing specialization; accordingly, they have rather low hearing sensitivities and are thus less affected by noise.

Wysocki and Ladich (2005b) investigated the effects of white noise exposure (158 dB) on the temporal resolution ability of the goldfish's auditory system. Fish communication sounds generally consist of series of pulses that differ mainly in pulse periods. Temporal patterns of pulses within sounds are important carriers of information in fish (Myrberg et al. 1978). Immediately after noise exposure, hearing sensitivity to click pulses was reduced on average by 21 dB and recovered within 1 week. Analysis of the response to double clicks showed that the minimum click period resolvable by the auditory system increased from 1.25 to 2.08 ms immediately after noise exposure and recovered within 3 days. Thus, environmental noise potentially impairs the detection of temporal patterns of sounds and subsequently gathering of information important for acoustic orientation and communication.

Other investigators examined the physiological and morphological effects of exposure to pure tones. Popper and Clark (1976) investigated the TTS after 4 h exposure to pure tones of 300, 500, 600, and 1,000 Hz at 149 dB. The TTS lasted for 2–4 h in goldfish. Recovery was complete. Exposure to very high sound pressure levels (~175–200 dB) resulted in morphological damage to sensory hair cells in various regions of the otolithic endorgans in the cod *Gadus morhua*, the cichlid *Astronotus ocellatus*, and the goldfish (Enger 1981; Hastings et al. 1996; Smith et al. 2011). In summary, fish lose their hearing abilities at least partly when exposed to levels of more than 100 dB above hearing thresholds.

4.2.2 Masking

Exposure to high levels of white noise deteriorates hearing sensitivity for hours or even days by shifting hearing thresholds and thus decreasing hearing sensitivities. Even much lower noise levels (below 110 dB), however, can decrease hearing abilities when the noise is present during sound detection, a phenomenon termed masking. Numerous authors investigated the masking effects from various points of views.

Fay (1974) showed that masking by broadband white noise increases the hearing thresholds of goldfish by a certain degree. The masking effect was lowest at 100 Hz with a signal-to-noise ratio (or critical ratio; critical ratio is defined as the sound pressure level of the tonal signal at thresholds minus the spectrum level of the noise) of 13 dB and highest at higher frequencies. Every increase in the spectrum level of the masking noise by 10 dB increases the hearing curve by

10 dB. Without elaborating on the critical ratio in more detail, the above experiments clearly showed that hearing abilities are limited by the level of noise and that any increase in the noise level decreases the sensitivity linearly in the goldfish, a well-studied species possessing hearing specializations.

Wysocki and Ladich (2005a) extended these investigations to fish taxa with differing hearing abilities and that use vocalizations for communication. They compared data from the goldfish to representatives of Amazonian doradid catfishes (family Doradidae) and North American centrarchids. The hearing abilities of the lined Raphael catfish *Platydoras armatulus* were determined between 200 and 4,000 Hz and of the pumpkinseed sunfish *Lepomis gibbosus* (no hearing specialization known) between 100 and 800 Hz in the presence of white noise. Noise levels of 110 dB RMS elevated the thresholds by 15–20 dB in *C. auratus* and by 4–22 dB in *P. costatus*. White noise of 130 dB RMS elevated overall hearing thresholds significantly in the otophysines by 23–44 dB, whereas the sunfish's sensitivity declined only at the higher noise level by 7–11 dB. Wysocki and Ladich (2005a) illustrate that the occurrence and degree of the threshold shift (masking) depend on the hearing sensitivity of fishes (with pressure sensitive fish showing a higher degree of masking), on the frequency, and on the noise levels tested. Ramcharitar and Popper (2004) observed differences in TTS within drums (family Sciaenidae). The black drum *Pogonias chromis* showed significantly greater shifts in auditory thresholds than the Atlantic croaker *Micropogonias undulates*, particularly in the frequency range of 300–600 Hz.

Noise exposure and masking studies that applied white noise indicate that noise affects sound detection and subsequently limits the abilities of fish to analyze the acoustic scene (or soundscape; Fay 2009). This might affect acoustic communication and orientation of fishes, in particular of species having enhanced hearing abilities.

4.3 Effects of Ambient Noise on Hearing

Studies showing the negative effects of white noise on auditory sensitivity raise the question if and to which degree fish may be masked under natural ambient noise conditions. In this chapter the term ambient noise refers to natural nonhuman noise sources. Theoretically, we postulate that the auditory (and sound-producing) system of fish are well adapted to their environment under calm conditions and that signal detection will be occasionally masked by short noise pulses. If this hypothesis is correct, then we furthermore assume that the large diversity in hearing sensitivities—based on a large number of accessory hearing structures—evolved as an adaptation to varying ambient noise levels and spectra (Ladich and Popper 2004). In order to test this hypothesis, ambient noise levels (RMS levels) and spectra need to be measured and analyzed in various habitats, and the auditory sensitivities of fish need to be measured in the presence of the habitat noise.

4.3.1 Natural Ambient Noise

Wenz (1962) and Urick (1983) estimated and described ambient noise spectra in the ocean in dependence of sea states, wind speeds, depth, and oceanic traffic. The general conclusion from these largely theoretical descriptions is that the noise spectrum level increases with sea state, wind speed, precipitation, and decreases at higher frequencies. Nonetheless, a single set of noise curves for all oceanic habitats is much too general for a meaningful assessment of the noise situation in the habitat of a particular fish species.

Recently, the ambient noise of several freshwater and marine habitats have been compared with regards to the particular fish species that live in these environments.

Wysocki et al. (2007) described a broad range of aquatic habitats in Central Europe, including running waters such as creeks and rivers and stagnant waters such as lakes and backwaters. They found considerable differences in noise levels and spectral profiles between the twelve habitats investigated. Stagnant habitats are quiet, with overall noise levels below 100 dB re 1 μ Pa ($L_{Leq,1min}$, RMS) under no-wind conditions. Noise levels in fast-flowing waters were typically above 110 dB and peaked at 135 dB in a free-flowing section of the Danube River. Noise levels ($L_{Leq,1min}$, RMS) differed by more than 50 dB between habitats, making it necessary to consider each habitat separately when looking for masking effects in the field. Note that RMS noise levels merely provide a rough estimate of the overall noise situation in a habitat. It is important to examine spectral levels in order to determine how fish might be affected in their particular hearing range and how well sounds may propagate. Low levels of spectral noise energy in a limited frequency range, sometimes termed ‘noise windows’, are far more suitable for sound propagation and sound detection than high levels over a wider range of frequencies (Lugli and Fine 2003). Wysocki et al. (2007) showed that most environmental noise in stagnant habitats is concentrated in the lower frequency range below 500 Hz. In fast-flowing waters, high amounts of sound energy were present in the frequency range above 1 kHz, leaving a low energy “noise window” below 1 kHz (Fig. 4.1).

The soundscape of aquatic habitats can be quite diverse even for closely related species. Lugli (2010) investigated the ambient noise at the typical breeding sites of northern Italian and Mediterranean gobies (family Gobiidae) that inhabit stony streams, vegetated springs, brackish lagoons, and sandy as well as rocky shores. Noise spectral levels in the 50–500 Hz band differed by more than 40 dB; they were much lower in the vegetated spring (60–70 dB re 1 Pa²/Hz) and the stream (70–80 dB) than in the brackish/marine habitats (80–110 dB). The author concluded that lagoon and coastal gobies are exposed to higher levels of low-frequency masking noise than freshwater gobies (Fig. 4.2).

Studies by Lugli and Fine (2003) and Speares et al. (2011) showed that the ambient noise spectrum not only differs considerably between but also within habitats. Lugli and Fine (2003) measured quiet areas and areas adjacent to

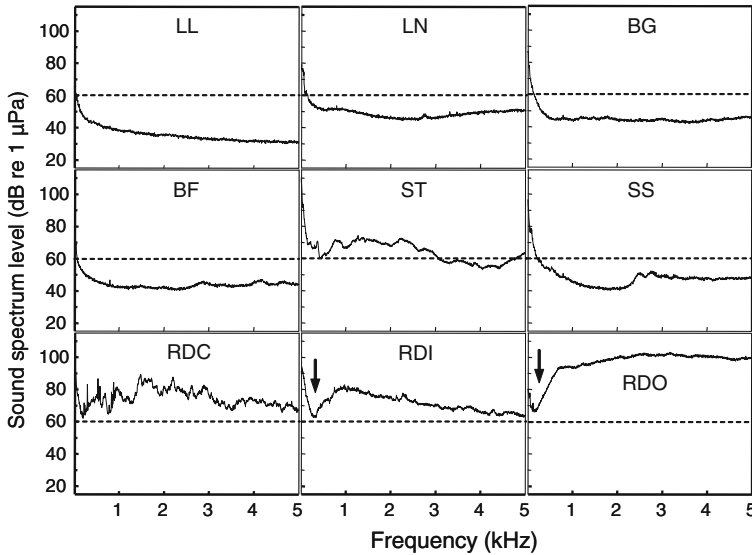


Fig. 4.1 Absolute amplitude spectra of the nine habitats within Central Europe illustrating the large diversity in ambient noise conditions. *BG* Backwater Gänsehauften Traverse; *BS* Backwater Schönauer Traverse; *LL* Lake Lunz; *LN* Lake Neusiedl; *RDC* Danube Channel; *RDI* Danube River at Danube Island; *RDO* Danube River at Orth; *SS* Schwarza stream; and *ST* Stream Triesting. Arrows indicate potential noise windows. Modified with permission from Wysocki et al. (2007). Copyright 2007, Acoustical Society of America

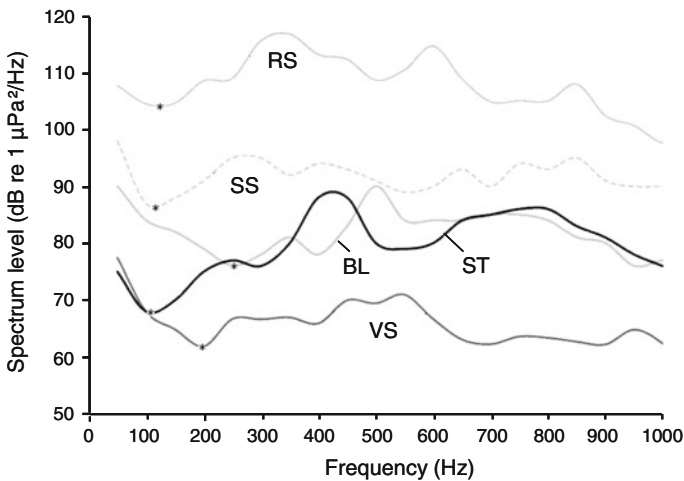


Fig. 4.2 Low-frequency spectra (0.05–1 kHz) of the ambient noise from five habitats inhabited by northern Italian and the Mediterranean goby species. Asterisks indicate the center frequency of the quiet window of the ambient noise. *BL* Brackish lagoon; *RS* Rocky shore; *SS* Sandy shore; *ST* Stony stream; *VS* Vegetated spring. Modified with kind permission from Springer Science + Business Media from Lugli (2010)

waterfalls and rapids in two shallow streams, the Stream Stirone in northern Italy and in the Serchio River in Tuscany in central Italy. Noise spectral levels differed by up to 50 dB in the frequency range below 1 kHz between quiet pools and locations close to rapids and waterfalls. Ambient noise from a waterfall attenuates as much as 30 dB between 1 and 2 m. Speares et al. (2011) investigated two creeks in Alabama, which are inhabited by small darter species (family Percidae), and reported that spectral levels differed between three microhabitats—a run, a riffle, and a pool—depending on the water flow velocity. The noisiest microhabitat in both streams was the fast-moving riffle. Spectral levels of the riffle were approximately 40–60 dB higher than levels of the other microhabitats in these creeks in the frequency range below 1 kHz. The observations that large water movements (running water, coastal surf) result in high noise levels (Wysocki et al. 2007; Lugli 2010) were corroborated by laboratory experiments. Flume experiments carried out by Tonolla et al. (2009) showed that increases in water velocity resulted in increased sound levels over a wide range of frequencies.

Changes in levels and spectral composition were not only found between and within habitats, but were also observed throughout the year in Central Europe. Amoser and Ladich (2010) determined that changes in sound pressure level (SPL) were smallest in the river (maximum: 10 dB), whereas higher changes were measured in stagnant habitats and streams (maximum: 31 dB). The spectral compositions of the ambient noise determined at different times of the year were similar at the river sites (mean cross-correlation coefficients: 0.85 and 0.94) and were weaker or not correlated at the other study sites (means: 0.24–0.76). Cross-correlation coefficients are measures of the similarity between the shapes of the amplitude spectra within each habitat. The mean cross-correlation coefficients of the ambient noise spectra were negatively correlated to changes in SPL, indicating that small changes in spectral composition (high coefficients) were accompanied by small changes in SPLs (RMS) and vice versa. These local and seasonal changes make the soundscape for fish rather complex, especially when fish migrate between habitats.

Besides large differences in noise conditions in freshwater habitats and microhabitats, pronounced differences were also described in marine habitats due to weather conditions and in coastal habitats due to tides. Chapman and Hawkins (1973) mentioned that the level of sea noise in Upper Loch Torridon on the west coast of Scotland, a typical habitat of cods (family Gadidae), was directly related to weather conditions. Any increase in wind speed, and hence surface motion, was accompanied by a proportional increase in the noise level. Heavy rain also considerably increased noise levels at higher frequencies.

Measurements in tidal zones were conducted by Coers et al. (2008). She and her colleagues investigated the ambient noise in the tidal zone of Fayal Island, the Azores, the preferred habitat of the rock-pool blenny *Hypsoblennius gilberti* (family Blenniidae). The researchers observed that the ambient noise revealed major spatial and temporal variation in levels throughout the tidal cycles. Overall levels (RMS) of ambient noise could increase up to 40 dB during high tide and up to 16 dB in spectral levels in the frequency range from 50 to 300 Hz.

Several studies described the ambient noise profiles of coral reefs in different contexts, such as to investigate guidance mechanisms for larvae, juveniles, and adult fish (Tolimieri et al. 2004; Kennedy et al. 2010; Radford et al. 2011). Reef noise is a combination of the sounds produced by reef-associated animals and various abiotic sources. Depending on the reef investigated, different high-energy peaks are found caused by vocal fish, crustaceans, and other marine invertebrates. Kennedy et al. (2010), for example, recorded the ambient noise at 40 reef sites of the Las Perlas archipelago in the Gulf of Panama and compared these sites to offshore sites. Acoustic recordings were taken at each site while the sea was calm. Each reef had a different spectral profile but a similar spectral peak at around 3 kHz, which was attributable to snapping shrimps. In contrast, offshore recordings were rather quiet and of lower levels, possessed a more flat spectrum and dropped off above 3 kHz (Fig. 4.3). Tolimeiri et al. (2004), in contrast, recorded the sea noise at the Feather reef in Northern Australia and found two energy peaks, one attributed to a fish chorus with energies below 1 kHz and a second to shrimps above 10 kHz.

In summary, several recent studies have described the acoustic environment of fishes in freshwater as well as marine habitats in much more detail than previously. These studies reveal that the noise situation is quite diverse, depending on a large

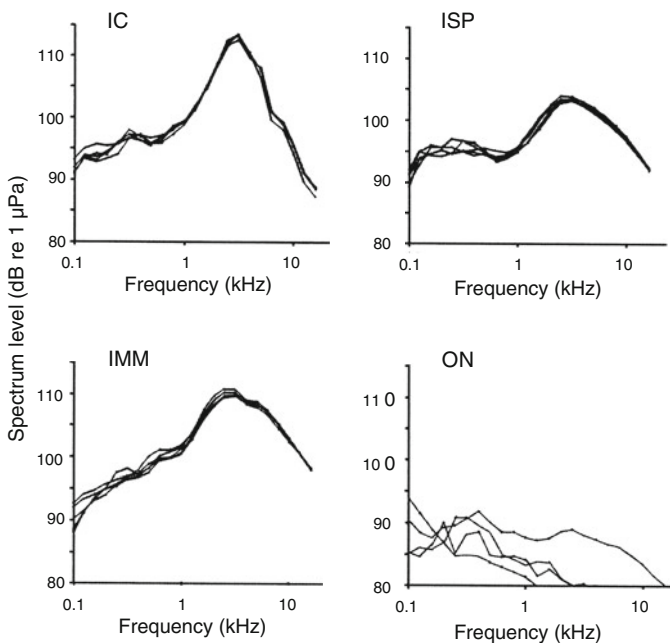


Fig. 4.3 Third octave spectra measured at several coral reef sites and at offshore sites measured in the Las Perlas Archipelago in the Gulf of Panama. Each plot shows five ‘typical’ reef acoustic profiles during the 2 min recording period. *IC* Isla Contadora; *IMM* Isla Mongo Mongo; *ISP* Isla San Pablo; *ON* Offshore Noise. Modified from Kennedy et al. (2010). Copyright 2010, with permission from Elsevier

degree on the movement of waters caused by natural water flow (e.g., rivers), by winds, by tides, etc., but also on the acoustic activity of various vocalizing animals. The conclusion was that standing waters are much quieter than moving or densely populated waters. Much more work is required to get a comprehensive picture of the degree soundscapes facilitate or limit sound detection and acoustic communication in fish when living in habitats from a depth of a few centimeters down to the deepest oceans.

4.3.2 Masking by Ambient Noise

Studies examining the effects of ambient noise on hearing in fishes are sparse. They were either carried out in the field or by recording the ambient noise in the field and playing it back in the lab. Chapman and Hawkins (1973) and Chapman (1973) measured hearing in the cod *Gadus morhua* and other representatives of the family Gadidae in the field. Fish were tested in a Scottish Loch 15 m below the sea surface and 5 m above the sea bed. Only in calm sea conditions were unmasked thresholds obtained. The authors clearly showed that any change in the sea noise level was accompanied by corresponding shifts in the hearing threshold in gadids. This hearing threshold to spectral level of the sea noise ratio at a particular frequency was constant and independent of the sea noise level. The ratio increased from 18 dB at 50 Hz to 24 dB at 380 Hz in the cod. This masking effect of the sea noise was confirmed when the noise level was raised artificially by transmitting random noise through underwater speakers. These findings were corroborated by laboratory experiments using white noise at different levels (Wysocki and Ladich 2005a).

Based on this knowledge, Amoser and Ladich (2005) attempted to determine the degree to which fish are masked under ambient noise conditions in various European freshwater habitats and what this masking effect looks like in species possessing different hearing abilities. They recorded ambient noise in four different habitats (Danube River, Triesting stream, Lake Neusiedl, backwaters of the Danube River), and played it back to native fish species while simultaneously measuring their auditory thresholds using the auditory evoked potential (AEP) recording technique. The results showed that the carp *Cyprinus carpio*, a pressure sensitive species, is only moderately masked by the quiet habitat noise level of standing waters (mean threshold shift 9 dB) but is heavily affected by stream and river noise by up to 49 dB in its best hearing range (0.5–1.0 kHz) (Fig. 4.4). In contrast, the hearing thresholds of the European perch *Perca fluviatilis*, a species lacking hearing specializations, were only slightly affected (mean up to 12 dB at 0.1 kHz) by the highest noise levels presented. Their results indicated that hearing abilities of otophysines are well adapted to the lowest noise levels encountered in freshwater habitats and that their hearing is considerably masked in some parts of their distribution range. A parallel study on the topmouth minnow *Pseudorasbora parva*, a common Eurasian cyprinid, supports these conclusions (Scholz and

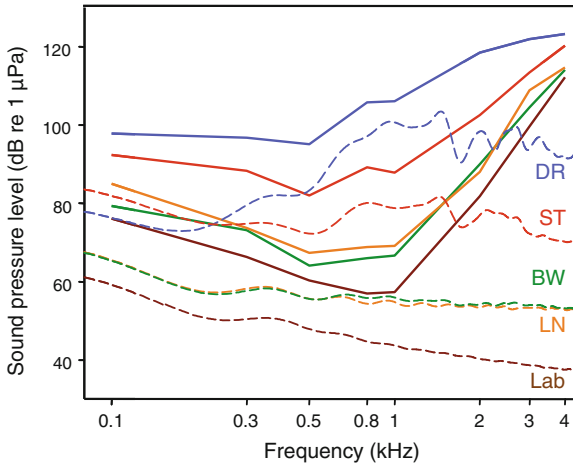


Fig. 4.4 Mean hearing thresholds of the carp *Cyprinus carpio* (solid lines) under laboratory conditions and in the presence of the different freshwater noise types (see also Fig. 4.1). Broken lines show the cepstrum-smoothed sound power spectra of the corresponding noise types. BW Backwater; DR Danube River; Lab Laboratory noise; LN Lake Neusiedl; ST Stream Triesting. After Amoser and Ladich (2005)

Ladich 2006). Their hearing sensitivity is slightly masked under ambient noise conditions recorded in their habitat. Their best hearing sensitivities were between 300 and 800 Hz at 57 dB re 1 μ Pa under quiet laboratory conditions and at 72 dB in the presence of lake noise.

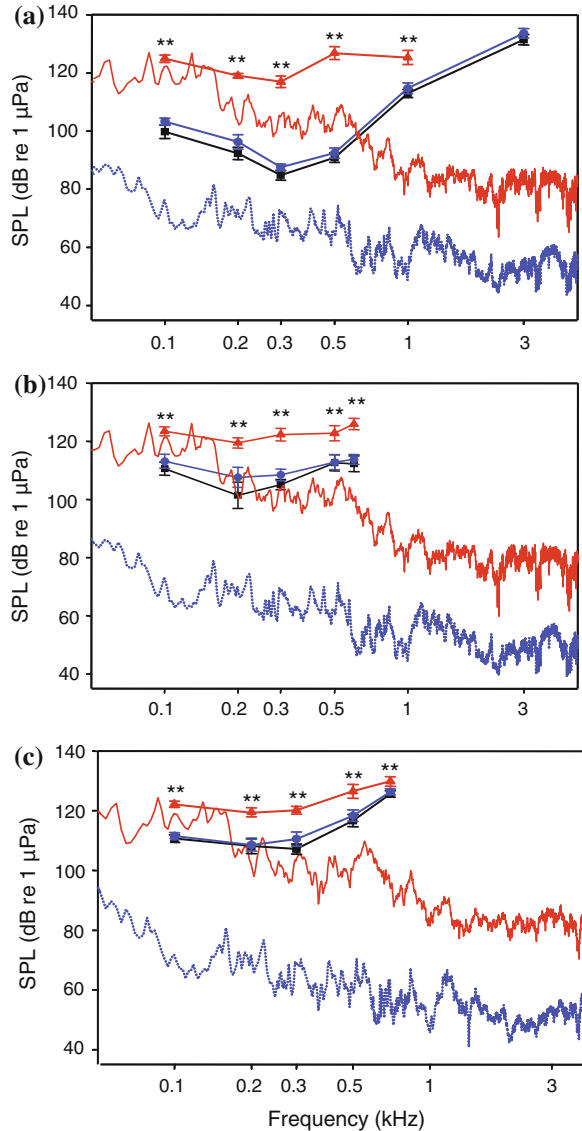
Hearing in species lacking accessory hearing structures is minimally impaired by the typical noise in natural habitats. Belanger et al. (2010) examined the hearing sensitivity of the round goby *Neogobius melanostomus* (family Gobiidae) at ambient noise conditions encountered in the Detroit River. This species has been (most likely accidentally) introduced from the Black and Caspian Sea region of Eurasia to the Great Lakes region and thus is not native to the Great Lakes. At natural noise levels (135 dB RMS), the authors did not observe any shift in auditory thresholds. Slight shifts of up to 10 dB were found at much higher noise levels, which according to the authors might occur under severe weather conditions.

To what degree are the hearing abilities of marine fish adapted to ambient noise? More recent studies on nonrelated taxa revealed that fish are well adapted to the ambient noise found during calm sea conditions. In addition to the study on cods by Chapman (1973), investigations on toadfish, on sciaenids or drums, damselfish, and gobies (family Gobiidae) revealed that the hearing sensitivities were only slightly masked. Vasconcelos et al. (2007) showed that ambient noise from the Tagus River estuary in Portugal affected the auditory sensitivity only at low frequencies (50–100 Hz) in the Lusitanian toadfish *Halobatrachus didactylus* compared to quiet lab conditions. Codarin et al. (2009) observed that the hearing sensitivity in the red-mouthed goby *Gobius cruentatus*, the Brown meagre *Sciaena*

umbra (family Sciaenidae) and the Mediterranean damselfish *Chromis chromis* (family Pomacentridae) changed by less than 3 dB when exposed to the ambient noise recorded in their habitat, the Miramare Natural Marine Reserve in the Adriatic Sea (Fig. 4.5).

Lugli (2010) described a large diversity in noise profiles in goby habitats (Fig. 4.2). How does this large diversity affect hearing in representatives of this perciform family? The conclusion, based on the lack of threshold shifts in species lacking hearing specializations such as the European perch, the red-mouthed and

Fig. 4.5 Mean (\pm S.E.) hearing thresholds of (a) the sciaenid *Sciaena umbra*, (b) the Mediterranean pomacentrid *Chromis chromis* and (c) the gobiid *Gobius cruentatus* under laboratory conditions (“baseline”; squares) and during playback of the ambient (circles) and boat noise (cabin-cruiser; triangles) compared to sound spectra of ambient (dotted line, blue) and cabin-cruiser (continuous line, red) noises. ** = $p < 0.001$ (repeated measure ANOVA). Modified from Codarin et al. (2009). Copyright 2009, with permission from Elsevier



round goby, and the Mediterranean damselfish (Amoser and Ladich 2005; Codarin et al. 2009; Belanger et al. 2010), is that the hearing sensitivities of northern Italian gobies are minimally or not at all affected by the different noise levels in their habitats under calm conditions. This changes as we will see in the next chapter under anthropogenic noise and perhaps under severe weather conditions.

4.3.3 Anthropogenic Noise and Masking

The following section concentrates on how human-made noise changes the natural soundscape and how this affects sound detection (for the implications of anthropogenic noise for the conservation of fish and other animals see Chap. 14). The potential deterring or tissue-damaging effects of anthropogenic noise have been reviewed elsewhere (e.g., Popper and Hastings 2009a, b).

Boats and ships produce an increasing amount of noise, which could change the acoustic scene when a vessel passes, during certain seasons or even throughout a year. In the last decades, noise levels in many habitats have generally increased due to intense ship traffic close to coasts. Andrew et al. (2002, 2011) described an increase in noise levels at the North American west coast of approximately 10 dB at low frequencies. Shipping is the number one factor for this increase. Seasonal changes are pronounced in temperate zones due to human boating and recreational activities during the summertime. Such a seasonal change has been convincingly described by Samuel et al. (2005) in the Peconic Bay Estuary system in Long Island, New York. Between Independence Day and Labor Day the coastal habitats of New York waters are flooded with anthropogenic noise in the frequency range up to 1200 Hz, i.e., within the main hearing and communication range of fishes. During the period of highest human activity, average spectrum levels were about 26 dB higher than during the lowest period of human activity. Although the authors did not concentrate on fishes in particular, their study illustrates that human seasonal activity increases noise levels in coastal waters and that this is probably a worldwide phenomenon.

The main sound energy of surface vessels is almost always located at low frequencies and thus quite often within the hearing and communication range of fishes. The characteristic features of noise of ships and boats depend on propeller, engines, and load and may vary to a certain degree. Amoser et al. (2004) showed that the noise energies emitted by a Class 1 powerboat during a race at Lake Traunsee in Upper Austria peaked at 415 Hz, which is well within the most sensitive hearing range of cyprinids such as the carp *C. carpio* or the roach *Rutilus rutilus* inhabiting this lake. Cyprinids may be masked by this noise up to a distance of several hundred meters but fish lacking hearing specializations such as the coregonid *Coregonus lavaretus* (family Coregonidae) will be affected only at close distance.

The effects of anthropogenic noise from ships and boats on hearing sensitivity of fishes are similar to intense white noise described above in Sect. 4.2.2. Exposing fathead minnow *Pimephales promelas* (family Cyprinidae) to boat noise for 2 h

elevated the hearing threshold in the minnow's most sensitive hearing range (Scholik and Yan 2002b). Masking effects have been demonstrated in representatives of several marine fish families. Vasconcelos et al. (2007) and Codarin et al. (2009) found that ferry and boat noise decrease the hearing sensitivities in the toadfish *H. didactylus*, the goby *G. cruentatus*, the sciaenid *S. umbra*, and the damselfish *C. chromis* between 10 dB and more than 30 dB (Figs. 4.5 and 4.8). The masking effect caused by ship noise as compared to ambient noise was more pronounced in the sciaenid than in representatives of the other families investigated because of its generally higher hearing sensitivities.

While ship traffic noise is the most ubiquitous anthropogenic noise source in aquatic habitats, other noise sources such as, e.g., construction sites or geological surveys can also affect hearing in fishes. Popper et al. (2005) reported 24 h threshold shifts in the northern pike *Esox lucius* (family Esocidae) and the lake chub *Couesius plumbeus* (family Cyprinidae) when exposed to airgun shots of a geological survey in the Mackenzie River Delta.

4.4 Sound Production and Transmission

Representatives of numerous bony fish families possess sound-generating mechanisms and vocalize in agonistic and reproductive contexts (Ladich and Fine 2006; Ladich and Myrberg 2006; Myrberg and Lugli 2006). The main energies of sounds are often concentrated at low frequencies of around 100 Hz or slightly above, based on the contraction rate of drumming muscles (100–200 Hz). In contrast, broadband high-frequency sounds with main energies at or above 1 kHz are found in gouramis, catfishes, and some cyprinids (Ladich 1988, 1997; Ladich et al. 1992) and are produced by sonic mechanisms other than swim bladders (Ladich and Bass 2011).

Are the main energies of sounds and thus sound-generating mechanisms adapted to ambient noise conditions? Do fish produce sound energies at low frequencies to optimize sound transmission and thus increase communication distances? Lugli and Fine (2003) suggest that vocal gobies utilize noise windows for communication. The authors found a quiet window or 'notch' around 100 Hz at noisy locations in shallow streams in northern Italy. The window lies between two noise sources, a low-frequency one attributed to turbulence, and a high-frequency one between 200 and 500 Hz attributed to bubble noise from water breaking the surface (Lugli and Fine 2007). Freshwater gobies such as *Padogobius martensii* and *Gobius nigricans* emit sounds with main frequencies in the 80–200 Hz band (Lugli et al. 2003). Therefore, both species utilize frequencies for sound communication that fall within the low-frequency quiet region of their habitats (Lugli et al. 2003).

In a subsequent paper, Lugli and Fine (2007) extended these observations by investigating particle motion of ambient noise and of vocalizations in addition to acoustic pressure. Gobies lack accessory hearing structures and will therefore only

detect particle motion (particle velocity of particle acceleration) in a sound field but not the sound pressure components. So far the description of sound spectra and vocalizations in fish are almost exclusively based on sound pressure due to a lack of appropriate particle motion detectors. Lugli and Fine (2007) measuring both components with a new underwater acoustic pressure velocity probe found that the ambient noise spectrum is generally similar for sound pressure and particle velocity including the quiet window at noisy locations. The energy distribution of the velocity spectrum is shifted up by 50–100 Hz. The energy distribution of vocalizations was similar for sound pressure and particle velocity for the tonal sound, whereas the pulse-train sound exhibited larger differences. Transmission loss was high for both sound components and amplitudes declined by 6–10 dB/10 cm. The ratio between pressure and velocity did not change with distance from the sound source. The authors argued that SPL measurements, either for environmental noise or sounds emitted by a particle motion sensitive teleost are likely relevant for characterization of the dominant frequencies used for communication in the near field of a sound source.

Lugli (2010) investigated additional habitats such as rocky or sandy shores and found similar quiet windows at 100 Hz (stream, sandy/rocky sea shore) or at 200 Hz (spring, brackish lagoon) (asterisks in Fig. 4.2). The spectrum of the ambient noise showed that fish sound frequencies match the frequency band of the quiet window in several goby habitats (Fig. 4.8). In a further step, Lugli (2010) generalized this result by comparing the main frequencies of mating sounds of representatives of gobies, toadfishes (family Batrachoididae), sculpins (family Cottidae), minnows (family Cyprinidae), and darters (family Percidae) to the frequency band of the quiet window that he found in his study on goby habitats. Although this is only a rough comparison because the noise characteristics of each species' habitat need to be analyzed in detail, it indicates that fish other than gobies might utilize noise windows too (Fig. 4.6).

Crawford et al. (1997) and Speares et al. (2011) described acoustic or noise windows at higher frequencies than those observed by Lugli and coauthors. Crawford et al. (1997) investigated acoustic communication in the weakly electric mormyrid *Pollimyrus isidori* in shallow floodplains of the Niger River in Mali. The main energies of their vocalizations range from 300 Hz up to 2 kHz and fall within an acoustic window, thereby minimizing potential interference with sound sources from other abiotic and biotic sources. Strong high-frequency noise above 4 kHz was thought to emanate from stridulating aquatic insects. Speares et al. (2011) studied the aggressive vocalizations produced by two closely related species of darters, genus *Etheostoma* (family Percidae), and compared the spectrum to that of the ambient noise in their respective microhabitats, namely creeks in Alabama. Dominant frequencies of darters' aggressive drum sounds are concentrated between 100 and 400 Hz, thus avoiding high ambient noise levels at lower frequencies.

Nonetheless, this match of ambient noise windows and sound frequencies in gobies (and perhaps other vocal teleosts) should not conceal that the communication distances are quite short due to low sound levels and due to physical

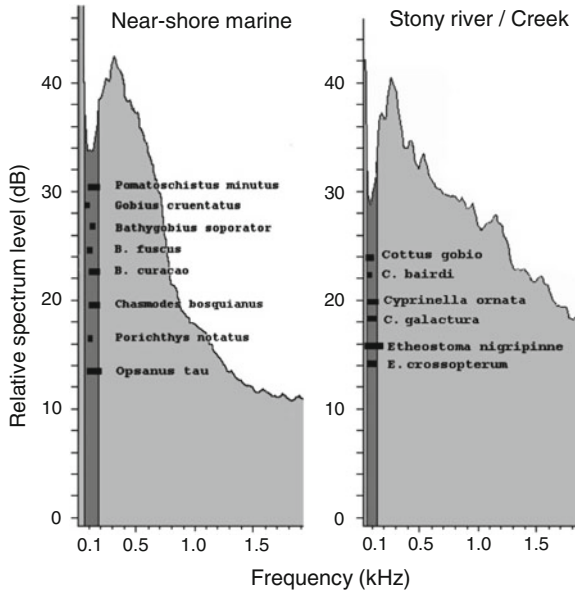


Fig. 4.6 Main frequencies of the mating sound (*dark horizontal bars*) emitted by vocal fish species breeding in near-shore marine habitats (*left graph*) or stony streams and creeks (*right graph*), superimposed on a generic ambient noise spectrum of a breaking wave (*left*), and a small waterfall (*right*), chosen among those available from the study (breaking wave noise spectrum: Rosolina beach, waterfall noise spectrum: Stream Stirone) by Lugli (2010). The low-frequency AN spectrum of both noise sources features a narrow quiet window at around 100 Hz (*dark gray area*). Modified with kind permission from Springer Science + Business Media from Lugli (2010)

constraints in shallow water habitats. Theoretically, only sounds will propagate that have a wavelength shorter than approximately four times the water depth, a phenomenon known as the frequency cutoff phenomenon (Rogers and Cox 1988). For example, frequencies below 750 Hz will not propagate in water shallower than 50 cm, which means that almost all low-frequency sounds produced by fish such as drumming sounds will not propagate at all. Fine and Lenhardt (1983) studied sound propagation and transmission loss of the mating call of the oyster toadfish *Opsanus tau* in water 1 m in depth and found that the fundamental frequency (200 Hz) was 16 dB lower at 1 m and 29 dB lower at 3 m. They conclude that over a sandy bottom communication is restricted within a range of a several meters. Field measurements by Lugli and Fine (2003) on courtship sound transmission in *P. martensii* indicate an attenuation of 15–20 dB over 20 cm at a water depths of 50 cm. Due to the low amplitude of goby sounds (90–120 dB at 5–10 cm), call levels are below the noise level 50–60 cm from the source, even under quiet conditions.

In addition, acoustic windows are not typical in fish utilizing low frequencies for vocalizations. Coers et al. (2008) reported that the ambient noise in a tidal zone

was most pronounced for frequencies below 250 Hz, thus overlapping most of the frequency range used by rock-pool blennies *Parablennius parvicornis* (family Blenniidae) for communication. Similarly to gobies, communication distances are quite short, reaching 25 cm under calm (low tide conditions) and no doubt less under high tide conditions.

In reefs, communication distances are obviously larger than in tidal zones or the very shallow creeks mentioned above. Mann and Lobel (1997) and Mann (2006) estimated that male damselfishes such as *Dascyllus albisella* (family Pomacentridae), which produce pulsed courtship sounds (chirps) to advertise their territories, will be detectable at or beyond 11–12 m from the source. At larger distances, reflection and refraction will affect the temporal, amplitude, and spectral patterns of fish sounds (Fig. 4.7). Studies on the short-range propagation of damselfish sounds showed that amplitude, pulse duration, and pulse frequency varied by as much as 50 % over 10 m (Mann and Lobel 1997). The pulse period of the sound varied the least (by 4 %) of the sound characteristics measured.

Detection distances were also calculated for the silver perch *Bairdiella chrysoura* (family Sciaenidae, drums or croakers) in North Carolina waters by Sprague and Luczkovich (2004). Source levels of individual fish in a chorus ranged from 128 to 135 dB. The maximum distance at which an individual silver perch could be detected by the hydrophone depends on the background noise level

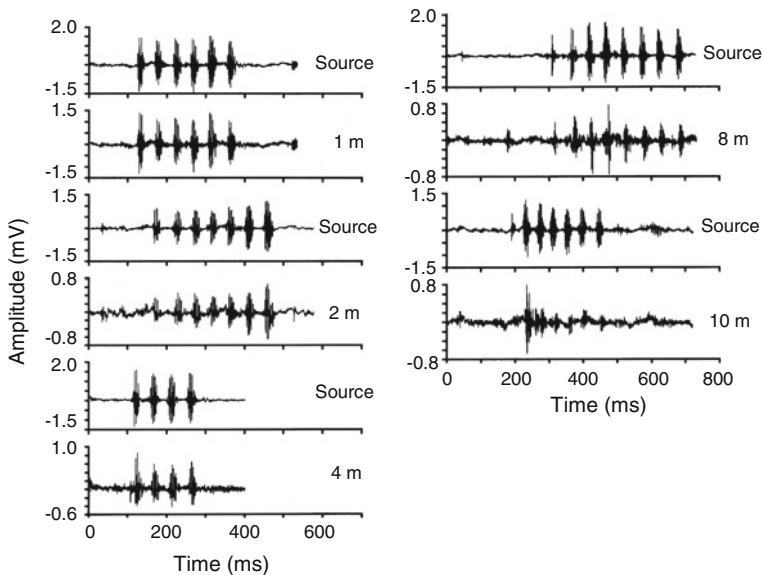


Fig. 4.7 Waveforms illustrating the propagation of damselfish sound over a range of distances. The source waveform shows the damselfish sound at 1 m from the hydrophone, the lower waveform the recording at distances from 1 up to 10 m. The lower waveforms show that amplitudes and pulse duration decrease with distance. Modified with permission from Mann and Lobel (1997). Copyright 1997, Acoustical Society of America

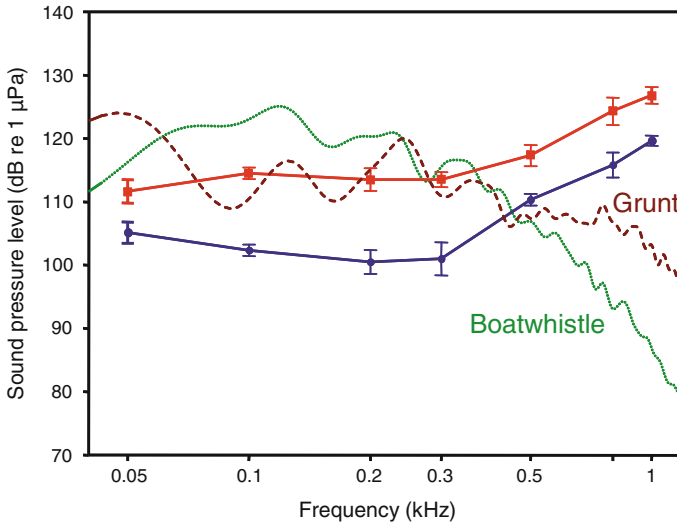


Fig. 4.8 Mean (\pm S.E.) hearing thresholds of the Lusitanian toadfish in the presence of ambient (blue line/circles) and ship noise (red line/squares) as well as power spectra of sounds (boatwhistle—dotted green line; grunt—dashed brown line). The boatwhistle spectrum was calculated from a distance of 20 cm, the grunt train 10 cm away from the calling animals. Modified after Vasconcelos et al. (2007)

and may vary considerably. For the loudest background level recorded a silver perch 1 m from the hydrophone would be undetectable. On the other side on a quiet morning an individual could be heard at more than 100 m. Under conditions recorded in the study, fish were detectable by the hydrophone at 1–7 m.

Investigations on fish communication distances are limited because direct observations are sparse and playback experiments were successful in only a few cases. Proving that fish detect sounds at a certain distance requires observing a phonotactic response (approach to the speaker): ideally, females should approach a speaker so that females are not attracted by visual signals. Field playback experiments in the damselfish *Stegastes partitus* showed that females approach conches, where male sounds emanate over a distance of approximately 10 m (Myrberg et al. 1986). Communication distances in fish beyond this distance have not been proven unambiguously so far. Some fishes, under certain conditions, might be able to communicate acoustically over much larger distances, but communication distances are typically much shorter, on average less than one meter, in many cases merely a few centimeters.

It is interesting to ask why acoustic communication distances in fish are much smaller than those of terrestrial animals such as frogs (Chaps. 5 and 6) or birds (Chaps. 7 and 8) and aquatic mammals such as whales (Chaps. 9 and 10). The reasons for this difference might be the lower levels of fish sounds (e.g., approximately 120 dB at 10 cm in croaking gouramis, family Osphronemidae—Ladich

2007; 126 dB at 1 m in toadfish, family Batrachoididae—Barimo and Fine 1998; 90–120 dB at 5–10 cm in gobiids—Lugli and Fine 2003; 130 dB in drums at 1 m distance—Sprague and Luczkovich 2004) as compared to whales, which reach up to 180 dB and more at 1 m distance (Chap. 9). The frequency cutoff phenomenon in shallow waters may also play a role, making it difficult to propagate low-frequency sound. Despite this frequency cutoff phenomenon, most fish concentrate their sound energies between 100 and 300 Hz (Amorim 2006; Ladich and Myrberg 2006). In contrast, baleen whales utilize low-frequency sounds to communicate over very long distances—hundreds of meters or even several kilometers (Chaps. 9 and 10)—quite the opposite of what is found in fishes. This discrepancy can be explained by differences in the biology of fishes and whales. Fish vocalize regularly close to substrates such as crevices, bottoms of their habitats, coral reefs, floating plants, etc., mostly in shallow waters (cm to m), whereas whales vocalize in open waters at much greater depths, where low frequencies propagate readily.

4.5 Communication

The previous section showed that the auditory sensitivities of fishes are adapted to the ambient noise (at calm conditions) and that fish with improved hearing are masked in noisier regions of their habitats or during noisier time periods (tides, wind, etc.). Communication is not only limited by masking, which decreases the hearing sensitivities, but also by restrictions in sound production and transmission. Most sound-production mechanisms emit low-amplitude low-frequency sounds, which limits the communication distances because of several physical factors in the environments. Factors include the high levels of ambient noise at low frequencies (Figs. 4.1, 4.2, 4.8) and the frequency cutoff phenomenon. Quiet windows at low frequencies may improve communication distances in some habitats, but communication distances remains quite short (<0.5 m). Any increase in the noise level will lower the communication distances even further.

4.5.1 *Animal Acoustic Adaptations to Anthropogenic Noise*

Animals exhibit strategies to cope with anthropogenic noise in their environment. Several animal taxa such as frogs, birds, and mammals, including whales, are able to adapt their vocalizations to increasing noise levels. Frogs can decrease their calling rate and time calling in the presence of anthropogenic noise (Chaps 5. and 6). A number of songbird species such as great tits, nightingales, blackbirds, and robins change their singing behavior in cities as compared to forests and other habitats that are minimally affected by traffic or industrial noise. The main strategies include increasing the SPL or dominant frequencies of songs or shifting

singing to quiet periods of the day (Chaps. 7 and 8). Increasing the sound level is a well-known phenomenon termed Lombard effect (Brumm and Zollinger 2011).

Mechanisms to compensate for increased noise have also been observed in aquatic habitats, where human-made noise has increased significantly over the past century. Aquatic mammals such as whales and manatees change frequencies, sound levels, or call duration in the presence of noise (Chaps. 9 and 10).

4.5.2 Anthropogenic Noise and Communication in Fish

Do certain fish species react similarly to birds and whales in the presence of noise? So far none of these behavioral responses has been described in fishes. We do not know if fish are able to adapt their vocal output to increasing noise levels by calling louder, longer, or at higher frequencies. Our lack of information could reflect the inability of fish to adapt to different conditions in ways similar to birds and mammals or perhaps the inability of researchers to collect long-term data or conduct appropriate experiments in the field or in the lab. Physiological experiments indicate that it is unlikely that there is a Lombard effect in fishes which utilize swim bladder muscles for sound production. Fine et al. (2001) found a small dynamic range in electrically stimulated toadfish sounds. Therefore, toadfish will not be able to increase the amplitude of their sounds. As long as a Lombard effect has not been shown in fishes, we have to assume that increasing noise levels will reduce communication distances. Two recent papers point into this direction. Vasconcelos et al. (2007) investigated the hearing abilities and the ability to detect conspecific sound in the Lusitanian toadfish *Halobatrachus didactylus* (family Batrachoididae) in the Tagus River estuary in the presence of ambient noise and ferry-boat noise. This species has best hearing sensitivities at low frequencies between 50 and 200 Hz, and the main energies of the ferry-boat noise were within the most sensitive hearing range, considerably masking their hearing abilities (Fig. 4.7). Comparisons between masked hearing thresholds and sound spectra of the toadfish's mating and agonistic vocalizations revealed that ship noise decreased the ability to detect conspecific acoustic signals and thus reduced communication distance. Accordingly, we must assume that acoustic communication, which is essential in nest advertisement, during nest defence and mate attraction, is restricted in coastal environments in the presence of human-made noise.

Codarin et al. (2009) examined the effects of hearing and the detection of conspecific sounds in the presence of boat noise in vocal representatives of different families in the Adriatic Sea near Trieste. They investigated the auditory sensitivities, in the presence of boat noise, of the brown meagre *S. umbra*, the Mediterranean damselfish *C. chromis*, and the red-mouthed goby *G. cruentatus*. The thresholds to conspecific sounds were 98 dB for *S. umbra* and 101 dB for *C. chromis* under both quiet lab noise and ambient noise conditions (calm sea), but increased in the presence of boat noise by approximately 20 dB (Fig. 4.9). The

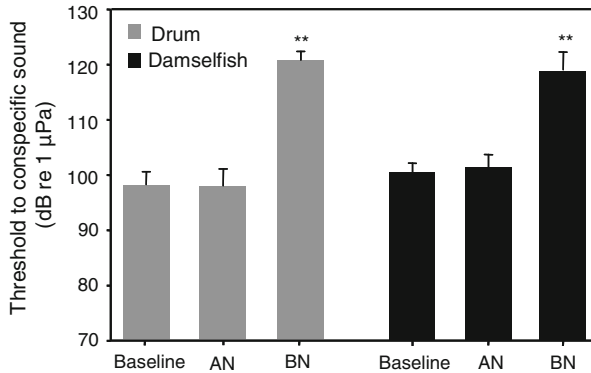


Fig. 4.9 Mean hearing thresholds (\pm S.E.) to conspecific sounds under lab (*baseline*), ambient noise (AN) and boat noise (BN) conditions in the drum *S. umbra* and the damselfish *C. chromis*. Asterisks indicate significant differences between BN and other conditions. Modified from Codarin et al. (2009). Copyright 2009, with permission from Elsevier

authors estimated that the detection distance for the drum's sounds will decrease from more than 100 m down to less than 1 m under boat noise conditions. In the damselfish, which has lower hearing sensitivities, they calculate that, under ambient noise conditions, sounds will be detectable up to 10 m; boat noise, however, would completely mask the signal even at a distance to the vocalizing fish of less than 1 m.

We know little about the responses of fish to increasing ambient noise levels. We do know that fish can modify their vocalizations in response to con- or heterospecifics. Fish such as male haddock *Melanogrammus aeglefinus* (family Gadidae) can modify their fundamental frequency during courtship to a certain degree (Hawkins 1993; Ladich 2004). Note that these frequency modulations were found during courtship or agonistic encounters and reflect different motivational levels. It is unknown if fish can increase their sound frequencies to avoid interference with low-frequency ambient noise. Other potential behavioral responses such as shifting the calling activity to more quiet periods of the day, postponing calling until the noise fades away or alternatively lengthening call durations have also not been described so far. Decreasing the calling activity in the presence of another sound source has been observed in the silver perch *Bardiella chrysoura* (family Sciaenidae) and the gulf toadfish *Opsanus beta* (family Batrachoididae). Luczkovich et al. (2000) found that bottlenose dolphin whistles suppress mating choruses of silver perch and Ramage-Healey et al. (2006) reported that the call rate of the gulf toadfish declines when pop sounds of the bottlenose dolphin were played back.

While acoustic responses to noise have not been observed, we know that fish may avoid loud sound sources. Some flee from rapidly approaching loud underwater noise sources. Underwater video recordings of roaches *Rutilus rutilus* and rudds *Scardinius erythrophthalmus* (both family Cyprinidae) in the Meuse River in

Belgium showed that the fishes actively avoided high-speed boats (Boussard 1981). The flight reactions started at distances of approximately 5 m. Similar responses have been reported regarding fishing vessels: cods *Gadus morhua* significantly altered their behavior during and after the passage of a bottom trawling vessel. According to Handegard et al. (2003), cods initially reacted by diving, then with horizontal movements away from the ship. Besides triggering avoidance behavior, noise can affect the foraging behavior and cause stress in fishes. Purser and Radford (2011) found strong evidence that adding noise affects the attention of fish and increases food handling errors. Furthermore, Wysocki et al. (2006) observed that the common carp *C. carpio*, the gudgeon *Gobio gobio* (both family Cyprinidae), and the European perch *Perca fluviatilis* (family Percidae) responded with increased cortisol secretion when exposed to ship noise (Wysocki et al. 2006). The data indicate that ship noise, characterized by amplitude and frequency fluctuations, constitutes a potential stressor for all three species independently of their different hearing sensitivities (for the implications of anthropogenic noise for the conservation of fish and other animals see Chap. 14).

4.6 Summary and Conclusion

Bony fishes evolved a large number of sonic organs, indicating the importance of sound communication in these animals. Moreover, at least one-third of fishes possess structures enabling them to extend their hearing range to several kilohertz and low sound levels. Numerous studies showed that hearing sensitivities, in particular of taxa with hearing enhancements, decreased when exposed for longer periods to high noise levels or in the presence of moderate noise levels due to masking. Aquatic habitats are characterized by large differences in noise levels and spectral profiles due to numerous abiotic and biotic factors such as running water, wind, tides, vocalizing animals, etc. Currently, we do not know if and how ambient noise and physical constraints such as the frequency cutoff phenomenon limit acoustic communication in fishes. Some light has been shed on these questions; recent studies showed that fish are adapted to ambient noise under calm conditions and that their hearing is masked under more noisy conditions (severe weather conditions, running water).

Most of the fishes communicate over short distances (<0.5 m), probably because of low sound levels and low sound frequencies produced and because of the ambient noise conditions. Some species, e.g., gobies, partly overcome these limitations by exploiting quiet windows in the ambient noise (frequencies of low spectral noise levels) for acoustic communication. However, it remains unclear whether these are adaptations or coincidences, and many more groups need to be investigated to answer this question.

Human-made noise such as ship noise masks hearing and potentially hinders acoustic communication in several marine fish families. We do not yet know if fish are able to cope with noise pollution similar to songbirds and whales by modifying

sound characteristics or calling behavior. It will be an important goal to close these gaps in our knowledge on acoustic communication in fishes in near future. This will help us to assess the impacts of aquatic noise pollution on the fitness of fishes and on fish populations.

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