

Invited Review

Acoustic communication in a noisy world: can fish compete with anthropogenic noise?

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Received 15 September 2013; revised 24 January 2014; accepted 12 February 2014; Advance Access publication 11 March 2014.

Anthropogenic (man-made) noise has changed the acoustic environment both on land and underwater and is now recognized as a pollutant of international concern. Increasing numbers of studies are assessing how noise pollution affects animals across a range of scales, from individuals to communities, but the topic receiving the most research attention has been acoustic communication. Although there is now an extensive literature on how signalers might avoid potential masking from anthropogenic noise, the vast majority of the work has been conducted on birds and marine mammals. Fish represent more than half of all vertebrate species, are a valuable and increasingly utilized model taxa for understanding behavior, and provide the primary source of protein for >1 billion people and the principal livelihoods for hundreds of millions. Assessing the impacts of noise on fish is therefore of clear biological, ecological, and societal importance. Here, we begin by indicating why acoustic communication in fish is likely to be impacted by anthropogenic noise. We then use studies from other taxa to outline 5 main ways in which animals can alter their acoustic signaling behavior when there is potential masking due to anthropogenic noise and assess evidence of evolutionary adaptation and behavioral plasticity in response to abiotic and biotic noise sources to consider whether such changes are feasible in fish. Finally, we suggest directions for future study of fish acoustic behavior in this context and highlight why such research may allow important advances in our general understanding of the impact of this global pollutant.

Key words: acoustic signaling, adaptation, anthropogenic noise, behavioral plasticity, fitness benefits, hearing, masking, pollution.

INTRODUCTION

Anthropogenic (man-made) noise has changed the acoustic landscape of many areas around the globe and is now recognized as a pollutant of international concern (e.g., inclusion in the US National Environment Policy Act and the European Commission Marine Strategy Framework Directive, and as a permanent item on the International Maritime Organization Marine Environmental Protection Committee agenda). Noise-generating human activities in aquatic environments, such as commercial shipping, recreational boating, pile-driving, seismic exploration, and energy production, are widespread and occur with increasing frequency (McDonald et al. 2006; Normandeau Associates 2012). In terrestrial environments, the prevalence of transportation networks, resource extraction, and urban development, for example, is similarly greater now than ever before (Watts et al. 2007; Barber et al. 2009).

In addition to increasing the amount of noise, human activities often generate sounds that are very different from those arising from natural sources (Hildebrand 2009; Popper and Hastings 2009; Normandeau Associates 2012). Common and consistent ambient

noises can exert a strong selective influence on the frequencies used by species to communicate acoustically; adaptation to the acoustic environment can include utilization of available “windows” in the background frequency range (see Brumm and Slabbekoorn 2005; Lugli 2010). Anthropogenic noises often have prominent frequencies within those naturally occurring windows (McDonald et al. 2006; Barber et al. 2009) and thus have the potential to disrupt communication efficiency. More generally, anthropogenic noises may differ from abiotic or biotic sounds in such acoustic characteristics as constancy, rise time, duty cycle, and impulsiveness (Hildebrand 2009; Popper and Hastings 2009; Normandeau Associates 2012). For instance, pile-driving generates high-energy impulsive sounds, which are characterized by a rapid rise time to a maximal pressure value followed by a decay period during which there is gradual reduction in the oscillating maximal and minimal pressure fluctuations. Underwater transmission of explosions includes an initial shock pulse followed by a succession of oscillating bubble pulses. Anthropogenic noise, therefore, presents a very real, and often novel, challenge to animals.

It is well established in humans that anthropogenic noise can cause physiological, neurological, and endocrinological problems; cognitive impairment; sleep disruption; and an increased risk of

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coronary disease (World Health Organization 2011; Le Prell et al. 2012). In the last decade, there has also been a burgeoning research interest in the potential impacts of noise on nonhuman animals; a recent survey of the peer-reviewed literature showed that more than 30% of studies published by the end of 2011 appeared within that last year alone (Radford et al. 2012; see also Morley et al. 2014). Effects have been demonstrated in a variety of taxonomic groups across a range of scales, from the physiology and behavior of individuals to changes at the population and community level (see Tyack 2008; Barber et al. 2009; Slabbekoorn et al. 2010; Kight and Swaddle 2011 for reviews). Despite the overall breadth of considered impacts, one topic—acoustic communication—has dominated research attention; nearly 60% of terrestrial studies, for example, have considered this aspect of behavior (Radford et al. 2012; Morley et al. 2014).

The most obvious way in which anthropogenic noise can disrupt acoustic communication is through masking, whereby there is an increase in the threshold for detection or discrimination of one sound as a consequence of another (Fay and Megela-Simmons 1999; Brumm and Slabbekoorn 2005). Masking can be complete, when the signal is not detected at all, or partial, when the signal is detectable by the listener but the content is hard to understand (Clark et al. 2009). Communication gets more difficult as background sounds increase for all vertebrates that have been studied, including birds, marine mammals, fish, and amphibians (see Fay and Megela-Simmons 1999; Brumm and Slabbekoorn 2005; Clark et al. 2009; Dooling et al. 2009). Individual fitness can consequently be compromised, either through effects on survival, if say signals indicating a predation threat are unheard or altered (Lowry et al. 2012), or as a result of impacts on reproductive success, arising from incorrect assessment of the quality of rivals or potential mates (Halfwerk et al. 2011) or from disrupted communication between parents and offspring (Leonard and Horn 2012). Numerous studies have, therefore, investigated how effective acoustic communication can be maintained despite rising levels of anthropogenic noise; in particular, research has focused on how signalers may enhance the likelihood of being heard and of conveying their intended message accurately.

The vast majority of the work examining how anthropogenic noise affects acoustic signaling behavior has been on birds and marine mammals (e.g., Miller et al. 2000; Slabbekoorn and Peet 2003; but see Sun and Narins 2005; Rabin et al. 2006; Lampe et al. 2012 for exceptions). Although it has become increasingly apparent in recent decades that many fish species also communicate acoustically (Ladich et al. 2006) and that noise has the potential to alter the likelihood of detection of these signals (Amoser et al. 2004; Vasconcelos et al. 2007), the ways in which the acoustic behavior of this taxonomic group is affected by anthropogenic noise has received virtually no direct empirical attention (see Picciulin et al. 2012 for an exception). Fishes represent more than half of all vertebrate species, possess a broad range of hearing and sound-production mechanisms, and exhibit a diverse array of vocal, reproductive, and social traits (Bone and Moore 2008). Consequently, fish are a valuable, and increasingly utilized, model taxa for understanding behavior. Additionally, fish provide the primary source of protein for >1 billion people and the principal livelihoods for hundreds of millions (FAO 2012). Because the majority of fish species live in coastal or freshwater environments, they are exposed to many forms of anthropogenic noise. Therefore, assessing the impacts of noise on fish is of clear biological, ecological, and societal importance.

Here, we begin with brief overviews of acoustic communication in fish and of the evidence that fish can indeed be affected by noise generated from human activities (full reviews of these topics are provided elsewhere). Combined, these bodies of work suggest that fish acoustic communication is likely to be disrupted by anthropogenic noise. We then use studies on other taxa to outline 5 main ways in which animals can alter their acoustic signaling behavior when there is potential masking due to anthropogenic noise and use evidence of evolutionary adaptation and behavioral plasticity in response to abiotic and biotic noise sources to consider whether such changes are feasible in fish. Finally, we suggest directions for future study of fish acoustic behavior in this context and highlight why such research may allow important advances in our general understanding of the impact of this global pollutant.

WHY MIGHT THE IMPACTS OF ANTHROPOGENIC NOISE ON ACOUSTIC COMMUNICATION BE OF RELEVANCE TO FISH?

Acoustic communication in fish

More than 800 species of fish from over 100 families have been documented to produce sounds, and many more are likely to do so (detailed reviews in Tavolga 1971; Myrberg 1981; Hawkins and Myrberg 1983; Ladich et al. 2006; Bass and Ladich 2008). As in other taxa, acoustic characteristics of the sounds produced can vary considerably between species and populations, in relation to gender and size, and with fluctuations in motivation (Hawkins and Rasmussen 1978; Myrberg et al. 1993; Parmentier et al. 2005; Verzijden et al. 2010). Sounds generated by fishes, therefore, provide valuable information in a variety of different contexts, including during territorial disputes and competition for food, predatory attacks, courtship interactions, and spawning aggregations (Myrberg et al. 1986; Hawkins and Amorim 2000; Amorim and Neves 2008). Consequently, there is mounting evidence that acoustic communication can affect the survival and reproductive success of fish (Rowe et al. 2008; Verzijden et al. 2010).

Fishes produce sounds in many varied ways, but they can be broadly divided into those that arise incidentally from another activity and those generated, often by specialized organs or structures, for communication (Tavolga 1971; Bass and Ladich 2008). Unspecialized sounds include those resulting from feeding, movement, or respiration. It is unlikely that these incidental sounds are either under selection pressure or can be controlled flexibly by the individual and thus they probably do not adapt across evolutionary time or exhibit plasticity in response to noise. Actively produced acoustic signals include stridulation, drumming, and stringing. Stridulation involves the rubbing together of mobile bony elements such as teeth, jaws, fin rays, and vertebrae. For example, when damselfish and clownfish open and close their mouths, bringing into contact their pharyngeal teeth, sounds described as pops and chirps are the result (Parmentier et al. 2007). Drumming sounds arise from the high-frequency contraction and relaxation of sonic muscles, which induces vibrations of the swim bladder wall. Cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*), for instance, use this mechanism, with their sounds described as knocks and grunts (Hawkins and Rasmussen 1978). Some species, such as croaking gouramis (genus *Trichopsis*), also generate sound through vibrations of tendons within the pectoral fins (Henglmüller and Ladich 1999). It is more plausible to expect that anthropogenic

noise might result in changes in these specialized types of sounds generated for communicatory purposes.

In general, sounds produced by fish for communication are made up of pulses (Winn 1964; Myrberg and Spires 1972; Bass and Ladich 2008). The wide interspecific diversity in sound characteristics will influence the likelihood of a given species being able to respond to noise created by human activities (see Francis et al. 2011). Moreover, the type and extent of intraspecific variation will determine the capacity to minimize masking arising as a consequence of anthropogenic noise. Although fish sounds most commonly vary in temporal patterning, with receivers usually extracting information from pulse number, duration, and repetition rate, interindividual differences in fundamental and dominant frequency, bandwidth, harmonic structure, and amplitude ratio have also been documented in various species (Hawkins and Rasmussen 1978; Myrberg et al. 1993; Bass and Ladich 2008). Thus, there is certainly the basis for adaptation across evolutionary time. Intraindividual variation in acoustic structure is also known to occur in a range of fishes, with fluctuations in relation to season, time of day, context, level of competition, and motivation (see Bass and Ladich 2008). Although some of this variation is due to differences in parameters such as temperature and circulating androgen levels, which are not under the control of the individual, examples of behavioral plasticity in sound production are becoming apparent (Parmentier et al. 2010; Amorim et al. 2011).

Known impacts of anthropogenic noise on fish

Fish species differ greatly in their hearing abilities as a consequence of differences in ear structure and other anatomical features, such as the presence of a swim bladder (Popper and Fay 1999; Bone and Moore 2008; Popper and Schilt 2008). The most valuable measurements of fish hearing have considered both particle motion and sound pressure (although all fishes can detect the former, only some are sensitive to the latter) and have been carried out in the free field or at specialized acoustic facilities (e.g., Hawkins and Chapman 1975; Popper et al. 2007; Halvorsen et al. 2012). Many other studies have created audiograms (plots of the lowest sound levels detectable at different frequencies) using auditory evoked potential methods in standard tank conditions, which is an approach that is now questioned (see Fay and Popper 2012 for a full discussion). Accurate assessments of precise hearing abilities are therefore relatively rare, but it is clear that although there are some species that can hear above 100 kHz, and many with capabilities above 3 kHz, the majority of fishes are likely to be able to detect sounds from below 50 Hz up to at least 500–1500 Hz (Popper and Fay 1999; Normandeau Associates 2012). Because most anthropogenic activities generate considerable noise at frequencies below 1 kHz (Normandeau Associates 2012), the potential for an impact is readily apparent.

Conclusive empirical evidence for a negative impact of anthropogenic noise on fish is rarer than for other taxa, most notably birds. This is partly due to a smaller research effort to date, partly because observational studies in natural conditions are often difficult to interpret, and partly because experimental work conducted in captivity can indicate an effect of increased noise but lacks ecological validity (see Normandeau Associates 2012; Slabbekoorn 2014 for a full discussion). However, there is sufficient information to suggest that the same range of impacts as found in other taxonomic groups—behavioral responses furthest from the source, with an increasing likelihood of physiological impacts, hearing damage, injury, and death with increasing proximity (Dooling et al.

2009)—may be apparent in fish (see Popper and Hastings 2009; Slabbekoorn et al. 2010; Normandeau Associates 2012 for reviews). It is important to note, though, that different noises can have different effects, and the same or similar noise sources may not affect all species in the same way; intraspecific differences are also likely (see Radford et al. 2014). For example, some fish species but not others may suffer injury or even death when very close to certain, particularly impulsive, sound sources (Keevin and Hempen 1997; Halvorsen et al. 2012). Likewise, some sources of anthropogenic noise have been shown to cause, for instance, temporary threshold shifts (transient reductions in hearing sensitivity) and stress, but only in some of the tested species (Popper et al. 2005, 2007; Wysocki et al. 2006, 2007). Catch rates, as indicators of movement away from a sound source, have also produced contrasting results in different studies (Engås et al. 1996; Løkkeborg et al. 2012).

In general, because they can be caused by lower sound intensities than other potential effects, the most important impacts might be those on behavior, including acoustic communication. The acoustic signals produced by many fish fall within a frequency band between 100 Hz and 1 kHz, making them vulnerable to anthropogenic noise from a variety of sources (Ladich et al. 2006; Bass and Ladich 2008; Normandeau Associates 2012). Several studies have suggested that noise from boat traffic, for example, could reduce the effective range of communication signals and therefore the signaling efficiency between individuals (Amoser et al. 2004; Vasconcelos et al. 2007; Codarin et al. 2009). This is because detection distances are reduced through masking (Codarin et al. 2009) and/or the auditory sensitivities of receivers are diminished (Vasconcelos et al. 2007). Only one study, however, has directly examined how noise might impact fish acoustic behavior. Picciulin et al. (2012) found that the mean pulse rate of brown meagres (*Sciaena umbra*) was higher following repeated, though not single, boat passes compared with during ambient conditions (it was assumed that the noise generated by the boats was the causal effect, although this was not tested directly). The observed increase in vocal activity could have arisen either from an increased density of callers or from an increased acoustic output by those individuals already calling (Picciulin et al. 2012).

HOW MIGHT FISH ACOUSTIC SIGNALERS RESPOND TO ANTHROPOGENIC NOISE?

Fish have not evolved in a quiet environment; as with most animals that communicate acoustically, they face the problem of naturally occurring, potentially masking, noise arising from abiotic sources including wind, rain, and waves and biotic noise from chorusing conspecifics or heterospecifics (see Luther and Gentry 2013). Solutions to ensure the audibility of signals over background noise could be manifested over 3 different time frames (see Brumm and Slabbekoorn 2005). First, acoustic signals might be shaped by natural selection across evolutionary time. Long-term adaptations in response to natural noise have been demonstrated in some fishes (Lugli et al. 2003; Lugli 2010), with interspecific and interpopulation differences in frequency range recorded in a number of species (Hawkins and Rasmussen 1978; Parmentier et al. 2005). Second, an animal could potentially reduce the masking effects of habitat-specific noise by making adjustments to signal properties during its lifetime. Such ontogenetic changes are feasible in species that exhibit vocal learning (e.g., passerine birds; Catchpole and Slater 2008) but are perhaps less likely in fish; although there is evidence of changes in the acoustic characteristics of some fish signals with age, vocal flexibility in this regard has not been documented (see

Vasconcelos and Ladich 2008). Third, animals may exhibit behavioral plasticity to temporary changes in background noise. Some fishes are known to be capable of such acoustic flexibility in certain contexts (Luczkovich et al. 2000; Parmentier et al. 2010; Amorim et al. 2011) although this may be less common than evolutionary adaptation.

Studies of the impact of anthropogenic noise on acoustic signaling in other taxa, primarily in relation to mate choice and territory defense (e.g., Miller et al. 2000; Slabbekoorn and Peet 2003; Luther and Baptista 2010; Bermudez-Cuamatzin et al. 2011), but also parent–offspring communication (Leonard and Horn 2012) and alarm calling (Lowry et al. 2012), suggest 5 main ways in which fish might alter their acoustic behavior. These are not necessarily mutually exclusive—multiple adaptations for communication in noisy conditions could occur (Brumm et al. 2004)—and there may be a trade-off between them—for example, increasing amplitude may be energetically costly and so result in a compromise in terms of signal duration (Fernandez-Juricic et al. 2005). Research investigating responses to nonanthropogenic noise sources allows an assessment of whether these putative changes in signaler behavior might be feasible in fish. However, it is important to note that relevant studies have been conducted on only a small minority of the >32 000 species of known fish; given their great diversity, generalizations should be avoided.

Avoidance of noise

The simplest means of avoiding the potential impacts of anthropogenic noise is to move away from the source. However, this is not always possible if the source dominates certain frequencies, as is the case with low-frequency shipping noise (Wright et al. 2007), or if an entire area is affected, as might occur in harbors and estuaries subjected to large amounts of shipping. Also, if a species is dependent on a particular area because of crucial resources, such as food or nesting sites, or is restricted by the geography of the region, then there may be no option but to remain despite the noise. An alternative way to maximize signal transmission is through temporal adjustments in communication, taking advantage of inherent gaps or fluctuations in competing noise to enhance the likelihood of signal detection and discrimination. A number of diurnal bird species have been shown to sing more at night when there is greater daytime competition from similar sounding species (see La 2012) and that adjustment in timing might also be selected for in response to sources of anthropogenic noise that are variable over time. For example, by singing at night in areas where there are high levels of daily urban noise, European robins (*Erithacus rubecula*) may benefit from minimizing acoustic competition or from an increase in the clarity of their signal (Fuller et al. 2007).

A single study of silver perch (*Bairdiella chrysoura*) provides the only suggestion to date that adaptive suppression of calling in response to external stimuli might occur in fish. Following natural occurrences or playbacks of whistles from bottlenose dolphins (*Tursiops truncatus*), a major predator of the perch, sound levels recorded from the chorusing fish were significantly reduced (Luczkovich et al. 2000). This reduction is most likely due to the cessation of calling by individuals close to the sound source, although it is also possible that fish in the vicinity moved away from the potential danger, causing a decrease in the amplitude of the chorus (Luczkovich et al. 2000). Either response would also aid in minimizing acoustic overlap with a nonthreatening but potentially masking influence (i.e., anthropogenic noise) although that remains to be tested directly. Moreover,

it is currently unknown if the ability to adjust calling flexibly in this way exists in other fish species.

Temporal adjustments

Perceptual studies have shown that the detectability of brief acoustic signals is considerably enhanced by increasing their duration, as a consequence of the temporal summation of signal energy in the peripheral auditory system of receivers (see Brumm and Slabbekoorn 2005). Some animals, such as common marmosets (*Callithrix jacchus*) and killer whales (*Orcinus orca*), appear to take advantage of this effect by extending the duration of their calls in response to temporarily elevated, man-made noise (Brumm et al. 2004; Foote et al. 2004). For longer acoustic signals, an increase in duration cannot be explained by exploitation of temporal summation but could increase the probability that some of the signal is given during a quieter period in terms of the background noise; this could be the case with some whale vocalizations (e.g., Fristrup et al. 2003; Di Iorio and Clark 2010). The likelihood of detection can also be enhanced through increased redundancy, achieved either by repeating the signal or through an increase in the rate of calling. Various whale, frog, and bird species have been shown to respond in this way to either playback or natural sources of anthropogenic noise (Lesage et al. 1999; Kaiser and Hammers 2009; Diaz et al. 2011).

The potential for evolutionary changes in the temporal structure of fish acoustic signaling is evidenced by the geographic variation observed in the skunk clownfish *Amphiprion akallopisos*, with populations in Indonesia and Madagascar having different call characteristics (Parmentier et al. 2005). The pulse duration of “short pops,” 1 of 3 call types produced, is longer in the Madagascan population, but the number of peaks per pulse is higher in the Indonesian population. For “long pops,” pulse period is longer, but the number of peaks is lower in the Indonesian population compared with the Madagascar population. It is not known whether the call parameters are different because of adaptation to different local abiotic or biotic sources of noise or as a consequence of genetic drift in reproductively isolated populations (Parmentier et al. 2005). However, there clearly exists the capacity for changes in the duration and rate of calling over evolutionary timescales, at least in this species.

There is also evidence that some fishes can respond flexibly in terms of the temporal structure of their calling. For example, certain damselfish (Pomacentridae) produce acoustic signals with different pulse rates depending on whether they are interacting agonistically with conspecifics or heterospecifics (Mann and Lobel 1998; Parmentier et al. 2010). Other species, such as the gulf toadfish (*Opsanus beta*), reduce their call rate when a predator is nearby (Remage-Healey et al. 2006). Male gulf toadfish, which produce a characteristic boatwhistle advertisement call to attract females, have also been shown to increase their call rate to compete acoustically with nearby rivals (Fine and Thorson 2008). A more recent study on Lusitanian toadfish (*Halobatrachus didactylus*) has demonstrated that males reduce their call duration and pulse period at low tide (Amorim et al. 2011), potentially because low-frequency sound rapidly attenuates in shallow water, so any calls produced would not be detected by distant females (Mann 2006). Behavioral plasticity in response to anthropogenic noise might, therefore, be feasible in terms of such acoustic characteristics.

Amplitude shifts

Animals experiencing elevated noise levels may increase the signal-to-noise ratio during communication by raising the amplitude of

their vocalizations, a response known as the “Lombard Effect” (Brumm and Zollinger 2011). To date, the Lombard Effect in response to anthropogenic noise has been demonstrated in a variety of species, including beluga whales (Lesage et al. 1999), killer whales (Holt et al. 2009), common marmosets (Brumm et al. 2004), domestic fowl (*Gallus gallus domesticus*: Brumm et al. 2009), and nightingales (*Luscinia megarhynchos*: Brumm and Todt 2002; Brumm 2004). Nightingales in noisier territories were neither bigger nor heavier than those in quieter territories, eliminating the possibility that the ability to sing at higher amplitudes is only exhibited by individuals that are big enough to enable them to do so (Brumm 2004). Brumm and Todt (2002) also demonstrated that nightingales do not just sing at maximum amplitude but regulate vocal intensity depending on the level of masking noise and whether it is within the spectral region of their own songs.

To date, there is little evidence that fish adjust the amplitude of their acoustic signaling in response to background noise. Whether they have the capacity to do so is likely to be constrained by body size as well as by the energetic costs of producing louder sounds (see Oberweger and Goller 2001). It is notable that all the existing examples of the Lombard effect are from birds and mammals. Although anurans, for example, are capable of varying the amplitude of their calls, there is no evidence that they do so in response to elevated noise levels (see Love and Bee 2010). It is also likely that noise-dependent regulation of signal amplitude does not occur in insects because there seems to be strong selection for increased loudness in this group, meaning they are often signaling close to their power capabilities anyway (Gerhardt and Huber 2002). As with many insects and frogs, fishes often call in aggregations (e.g., Luczkovich et al. 2000; Amorim et al. 2011) where a Lombard effect would quickly escalate and lead to all males signaling at maximum levels (Brumm and Zollinger 2011). Another potential reason for a lack of control over the amplitude of acoustic output would be if auditory feedback does not play a role in sound production; this is known to be the case with stridulating insects (reviewed in Gerhardt and Huber 2002), but whether it is also the case in fish requires further research before conclusions can be drawn.

Frequency shifts

Laboratory studies have shown that sounds with a greater bandwidth and a higher rate of frequency modulation are harder to detect from noise (Lohr et al. 2003), and animals in habitats with high levels of natural noise converge on vocalizations with primarily pure tones (e.g., Dubois and Martens 1984). To date, only one study has documented such a change in response to anthropogenic noise, with red-winged blackbird (*Agelaius phoeniceus*) songs exhibiting increased signal tonality due to an emphasis on lower frequencies (Hanna et al. 2011). More commonly, birds and cetaceans produce songs or calls with a higher average minimum or fundamental frequency at times or in areas with more low-frequency noise from sources such as traffic and seismic surveys (Lesage et al. 1999; Slabbekoorn and Peet 2003; Fernandez-Juricic et al. 2005; Parks et al. 2007). There are also examples of animals adjusting the relative amplitude of different frequency components: California ground squirrels (*Spermophilus beecheyi*), for instance, shift the peak energy of their calls from lower to higher harmonics when there is low-frequency noise from wind turbines (Rabin et al. 2006). Frequency shifts in response to noise could arise through evolutionary adaptation, as evidenced by a 30-year study of white-crowned sparrow (*Zonotrichia leucophrys*) songs: there was an increase in minimum frequency as urban noise increased across time (Luther and

Baptista 2010). A frequency change could also come about through behavioral plasticity if individuals prioritize the use of higher frequencies within their existing repertoire. Such acoustic flexibility has been demonstrated experimentally in birds, with individual house finches (*Carpodacus mexicanus*) exposed to playback of urban noise increasing the minimum frequency of their song elements and also decreasing the frequency when lower levels of anthropogenic noise were transmitted (Bermudez-Cuamatzin et al. 2011).

Two Italian freshwater gobies (*Padogobius martensii* and *Gobius nigricans*) provide evidence that some fishes can adapt their call frequencies in response to abiotic noise sources. The gobies inhabit environments where waterfalls produce low-frequency noise but with a quiet window in the noise spectrum around 100 Hz (Lugli et al. 2003). Both species exhibit the highest sensitivity to sound at 100 Hz and produce sounds with a fundamental frequency from 73 to 200 Hz (Lugli et al. 2003). Frequency differences between different populations of the same species of skunk clownfish (*A. akallopisos*) (Parmentier et al. 2005) also suggest the possibility of adjustments over evolutionary timescales. Although it was initially considered unlikely that fish could flexibly modulate their call frequencies (see Bass and Ladich 2008), a recent study has shown that male Lusitanian toadfish calling at low tide increase their fundamental frequency; as low-frequency sound rapidly attenuates in shallow waters, this is likely to enhance the transmission of their calls to females (Amorim et al. 2011). There is thus at least the potential for such adjustments in response to anthropogenic noise. Species that characteristically have higher frequencies within their repertoire may be better able to respond to anthropogenic noise in such fashion (see Francis et al. 2011). Different fish species produce acoustic signals in different frequency ranges although they are often structurally much simpler than, for example, birdsong, which may provide reduced opportunities for immediate flexibility.

Change in signaling modality

Animals may also increase the efficacy of communication amid noise by shifting emphasis to another modality (Brumm and Slabbekoorn 2005; van der Sluijs et al. 2011). The “redundant signaling” hypothesis proposes that animals have multiple signals so that if one modality fails to transmit to the receiver, other signals will successfully convey the message (Johnstone 1996). Many animal displays include various signal components, often in 2 or more sensory modalities (e.g., Candolin 2003). However, to the best of our knowledge, empirical testing of this possibility in response to anthropogenic noise has yet to be undertaken in any taxa.

Some fish species are certainly capable of shifting signaling modalities depending on present conditions. For example, the relative importance of visual and olfactory cues in determining the mate preference of female three-spined sticklebacks (*Gasterosteus aculeatus*) differs in clear versus turbid water (Heuschele et al. 2009). The potential for anthropogenic noise to alter the relative importance of different sensory modalities, therefore, seems likely in at least some species. Mate selection in Lake Malawi rock-dwelling cichlids, for instance, depends on visual, chemical, and acoustic cues (Plenderleith et al. 2005; Amorim et al. 2008). If boat traffic noise were to increase the masking of the latter, then a shift toward one or other modality might be expected. It is worth bearing in mind that signals in different modalities have different advantages and disadvantages. In most terrestrial habitats, for example, visual displays act at a much shorter range than acoustic signals and thus long-range aspects of acoustic cues may not be readily compensated for by visual alternatives. However, the more intense the

background noise (and, as a result, the shorter the communication range of acoustic signals), the more important short-range visual signals will become. For fishes, the trade-off may be somewhat different, as acoustic communication tends to be over relatively short distances compared with, say, birdsong.

MOVING FORWARD

Although there is undoubtedly a rapidly increasing research interest in the impacts of anthropogenic noise in general, and on acoustic communication in particular, there are a number of steps that we suggest would enhance considerably our current understanding.

Realistic masking experiments

Much early research examining the potential impact of anthropogenic noise used correlative, observational data and thus did not provide suitable controls for potential confounding factors (see Radford et al. 2012; Morley et al. 2014). If the effects of noise at different natural sites are to be compared, ideally these should be matched for other variables (see Francis et al. 2009, 2011). Ultimately, however, it is carefully controlled experimental manipulations (e.g., Bermudez-Cuamatzin et al. 2011; Halfwerk et al. 2011) that are crucial to tease out the direct effect of noise and thus provide the strongest possible conclusions.

High-quality noise-related experiments require accurate and suitable characterization of the sound source (see Schaub et al. 2009; Morley et al. 2014). Underwater sound includes 2 components: pressure (as detected by humans) and particle motion, which results from the oscillatory displacement of particles back and forth within a propagating sound wave. Although some fish species are sensitive to sound pressure, all detect particle motion and thus measuring this element of a sound source and determining the masking impact are critical (see Normandeau Associates 2012). Moreover, variation in characteristics beyond just absolute amplitude should be considered; for instance, differences in temporal patterns and fluctuations in periodicity, frequency, and amplitude may well result in different impacts. Relatively loud, continuous noise might be expected to lead to long-term acoustic adjustments, whereas fluctuating noise levels might result in acoustic plasticity (see Luther and Gentry 2013 and references therein).

As with all experimental research, there are likely to be advantages and disadvantages to different approaches (Slabbekoorn 2014). Captive studies often allow behaviors to be examined in greater detail than those conducted in the wild, as well as offering potentially more control over the conditions and contexts of the focal animals. However, aquatic tank setups result in complex sound fields (e.g., Parvulescu 1964); although it is possible to determine the potential for an effect of additional noise, assessments of absolute values for masking and the scale of impact are not feasible. Moreover, captive animals are usually more constrained than in the wild and may not exhibit their full behavioral repertoire. Studies in the wild do not suffer from these issues, thus providing ecological validity, but they can be logistically much more challenging and do not normally allow the same level of control, providing more limited information in terms of subtle responses. Given the current dearth of detailed knowledge relating to the impact of anthropogenic noise in general, and on acoustic signaling in fish in particular, we would advocate a complementary approach, including full consideration of the relevant limitations where appropriate (see also Slabbekoorn 2014). In general, masking experiments should include readily controllable noise sources; the potential to

manipulate and measure the magnitudes, direction, and spatial characteristics of both particle motion and sound pressure; and the ability to collect and analyze response variables of most relevance.

Receiver's perspective

Acoustic communication of course entails not only the actions of the signaler, as considered in this review, but also signal perception and discrimination on the part of the receiver. Sensory adaptations and perceptual flexibility to enhance extraction of signals from background noise include selective attention and auditory stream segregation, mechanisms to counteract constraints on discrimination, and improvements in detection thresholds (see Brumm and Slabbekoorn 2005). Such evolutionary adaptations and behavioral plasticity are relevant not only to acoustic communication but also to the use of natural sounds for habitat selection, settlement, predator avoidance, and prey detection (e.g., Simpson et al. 2005, 2011; Schaub et al. 2009). However, although examples of these receiver abilities in relation to natural noise sources are readily apparent in a variety of taxa, including fish (Fay and Edds-Walton 1997; Lugli et al. 2003), far less research attention has focused on how anthropogenic noise affects receivers compared with signalers. Moreover, assessments of fish hearing have rarely been conducted in acoustical conditions that allow accurate measurement of the true sound field in terms of both sound pressure and particle motion (Fay and Popper 2012) and thus precise hearing thresholds for most species are not yet known (see above). Use of current hearing-assessment methods do potentially allow comparative research, as long as all measurements are conducted in the same laboratory using the same equipment, and thus provide an important tool when considering the possibility of temporary or permanent threshold shifts; if the hearing ability of the receiver is detrimentally affected by anthropogenic noise, then acoustic communication will be compromised (Vasconcelos et al. 2007).

Nonmasking effects of noise

In addition to masking signals, anthropogenic noise might also affect acoustic communication in various indirect ways (Naguib 2013). For instance, studies have shown that noise can cause stress in a range of taxa, with some preliminary indications in fish (e.g., Wysocki et al. 2006, but see Wysocki et al. 2007), and stress can affect individual performance and decision making, with consequences for any behavior, including communication (Kight and Swaddle 2011). Moreover, noise may be distracting, shifting attention away from signals of relevance as well as impairing cognitive performance; animals have a finite capacity to attend simultaneously to multiple stimuli (Chan and Blumstein 2011). Work in non-communicative contexts has demonstrated that additional noise in the environment can potentially distract fish and detrimentally affect behavioral performance (Purser and Radford 2011). Noise can also influence habitat choice, individual spacing, and population density (Francis et al. 2009; Simpson et al. 2010); although less is known about such effects in aquatic environments compared with terrestrial species, there is evidence that anthropogenic noise can at least temporarily affect space use by fish (Engås et al. 1996; Holles et al. 2013). Alterations in the way conspecifics are distributed in the environment could have consequences for the likelihood of detecting particular signals, the number of rivals or potential mates that can be assessed, and the effort and resources needed to acquire that information; noise could influence not just individual communicative interactions but information flow through conspecific

networks and whole communities (Naguib 2013). As yet, there is hardly any empirical work assessing these indirect consequences of anthropogenic noise on acoustic communication, and certainly not in fish.

Fitness consequences

The vast majority of experimental studies investigating anthropogenic noise have, to date, considered relatively short-term effects (see Radford et al. 2012; Morley et al. 2014 and references therein). However, both for fundamental scientific progress in this field and for successful policymaking and mitigation, assessments of the likely impacts on individual survival and reproductive success are vital. Some short-term effects (e.g., increased predation risk) can be translated relatively easily into ultimate fitness consequences; others, including acoustic communication, need more careful consideration because animals may be able to compensate in some way and thus there may be no direct link between short- and long-term impacts (Bejder et al. 2006). Although the masking of communication signals elicits demonstrable behavioral changes in many passerine bird species and marine mammals, for instance, there is little evidence to support resultant changes in fitness. That is not to say changes in fitness do not arise, but rather that the experiments required to determine them have rarely been conducted (but see Halfwerk et al. 2011; Kight et al. 2012). Moreover, adjustments in acoustic signaling may result in greater energetic needs, an increased likelihood of detection by predators, or the loss of vital information, but these costs are rarely considered (see Read et al. 2014). Among aquatic organisms, fish offer a more feasible opportunity than marine mammals for a direct examination of the benefits and costs of acoustic alterations made in response to anthropogenic noise and thus to determine the impact on individual fitness and population viability.

CONCLUSIONS

The human population is projected to increase by 2.3 billion between 2011 and 2050 (United Nations 2011) and thus noise pollution is not just a pressing issue, but one of growing concern. There is increasing recognition that sublethal impacts of anthropogenic noise are perhaps the most important considerations for populations of animals. Potentially, our greatest knowledge in this regard currently relates to acoustic communication and particularly the way signalers minimize the risk of masking; certainly, this is the research topic that has so far received the most attention. But, there is a strong taxonomic bias in those studies that have been conducted; the majority focus on birds and marine mammals. Although the range of sounds made by fishes is not as diverse as in those taxa, their acoustic communication is also likely to be affected by anthropogenic noise and their biological and societal value mean that research into potential negative impacts is important.

The evidence available from other fields suggests that some species of fish have the potential to compete with anthropogenic noise; there are at least some of the same capabilities as birds and mammals in terms of adaptation or flexible adjustment in their acoustic signaling. Perhaps the most likely responses to anthropogenic noise are changes in temporal patterning and signal modality although alterations in frequency parameters and when to call may also be feasible in some cases. The likelihood that a given species will be able to respond in suitable fashion to a particular noise source, and thus maintain efficient acoustic communication, will depend on the mechanism of its sound production (not something that varies so considerably in birds and mammals), the types of sound produced,

and the intraspecific and intraindividual levels of variation shown. It is worth emphasizing that the body of relevant empirical work is currently very limited, and the huge diversity among the more than 32 000 species of fish means that extrapolations should be treated with extreme care. The same noise may affect species differently, different impacts can be expected at different spatial scales, and there may also be variation between individuals of the same species and even differences by the same individual depending on condition, state, and motivation. Clearly what is needed now are experimental tests of these ideas, both to enhance our understanding of how fish respond to anthropogenic noise and because studies of this taxonomic group present an ideal opportunity to take the whole field forward in exploring the ultimate effects of this global pollutant on individual fitness, population viability, and community structure.

FUNDING

A.N.R. and S.D.S. were partly supported by Department for Environment, Food and Rural Affairs (DEFRA) contract ME5207; S.D.S. was also supported by Natural Environment Research Council (NE/J500616/2).

We are grateful to J. Purser, R. Bruinjes, E. Morley, I. Voellmy, S. Holles, M. Wale, K. Everley, and T. Hawkins for fruitful discussions and to 2 anonymous referees for helpful comments on the manuscript.

Forum editor: Sue Healy

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