The Effects of Noise on Animals

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13.1 Introduction

Noise is ubiquitous in all animal habitats, often at substantial levels (Brumm and Slabbekoorn 2005). Habitats typically contain a myriad of geophysical, biological, and anthropogenic sounds, which constitute the local soundscape (see Chap. 7). Some of these sounds can interfere with the life functions of animals and hence are often referred to as "noise" (American National Standards Institute 2013).

Communication plays a critical role in animals' life functions as it is the foundation for social relationships among animals. However, acoustic communication often is constrained by background noise, which reduces the signal-to-noise ratio (SNR) and thus the signal detection and discrimination success of receivers. In terrestrial habitats, natural, abiotic noise is caused by wind, precipitation, thunder, running water, and seismicity. Birds, frogs, insects, and mammals create biotic noise. In aquatic environments, natural, abiotic noise is caused by wind, precipitation, breaking waves, polar ice break-up, and natural seismic activity. Biotic noise sources include shrimps, fishes, and marine mammals.

Such natural noise has been shown to interfere with sound usage by animals. For example, wind noise might interfere with marine mammal communication, and as a counteraction, humpback whales (*Megaptera novaeangliae*) increase the sound pressure level of their sounds as a function of increasing wind noise level (Dunlop et al. 2014). Also, animals of the same or different species can interfere with sound usage. Snapping shrimp are known to mask toothed whale biosonar (Au et al. 1974, 1985) and harp seals (*Pagophilus groenlandicus*) have been shown to

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increase their call repetition to be heard above the chorus of their conspecifics (Serrano and Terhune 2001). Similarly, king penguins (*Aptenodytes patagonicus*; Aubin and Jouventin 1998), zebra finches (*Taeniopygia guttata*; Narayan et al. 2007), and big brown bats (*Eptesicus fuscus*; Warnecke et al. 2015) communicate in a cacophony of conspecific calls. Animals have evolved sound production and reception capabilities in natural biotic and abiotic background noise. However, anthropogenic noise is fairly recent on evolutionary time scales. Researchers have tried to assess whether existing adaptations are sufficient for animals to deal with anthropogenic noise.

Anthropogenic noise in terrestrial environments originates from road traffic, trains, aircraft, industrial sites, energy plants, construction machinery, etc. Anthropogenic noise in aquatic environments originates from recreational boating, commercial shipping, commercial fishing, offshore hydrocarbon and mineral exploration, hydrocarbon production, mineral mining, marine construction, offshore renewable energy production, military activities, etc. Such anthropogenic sounds, in air or water, have distinct "sound signatures," and their contributions to the marine and terrestrial soundscapes are discussed in Chap. 7.

The effects of anthropogenic noise have been studied extensively in humans (Kryter 1994); however, less is known about how human-generated noise affects other animals. Four edited books (Brumm 2013; Popper and Hawkins 2012, 2016; Slabbekoorn et al. 2018a) and some journal special issues (Erbe et al. 2016b, 2019c; Le Prell et al. 2019; Thomsen et al. 2020) compile many examples outlining the effects of noise. The effects of anthropogenic noise on animals are a growing concern, having resulted in an exponential increase in the number of research publications on this topic (Williams et al. 2015).

What are the effects of anthropogenic noise? They can vary from mere auditory sensation, mild and temporary annoyance, brief behavioral changes, temporary avoidance of an area, and masking to long-term changes in the usage of important feeding or breeding areas, prolonged stress, hearing loss, barotrauma (in aquatic species), injury, and ultimately death (Kight and Swaddle 2011). In addition to such direct effects of noise, there may be indirect effects (e.g., when a prey species is impacted, leading to reduced prey availability). The effects of noise do not always have to be negative from the animals' point of view. In some cases, animals actually use anthropogenic sounds to their advantage. For example, the sound of a dumpster lid closing in a campground might indicate a food source to some birds and mammals. Underwater sounds from ships can increase the settlement, growth rate, and absolute growth of biofouling organisms such as bryozoans, oysters, calcareous tubeworms, and barnacles (Stanley et al. 2014). Sounds from fishing vessels may attract birds, seals, and dolphins, which then feed on the bait or catch (Söffker et al. 2015). This attraction to a food source elicited by anthropogenic noise is called the "dinner bell effect."

In terms of the potential negative effects of anthropogenic noise on animals, Fig. 13.1 shows a generalized view of increasingly severe effects closer to the noise source. Depending on where the noise source and the receiving animals are located in space, received noise will differ in spectral and temporal characteristics (see Chaps. 5 and 6 on sound propagation in air and water, respectively). While there are widely varying sound propagation conditions depending on the specific environment in which a sound is produced and received, received levels generally attenuate or decrease as sound propagates from its source. Given that no habitat is acoustically homogeneous or isotropic, received levels vary with azimuth (direction) and inclination (height or depth), leading to different impact ranges in all directions.

The absolute range and order of noise impact severity can differ based on features of the propagation environment, exposure context, and species involved (Ellison et al. 2012). In general, at the longest ranges, a noise might barely be audible to an animal and may be less likely to have any negative effect. Audibility of a noise depends on its amplitude and spectrum, propagation

Fig. 13.1 Sketch of generalized ranges from a noise source, at which different types of impact may occur
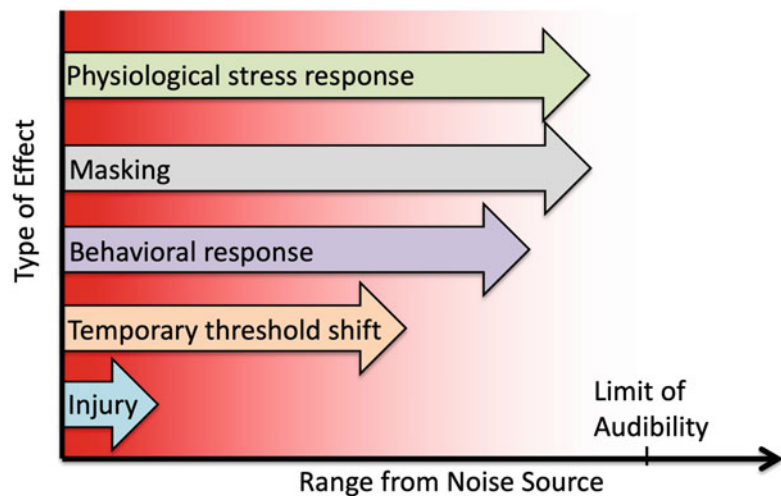
conditions from the source to the receiver, ambient noise conditions, and hearing abilities of the animal.

Stress is a physiological response, which might occur at long and short ranges and at low and high noise levels. Stress can be a direct response to noise (e.g., if a novel noise is suddenly heard) and an indirect response to noise (e.g., if masking causes stress). Stress can affect numerous life functions (including immune response, reproductive success, predator avoidance, etc.; Tarlow and Blumstein 2007).

Acoustic masking might occur over long ranges when a distant noise masks a faint signal. Masking is the process (and amount) by which the audibility threshold for a sound is raised by the presence of another sound (i.e., noise; American National Standards Institute 2013).[1] The higher the noise level is, the greater the masking effect. Masking can interfere with signals important to animals, such as their social communication calls, mother-offspring recognition sounds, echolocation signals, environmental sounds, or sounds by predators and prey (Dooling and Leek 2018). The animal's auditory system splits incoming sound into a series of overlapping bandpass filters, thus optimizing SNR in the

bands occupied by the signal and enabling parallel processing (Moore 2013). The critical ratio is the most commonly measured parameter related to auditory masking. It is defined as the mean-square sound pressure of a narrowband signal (e.g., a tone) divided by the mean-square sound pressure spectral density of the masking noise at a level, where the signal is just detectable (see Chap. 10 on audiometry; International Organization for Standardization 2017). There are two categories of masking. Energetic masking occurs when the masking sound overlaps with the signal in both frequency and time, such that the signal is inaudible. Informational masking occurs later in the auditory process; the signal is still audible, but it cannot be disentangled from the masker (Moore 2013).

Somewhat closer to the source, changes in behavior of varying severity might be seen. An animal might change its orientation, cease prior behavior (e.g., feeding), move away from the source, or alter its vocal behavior, which may have implications for social functions.

Animals must be closer to sound sources to receive sound levels sufficiently high for noise-induced hearing loss (NIHL). NIHL results from overstimulation of the sensory cells in the inner ear, leading to metabolic exhaustion of the hair cells, damage to the organ of Corti, and in extreme cases, degeneration of retrograde

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[1] ANSI/ASA S1.1 & S3.20 Standard Acoustical & Bioacoustical Terminology Database; https://asastandards.org/asa-standard-term-database/

ganglion cells and axons. NIHL includes both temporary and permanent loss of hearing, termed temporary threshold shift (TTS) and permanent threshold shift (PTS), respectively. Both TTS and PTS depend on the spectral and temporal (duration of exposure and duty cycle) characteristics of the noise received (Moore 2013; Saunders and Dooling 2018). TTS, by definition, is recoverable, but the time to recover depends on the amplitude, frequency, rise time, and duration of noise exposure. While experiencing TTS, animals could have a decreased ability to communicate, interact with offspring, assess their environment, detect predators or prey, etc. While TTS implies a full recovery without physical injury, TTS might still involve submicroscopic physical damage. Kujawa and Liberman (2009) showed that for high levels of TTS, sensory hair cells appear unharmed, yet afferent nerve terminals might be injured leading to cochlear nerve degeneration. Death of sensory hair cells in the ear, damage to the auditory nerve, or injury to tissues in the auditory pathway may lead to PTS (Liberman 2016).

At high levels of noise exposure, animals may incur injury (i.e., acoustic trauma) to tissues and organs, such as damage to ear bones, lungs, kidney, or gonads (Popper et al. 2014). In aquatic species, fast changes in pressure can cause blood gases to exit solution and gas-filled tissues or organs (e.g., swim bladders in fish) to expand and contract rapidly, which may damage surrounding tissues and organs (e.g., rupture the swim bladder). Rapid changes in sound pressure are more likely to cause damage than gradual changes (Popper et al. 2014).

Whether the effect of noise is auditory, behavioral, or physiological, individual animals of the same species or population respond at different ranges and in different ways. Age, health, sex, individual hearing abilities, prior experience (habituation versus sensitization), context, current behavioral state, and environmental conditions may all affect the responses of individuals. For example, bowhead whale (*Balaena mysticetus*) and gray whale (*Eschrichtius robustus*) responses to seismic surveys ranged from none-observed to moderate (i.e., changing vocalization rates and
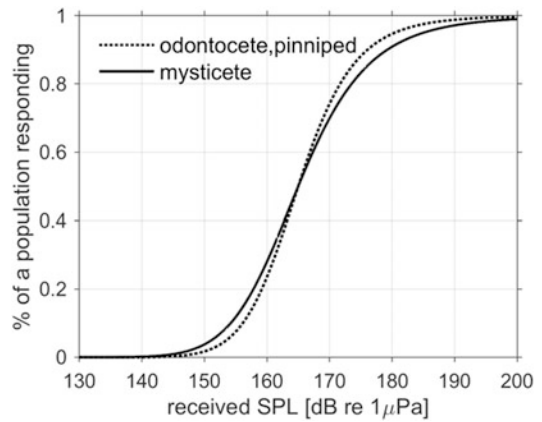

Fig. 13.2 Example of a historical dose-response curve based on received exposure level as a metric of sound dose used to assess the likelihood of bioacoustic impact from mid-frequency sonar (Department of the Navy 2008). Half of a population was modeled to respond at 165 dB re 1 μPa, with fewer animals responding at lower levels, and more animals responding at higher levels

swimming behavior; Blackwell et al. 2015; Malme et al. 1983; Miller et al. 2005). Therefore, some studies have developed a dose-response curve (Fig. 13.2) relating likelihood of response (or percentage of a population that might respond) to the received level of the specific source of noise under consideration (e.g., Hawkins et al. 2014; Miller et al. 2014; Williams et al. 2014).

The effects of noise discussed so far, and the concepts of impact ranges (Fig. 13.1) and dose-response curves (Fig. 13.2) relate to acute noise exposures (e.g., to a single discharge of a seismic airgun array or a single supersonic overflight). The scientific difficulty is to link short-term, individual impacts to long-term, population-level impacts, considering that animals might travel and be exposed to aggregate noise from multiple sources distributed through space and time. While some studies have documented long-term reductions in species abundance and diversity (e.g., near highways or in industrialized areas; Francis et al. 2009; Goodwin and Shriver 2011), in the majority of cases (i.e., species and noise sources), it remains unknown how the impacts on individuals accumulate over time (i.e., over multiple exposures) and over a population.
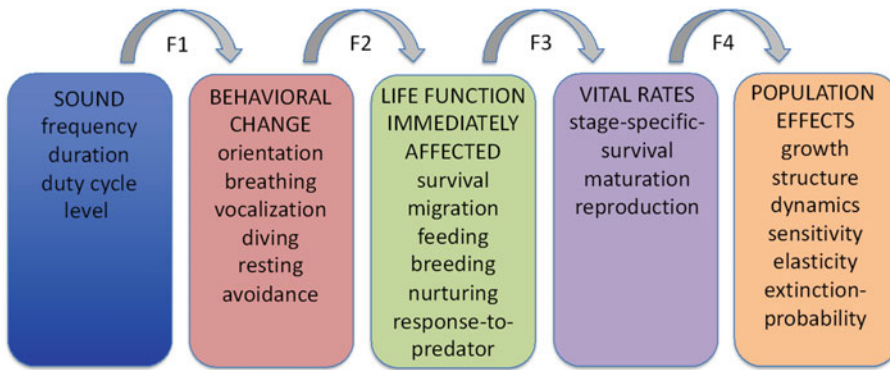
Fig. 13.3 Population Consequences of Acoustic Disturbance (PCAD) model (National Research Council 2005), which links noise exposure from individual to population-level consequences via a series of stages, connected by transfer functions

Extrapolating temporary effects on individuals to population-level effects is problematic. The Population Consequences of Acoustic Disturbance (PCAD) model (Fig. 13.3) was originally developed for marine mammals and provides a framework for the link between noise exposure and population impacts (National Research Council 2005). The link is broken down into five stages and four transfer functions.

Data to fully parameterize this model are not available for any species. However, progress has been made for a few selected species, with the elephant seal (*Mirounga angustirostris*) being an excellent model in the marine world, having been studied extensively over long periods (Costa et al. 2016). This conceptual model has recently been more fully developed mathematically and broadened to consider potential changes in vital rates to estimate population-level effects of any form of disturbance (New et al. 2014); the resulting framework is now more broadly termed the Population Consequences of Disturbance (PCoD) model. Furthermore, novel conceptual paradigms have been proposed to consider population consequences of noise exposure from multiple stressors, complex interactions of which may be additive, synergistic, or antagonistic (Ocean Studies Board 2016). These models have implications for other taxa and their conservation management.

One important aspect of noise impact management is mitigation. To reduce the risk of impacts from acute noise exposure (e.g., from a marine seismic survey or detonation), the surrounding area is commonly observed (e.g., visually or acoustically), and operations are changed (e.g., temporarily reducing power or shutting down) if animals are detected within the so-called safety zones (Fig. 13.4; Weir and Dolman 2007). Sometimes, alternative (e.g., quieter) technology is available. Also, noise barriers may be employed (e.g., temporary, sound-absorbing walls in terrestrial environments, or bubble curtains in marine environments; Bohne et al. 2019). Operations may be ramped up in an attempt to warn animals (e.g., Wensveen et al. 2017). Short-term operations may be timed to avoid biologically critical seasons or habitats.

In the case of chronic noise, such as from shipping, voluntary area-wide speed reductions reduced noise levels (Joy et al. 2019). Similarly, voluntarily turning off engines in drive-through national parks is encouraged (Fig. 13.5). For long-term operations or installations (such as highways), permanent sound barriers are commonly erected in the terrestrial environment. But these mitigation measures can reduce habitat connectivity. Instead, overpasses and long underground roadways may shelter large areas from noise exposure while concurrently increasing habitat connectivity. Understanding the role sound plays in habitat fragmentation will increase the ability to make barriers, underpasses, and overpasses more effective at reducing noise exposure, while also increasing landscape connectivity.
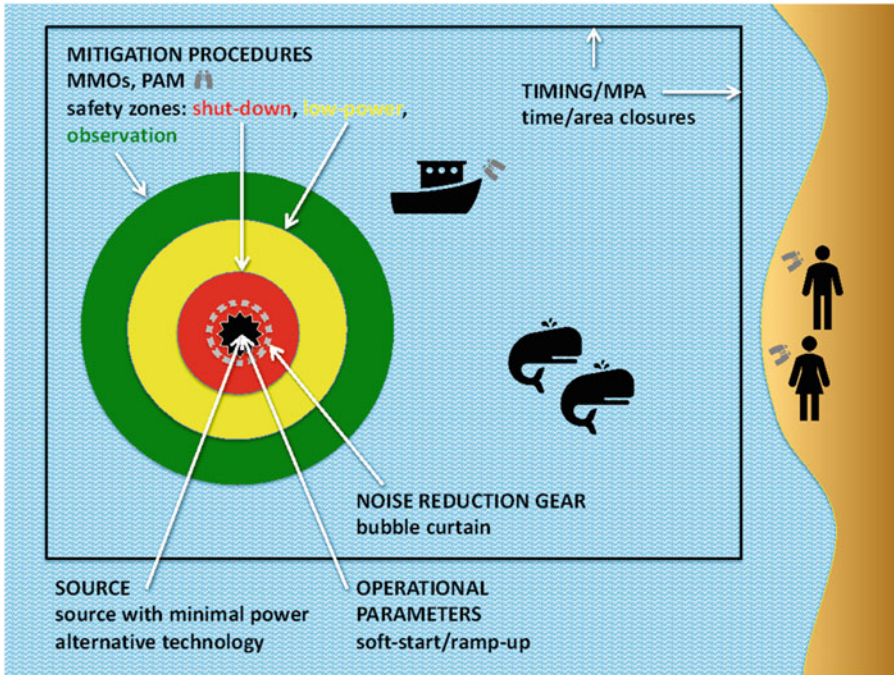
Fig. 13.4 Bird's-eye sketch of different mitigation methods employed in the marine environment to reduce the risk of noise impacts (Erbe et al. 2018). The offshore, noise-producing platform is indicated by the black star. It is surrounded by safety zones, which are observed in real time. MMO: marine mammal observer, who might be on shore, or on the operations platform, or on an additional vessel. PAM: passive acoustic monitoring using hydrophones, possibly as a towed array. Operations temporarily reduce power or shut down if animals are detected within these zones and resume once animals have departed. In addition, modifications might be possible to the source or its operational parameters. Noise reduction gear (e.g., a bubble curtain around pile driving in shallow water) is indicated by gray dots. MPA: marine protected area, which might only be accessible during low-risk seasons
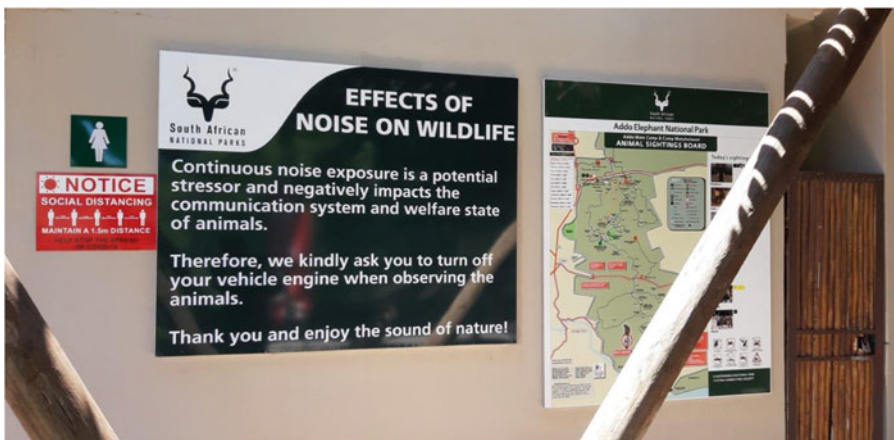

Fig. 13.5 Photograph from Addo Elephant National Park, South Africa, encouraging visitors to switch off their car engines to limit noise effects on wildlife (courtesy of Cathy Dreyer, Conservation Manager, Addo Elephant National Park)

Overall, the effects of anthropogenic noise are a challenge to researchers, noise producers, and policy makers. Often, stakeholders have data from only a few studies on a few species from which to develop criteria for noise exposure. This chapter gives examples of the effects of noise on a variety of animal taxa.

13.2   Behavioral Options in a Noisy Environment

When exposed to anthropogenic noise, animals have choices of responses. Behavioral changes are perhaps the most frequently observed and reported effects of noise. In many cases, such changes might be an "affordable" adaptation, for example when an animal temporarily moves away from the noise. The response (or lack thereof) is likely based on a cost-benefit ratio or the cost of change to improve fitness versus the magnitude of the benefit by changing. Although a variety of behavioral changes in response to noise have been studied in several species, their implications for biological fitness are difficult to determine.

13.2.1   Habituation

Animals sometimes habituate to anthropogenic noise. Habituation is a form of learning in which an animal reduces or ceases its response to a stimulus after repeated presentations; in other words, the animal learns to stop responding to anthropogenic noise when it learns there are no significant consequences. Habituation can be difficult to determine in the wild. A lack of observed behavioral response does not necessarily mean that there was no response or that the animal habituated; the response might have been too small to be observed, or it was of physiological type, or the animal's hearing sensitivity might have been reduced by prior exposure.

There are many accounts of animals living without apparent detrimental impacts in areas of high ambient noise, for example small mammals that live and breed along runways, railroad tracks,

or highways. The densities of white-footed mice (*Peromyscus leucopus)* and eastern chipmunks (*Tamias striatus*) did not decrease near roads. While both species were significantly less likely to cross a road than move the same distance away from roads, traffic volume (and noise level) had no effect (McGregor et al. 2008). Wale et al. (2013b) investigated the physiological responses of shore crabs (*Carcinus maenas*) to single and multiple ship-noise playbacks. Crabs consumed more oxygen, indicative of a higher metabolic rate and potential stress, when exposed to ship noise compared to ambient noise. However, repeated exposures to ship noise showed no change. The authors proposed that crabs exhibited the maximum response on the first exposure to ship noise, then habituated or became tolerant of the noise.

Even when no behavioral response is detectable, animals might accept noise exposure at levels that could have long-term hearing impacts, especially if there are benefits of sticking around. For example, each winter endangered manatees (*Trichechus manatus*) congregate around power plants in Florida likely in order to stay in the warm water effluence produced by the plant. In the process, they are potentially exposed to high levels of underwater noise for long periods. Seemingly, the benefit of the warm water outweighs the cost of noise exposure (JA Thomas, pers. obs.). Similarly, seals depredating at aquaculture sites might accept hearing loss inducing noise levels from acoustic harassment devices or "seal scarers" (Coram et al. 2014).

13.2.2   Change of Behavior

Temporary behavioral responses have been reported for gray whales that took a somewhat wider route around the noise from offshore oil drilling platforms, while continuing their normal round-trip migration from Alaska to Mexico (Malme et al. 1984). Such a subtle response likely won't have any long-term impact on fitness. Harbour porpoises (*Phocoena phocoena*), on the other hand, have been shown to forage almost

continuously around the clock and hence even moderate occurrences of anthropogenic disturbance might have significant fitness consequences (Wisniewska et al. 2016).

A permanent displacement from habitat has been suggested in egrets (*Ardea alba*) and great blue herons (*Ardea herodias*), judged by the altered distribution of nests along the Mississippi River, potentially in response to increased vessel traffic, such as tugboats and barges (JA Thomas, pers. obs.). A long-term displacement lasting six years occurred in killer whales (*Orcinus orca*) in response to acoustic harassment devices installed in parts of their habitat. Whales returned when devices were removed (Morton and Symonds 2002).

Noise affects not only animal movement but also other behaviors. Chaffinches (*Fringilla coelebs*) reduced their food pecking during increased background noise, which increased their vigilance; however, the increased alertness and hence reduction in predation risk might have reduced fitness via the reduction in food intake (Quinn et al. 2006). Similarly, California ground squirrels (*Otospermophilus beecheyi*) showed increased vigilance near wind turbines, potentially at the cost of other behaviors (Rabin et al. 2006). In the marine environment, anthropogenic noise interfered with the predator-prey relationship. Motorboat noise elevated metabolic rate in prey fish, which then responded less often and less rapidly to predation attempts. Predator fish consumed more than twice as much prey during boat noise exposure (Simpson et al. 2016).

Reinforcing an acoustic communication message with a visual display can enhance communication in a noisy environment. For example, male foot-flagging frogs (*Dendropsophus parviceps*) live in neotropical areas with fast-flowing streams, high levels of rain, and numerous other species of calling frogs. Foot-flagging frogs evolved the visual signal of stretching out one or two hind legs, vibrating their feet, or stretching out their toes while calling, assisting with their communication (Amézquita and Hödl 2004).

13.2.3 Change of Acoustic Signaling

Vocal behaviors can also change in response to noise. To reduce interference from urban daytime noise, chaffinches sang earlier in the day and European robins (*Erithacus rubecula*) changed vocal activities to nighttime (Bergen and Abs 1997; Fuller et al. 2007). The cost of this change in vocal behavior is unknown. Animals might also change the characteristics of their sounds to avoid masking. Changes in vocal effort such as increases in amplitude, repetition rate, and duration, or frequency shifts are collectively known as the Lombard effect, which has been demonstrated in several taxa, including frogs (Halfwerk et al. 2016), birds (Slabbekoorn and Peet 2003), and cetaceans (Scheifele et al. 2005). The Lombard effect has also been observed during odontocete echolocation: A captive beluga whale (*Delphinapterus leucas*) increased the amplitude and frequency of its echolocation signal when moved from a quiet habitat in San Diego to an area with high snapping shrimp noise in Hawaii (Au et al. 1985).

Some animal taxa might be limited in their ability to voluntarily and temporarily change the spectrographic features of their sounds—often called behavioral plasticity. Insects, for example, generate sound by stridulation of body parts, the resonance of which cannot be actively controlled. Consequently, a Lombard effect failed to be observed in *Oecanthus* tree crickets (Costello and Symes 2014); however, grasshoppers (*Chorthippus biguttulus*) from noisy habitats or those exposed to noise as nymphs produced higher-frequency sounds with higher duty cycles (i.e., increased sound-to-pause ratio), indicating developmental plasticity (Lampe et al. 2012, 2014).

A cessation of sound emission in the presence of anthropogenic noise can also occur. Thomas et al. (2016) studied the effects of construction noise on yellow-cheeked gibbons (*Nomascus gabriellae*) at Niabi Zoo. Before construction, a bonded pair and their four-year-old offspring

were quite soniferous. The pair commonly duetted in the early morning and displayed behaviors typical of a bonded pair. Once construction near their exhibit commenced, they gradually vocalized less often, and by the end of the four-month construction period, the pair bond had dissolved and the young became ill (possibly due to decreased quality of care with the loss of parent pair bond). For about a year, the pair remained distant from each other and did not vocalize. One of the authors (JA Thomas) played back recordings of the pair's own duet and those of wild gibbons. Already during the first playback, the pair slowly started to vocalize and move to the top of the exhibit where they normally performed their duet. They vocalized in response to their own duet as opposed to playbacks of other gibbon duets. The pair continued duetting for several more years of observation.

13.3 Physiological Effects

In addition to eliciting changes in fine- or gross-motor behavior and acoustic behavior, sound can also cause physiological impacts, like stress, hearing loss, or injury to tissues and organs. An animal with impaired hearing might exhibit different responses to sound and different acoustic behavior, compared to an animal with normal hearing.

A stress response may occur when noise is loud, novel, or unexpected (Wale et al. 2013a, b). Studies often concentrate on the effects of noise-induced stress on reproduction. However, stress also can result in: (1) a reduction or cessation of normal movement, with a reduced likelihood of escaping a predator; (2) reduced appetite, feeding, or food acquisition; and (3) excessive anti-predation behaviors. Attention is required to capture prey or avoid detection by a predator. Many animals use auditory cues to detect the presence of predators or prey, and any noise-induced distraction could limit this detection (Siemers and Schaub 2011). Chan et al. (2010) termed this the "distracted prey hypothesis".

The consequences of elevated stress levels can be far-reaching. Tarlow and Blumstein (2007) reviewed the effects of increased stress in birds resulting from human disturbances. The review documented changes in hormone levels, changes in heart rate, immunosuppression, changes in flight-initiation distance, disturbed breeding success, altered mate choice, and fluctuating anatomical asymmetry—all as a result of stress. While there have not been many long-term studies of noise-induced, chronic stress in animals, there is plenty of evidence from humans documenting, for example, hypertension and cardiovascular disease (Bolm-Audorff et al. 2020; Hahad et al. 2019; World Health Organization 2011).

Noise can further affect other non-acoustic sensing and information use (termed cross-modal impacts). For example, road noise impacted the ability of mongoose (*Helogale parvula*) to smell predator feces, leaving these mammals more susceptible to predation and loss of group cohesion (Morris-Drake et al. 2016). The effects of noise are complex and they differ by species. The following sections describe observed responses to sound by different taxa.

13.4 Noise Effects on Marine Invertebrates

Marine invertebrates comprise a great diversity of fauna with a corresponding diversity of sensory systems and modes of detecting sound or vibration. Only a few publications exist on the impacts of underwater sound on marine invertebrates.

13.4.1 Marine Invertebrate Hearing

Invertebrate species exhibit a diversity of sensory systems for detecting sound and vibration. Many crustaceans and molluscs have acoustic sensory systems that are an analogue to the fish otolith hearing system as they contain statocysts. These are small organs that house a dense mass (i.e., a statolith), which moves in response to sound and thus drives sensory hair cells, which create the

nervous response to the appropriate stimuli. Statocysts are involved in balance and motion sensing (e.g., in squids and cuttlefish; Arkhipkin and Bizikov 2000). Invertebrates can sense the particle motion of an incoming sound wave with the statocyst system, as reported, for example, in common prawn (*Palaemon serratus*; Lovell et al. 2005), octopus (*Octopus ocellatus*; Kaifu et al. 2008), and longfin squid (*Loligo pealeii;* Mooney et al. 2010).

Benthic molluscs, which are site-attached and fixed to the substrate, possess statocysts. These animals may be responsive to water-borne sound, to substrate-borne sound, or to sound waves traveling along the seabed-water interface. Some high-energy sound sources (e.g., impulsive seismic survey signals) can directly excite the ground (Day et al. 2016a). A benthic animal might derive information on nearby surf conditions or on an approaching predator grubbing along the seafloor from seabed-transmitted sound. Thus, benthic invertebrates, including molluscs and crustaceans, may be adapted to sense substrate-borne sound, as well as respond to water-borne sound.

Other invertebrates do not possess statocyst organs. Many invertebrates may be comprised primarily of soft tissue with no organs containing internal masses capable of exciting hair cells. Small animals of a single or few cells might merely vibrate in phase with the sound wave. Other vibratory sensory systems documented in invertebrates include single sensory hairs or antennal organs, such as in the copepod *Lepeophtheirus salmonis,* which responded to low-frequency vibrations or infrasound (<10 Hz; Heuch and Karlsen 1997).

Invertebrate larvae undergo multiple developmental stages of which the later stages, just before settlement, have the most developed sensory systems. These pre-settlement larvae are critical for recruitment success and thus of great concern with regard to anthropogenic impacts. Many late-stage larvae are responsive to sound cues for settlement; for example, those of corals (Vermeij et al. 2010) and crabs (Stanley et al. 2009). Information on the responses of late-stage larvae to anthropogenic sound is limited.

13.4.2 Effects of Noise by Taxon

Invertebrate statocyst systems can be over-excited by excessive motion of the statolith in response to intense sound, resulting in damage to surrounding hair cells or membranes, as observed in lobsters exposed to seismic airguns (Day et al. 2016a, 2019). There were no signs of repair over the 365-day holding period in these lobsters. While such damage likely results in a degradation of an animal's sensory capability, the degree to which the fitness of wild animals is affected remains unclear and in at least one documented case did not seem to alter population success (Day et al. 2020).

Invertebrates comprised of soft tissue with no dense masses might vibrate with a sound wave. In the case of intense impulse signals, this mechanical motion might cause physiological trauma to cells, although the onset level is not known (Lee-Dadswell 2011). Planktonic invertebrates with no statocyst systems but with sensory appendages and antennal organs have been shown to be susceptible to damage from intense impulse signals (McCauley et al. 2017).

Studies on noise effects on marine invertebrates show a range of impacts from none to severe, and results are difficult to compare due to vastly different experimental regimes. The following sections provide examples of study results on a species level.

13.4.2.1 Squid

Caged squid (*Sepioteuthis australis*) that were approached by a 20-in³ airgun moved away from the airgun at received sound exposure levels (SEL) of 140–150 dB re 1 μPa²s and spent more time near the sea surface; a strong startle response of the squid inking and jetting away from the airgun was observed when the airgun was discharged at about 30-m range with a received SEL of 163 dB re 1 μPa²s (Fewtrell and McCauley 2012; McCauley et al. 2003a). Two events of giant squid (*Architeuthis dux*) mass mortality in the Bay of Biscay in 2001 and 2003 were suggested to have been a result of marine seismic surveys, based on tissue damage (Guerra
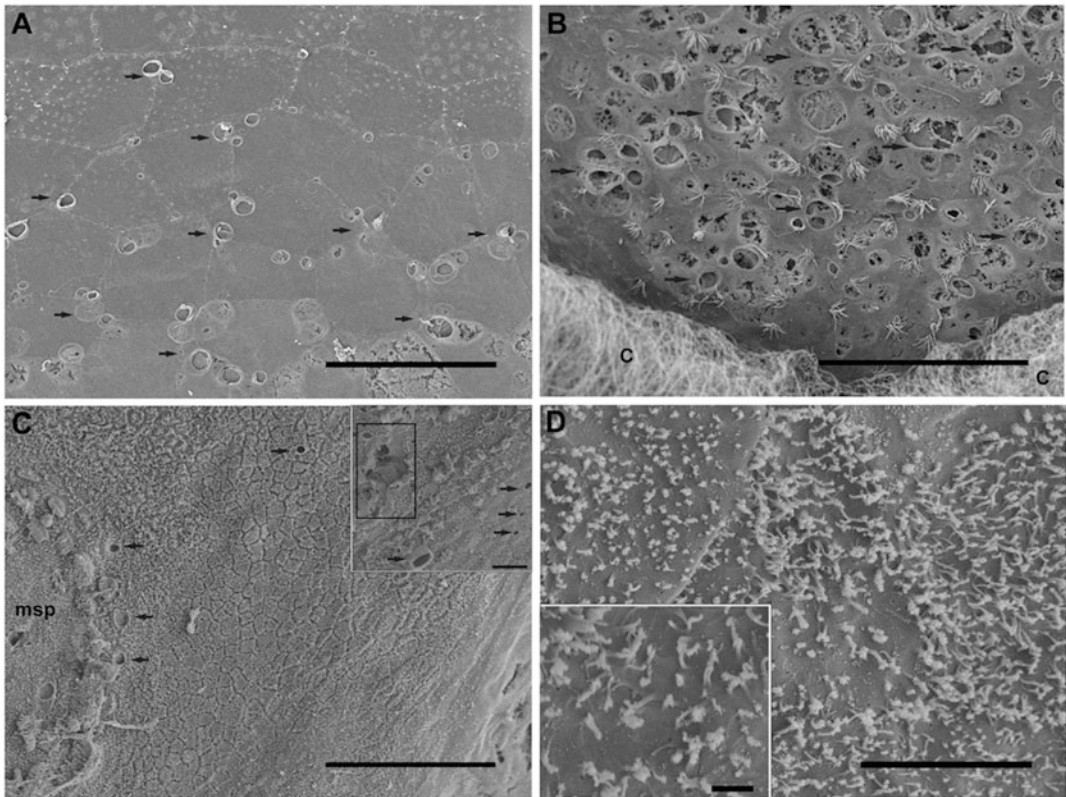
Fig. 13.6 Scanning electron microscope images of squid (*Illex coindetii*) epithelium 48 h after sound exposure. Arrows point to missing cilia and holes. Scale bars: A, B, C = 50 μm, D = 10 μm (Solé et al. 2013). © Solé et al.; https://journals.plos.org/plosone/article?id=10.1371/journal.pone.0078825; licensed under CC BY 4.0; https://creativecommons.org/licenses/by/4.0/

et al. 2004). Statocyst hair cell damage was found in cephalopods (cuttlefish and squid) subjected to simulated sonar sweeps in a laboratory tank (André et al. 2011; Solé et al. 2013; Fig. 13.6).

13.4.2.2 Scallops

Scallops (*Pecten fumatus*) exhibited behavioral changes as a result of exposure to a 150-in^3 airgun, which continued during the full 120-day post-exposure monitoring, suggesting damage to the statocyst organ, which controls balance (Day et al. 2016a, 2017). Physiological measures changed for the worse and mortality increased with dose from 1 to 4 passes of the airgun (Day et al. 2016a, 2017). A different study failed to find any significant effects of seismic airguns on scallops (Parry et al. 2002); however, animals had been removed from their seafloor habitat and were suspended in lantern nets in the water column where they would not have experienced substrate-borne and interface (i.e., at the seafloor) sound and vibration. Also, physiological measurements and long-term monitoring were not conducted. Przeslawski et al. (2018) made observations of wild scallops exposed to seismic airguns and found no discernible impacts, but the study had insufficient controls and no physiological measurements, and longer-term post-exposure sampling was not undertaken.

13.4.2.3 Crustaceans

Spiny lobsters (*Jasus edwardsii*) were exposed to single passes of a 45 or 150-in^3 airgun and monitored for 365 days after exposure (Day et al.

2016a). No mortality or significant morphological changes were found in adults or in egg viability (Day et al. 2016b). However, impaired righting ability correlating with damaged statocyst organs (ablated hair cells) and compromised immune function were reported (Day et al. 2019; Fitzgibbon et al. 2017). How these changes would impact wild lobsters is unclear, especially as another study using an apparently healthy lobster population found pre-existing statocyst damage and no further increase in damage after experimental airgun exposure, suggesting the animals had been exposed to intense noise *in situ* before the experiment but had adapted to the damage (Day et al. 2020). American lobsters (*Homarus americanus*) exposed to 202–227 dB re 1 µPa pk-pk airgun signals in a large tank exhibited physiological changes but no impact on righting times and no mortality (Payne et al. 2007). Andriguetto-Filho et al. (2005) compared shrimp (*Litopenaeus schmitti, Farfantepenaeus subtilis,* and *Xyphopenaeus kroyeri*) catch rates before and after airgun exposure (635 in^3) in shallow (2–15 m) water in north-eastern Brazil, finding no difference. The playback of ship noise as opposed to ambient noise negatively affected the foraging and antipredator behavior of shore crabs (*Carcinus maenas;* Wale et al. 2013a). Furthermore, oxygen consumption was greater during ship noise playback (possibly a stress response), and heavier crabs were more affected (Wale et al. 2013b). Evidently, there might be different responses to anthropogenic noise, depending on the size of an individual organism.

13.4.2.4 Coral

Experiments on the potential impacts of a 2055-in^3 3D seismic survey on corals were undertaken in the 60-m deep lagoon of Scott Reef, north-western Australia. Corals within and outside of the lagoon were exposed to airgun noise over a 59-day period. Some corals received airgun pulses from straight overhead (seismic source at 7-m depth, corals at ~60-m depth), whereas the full seismic survey passed within tens to hundreds of meters horizontal offset, yielding maximum received levels of 226–232 dB re 1 µPa pk-pk, 197–203 dB re 1 µPa^{2}s, and

214–220 dB re 1 µPa rms (McCauley 2014). No evidence of mechanical trauma (i.e., breakage), physiological impairment (i.e., polyp withdrawal or reduction in soft coral rigidity), or long-term change in coral community structure was found (Battershill et al. 2008; Heyward et al. 2018).

13.4.2.5 Larvae/Plankton

Noise and vibration from ships can enhance the settlement and growth of larvae of bryozoans, oysters, calcareous tubeworms, and barnacles, and thus increase biofouling (Stanley et al. 2014). The effects of a 150-in^3 airgun were studied by Day et al. (2016b) with berried (with eggs) spiny lobster (*Jasus edwardsii*) off Tasmania. No mortality of adult lobster or eggs could be attributed to the airgun at cumulative received SEL of up to 199 dB re 1µPa^{2}s. Some differences in exposed larvae morphology were noted (i.e., slightly larger than controls), but no differences in larval hatching rates or viability were found. These were early-stage larvae with under-developed sensory organs; results might differ for late-stage larvae. Parry et al. (2002) found no impacts on plankton from a 3542-in^3 seismic array, but their statistical power to detect impacts was low. Aguilar de Soto et al. (2013) exposed early-stage scallop larvae to airgun signals simulated by an underwater loudspeaker 9 cm away from the larval tank. Morphological deformities were found in all exposed larvae. However, the exact stimulus was unknown owing to the experimental setup and inherent acoustic limitations in small tanks.

McCauley et al. (2017) reported negative impacts, including a 2–3 times greater mortality rate, on various zooplankton out to 1 km from passage of a 150-in^3 seismic airgun. In contrast, Fields et al. (2019) exposed constrained adult North Sea copepods (*Calanus finmarchicus*) to a 520-in^3 airgun cluster with measured impacts limited to within 10 m. McCauley et al. stated that the "'copepods dead' category was dominated by the smaller copepod species (*Acartia tranteri*, *Oithona* spp.)". These species are ~0.5 mm in length as compared to the ~2.5-mm *C. finmarchicus*, suggesting a possible size dependency for impacts from airguns. The 1-km

impact range given by McCauley et al. (2017) was within the repeat range (400–800 m) within which a 3D seismic survey vessel would pass on an adjacent seismic line, so that the entire survey area could have its plankton field degraded. Richardson et al. (2017) ran ecological models to assess the scale of this impact. Assuming an area of strong tidal currents and consistent ocean current, a 3-day copepod turnover rate, and a three-fold increase in copepod mortality within 1.2 km, the copepod plankton field was modeled to recover within three days of completion of a mid-size 3D seismic survey. But, when Richardson et al. (2017) reduced the strength of the currents in the model, the impact persisted for three weeks. Many larger zooplankton have a longer than 3-day turnover rate (i.e., weeks to months) with larval forms having a once or twice per year recruitment cycle, enhancing impacts above the published model output. Given the central role zooplankton play in the ocean ecosystem, and given that not all turn over rapidly, the results of McCauley et al. (2017) are of concern for ocean health.

13.5   Noise Effects on Terrestrial Invertebrates

Soniferous terrestrial invertebrates include some crabs, spiders, and insects. Limited information exists on the impacts of sound on terrestrial invertebrates, with insects being the main group studied. Currently, little is known about how egg and larvae of terrestrial invertebrates respond to high-amplitude anthropogenic sounds. As a result, this section concentrates on adult insects as representatives of terrestrial invertebrates.

13.5.1   Insect Hearing

The ability to hear air-borne sound evolved independently at least 24 times in seven orders of insects (Greenfield 2016), either as tympanal hearing or hearing with antennae. These ears are sensitive to a very broad range of frequencies, from less than 1 kHz to high ultrasonics beyond

100 kHz. Signaling at these frequencies is important for mate attraction and localization, rivalry, and spacing of individuals within populations. In addition, many species use their ears to detect and avoid predators. Some species of flies eavesdrop on calling insects to locate and parasitize them.

An evolutionary adaptation to ambient noise from competing insect choruses is the modification of peripheral sensory filters, such as the sharpening of tuning in the cricket (Fig. 13.7). Such sharp tuning curves reduce the amount of masking noise within the filter (Schmidt et al. 2011).

However, the most prevalent form of insect communication involves substrate-borne sound. More than 139,000 described taxa are expected to exclusively use vibrational signaling and an additional 56,000 taxa use a combination of vibrational communication and other forms of mechanical signaling (Cocroft and Rodríguez 2005). The sensory organs monitoring substrate-borne sound (e.g., the subgenual organs in the legs) are tuned to frequencies below 1 kHz and are extremely sensitive.
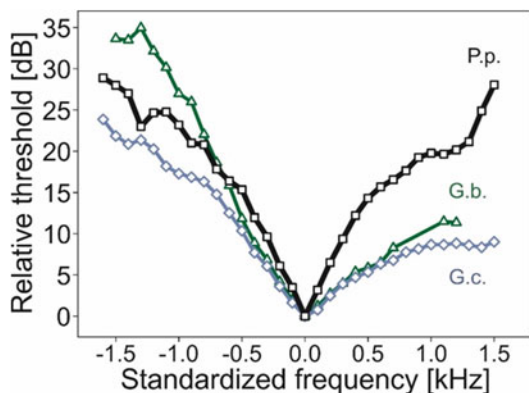

Fig. 13.7 Graph of standardized mean sensitivity tuning curves of auditory interneuron AN1 in three cricket species: *Paroecanthus podagrosus* (P.p.), a neotropical cricket communicating under strong background noise levels, and *Gryllus bimaculatus* (G.b.) and *G. campestris* (G.c.), field crickets in environments with less background noise. The increased steepness in tuning toward higher frequencies filters out competing frequencies from other crickets (Schmidt et al. 2011). © Schmidt et al.; https://jeb.biologists.org/content/214/10/1754. Published green open access; https://jeb.biologists.org/content/rights-permissions

Anthropogenic noise sources produce significant amplitudes of air-borne sound at frequencies from less than 10 Hz to 50 kHz (e.g., traffic on roads and railways, compressors, wind turbines, military activities, and urban environments). At the same time, airport, road, and railroad traffic and construction are significant sources of low-frequency, substrate-borne vibrations below 1 kHz. Such substrate-borne noise may be created directly by vibrating the substrate (e.g., by driving over it) or indirectly via air-borne noise that induces vibrations in the substrate. The relatively low-frequency sound produced by many of these sources suffers less attenuation and can thus travel farther from the source. Because many insects have very sensitive receptors for substrate-borne sound, with displacement thresholds less than 1 nm, they are likely to detect anthropogenic sources over long distances. Anthropogenic noise may therefore have a significant impact on the ability of insects to communicate and listen in both the air-borne and substrate-borne channel (reviewed by Morley et al. 2014; Raboin and Elias 2019).

13.5.2 Behavioral Effects

Anthropogenic noise may impact insects in various ways. It can mask communication signals, increase stress, affect larval development, and ultimately decrease lifespan (reviewed by Raboin and Elias 2019). The most common consequence of noise is masking, when noise overlaps in time and frequency with a signal. This decreases the signal-to-noise ratio and thus the detection and/or discrimination of signals. For example, Schmidt et al. (2014) found that anthropogenic noise resulted in less effective female cricket orientation toward signaling males (phonotaxis: orientated movement in relation to a sound source), which, in crickets, is the usual way to bring the sexes together. In another cricket species, males shortened their calls and paused singing with increasing noise level. However, males did not adjust the duration of intervals between song elements important for species identification (Orci et al. 2016). Apparently, these insects can

neither modify the fundamental frequency of their song nor increase the amplitude of their calls in noise (i.e., lack of a Lombard effect), as do some species of frogs and birds, to reduce masking by anthropogenic noise.

For insects using substrate-borne signals, experimentally induced noise may disrupt mating. Insects either respond less frequently to signals of the opposite sex, or they cease signaling during the initial part of communication (Polajnar and Čokl 2008). The fact that noise can disrupt substrate-borne communication between the sexes may be utilized in pest control in agriculture (Polajnar et al. 2015). For example, substrate-borne noise can mask the mating signals of species of leafhoppers, which represent a major pest in vineyards, resulting in reduced reproductive success. A similar approach was successful with pine bark beetles, when the substrate-borne noise spectrally overlapped with beetle signals (Hofstetter et al. 2014).

The failure to adjust the frequency or amplitude of mating signals in noise does, however, not exclude other means of behavioral plasticity. For example, the responses of male field crickets (*Gryllus bimaculatus*) to traffic noise depended on prior experience (Gallego-Abenza et al. 2019). Recordings of car noise were played back to males living at different ranges from the road and, therefore, with different prior experience to road noise. Males farther from the road decreased their chirp rate more than those nearer by, suggesting that "behavioral plasticity modulated by experience may thus allow some insect species to cope with human-induced environmental stressors" (Gallego-Abenza et al. 2019).

Developmental plasticity may also manifest in signal modifications in response to noise. The courtship signals of grasshoppers are more broadband in frequency than those of crickets. Specifically, male grasshoppers (*Chorthippus biguttulus*) from roadside habitats produced higher-frequency signals compared to grasshoppers in quieter habitats (Lampe et al. 2014). In an experiment that reared half of the grasshopper nymphs in a noisy environment and the other half in a quiet environment, adult males from the first group produced signals with higher-

frequency components, suggesting that developmental plasticity allows signal modifications in noisy habitats.

13.5.3 Physiological Effects

Strong anthropogenic noise can result in hearing loss. Auditory receptors in the locust ear showed a decreased ability to encode sound after noise exposure. The mechanism for such hearing loss reveals striking parallels with that of the mammalian auditory system (Warren et al. 2020). A series of experiments was conducted to determine whether exposure to simulated road traffic noise induces increased heart rates, as an indicator of a stress response (Davis et al. 2018). Larvae of the monarch butterfly (*Danaus plexippus*) exposed for 2 h to road traffic noise experienced a significant increase in heart rate, indicative of stress. Because these larvae do not have ears for air-borne sound, the likely sensory pathway involved vibration receptors. However, exposing larvae for longer periods (up to 12 days) to continuous traffic noise did not increase heart rate at the end of larval development; so chronic noise exposure may result in habituation or desensitization. However, habituation to stress during larval stages may impair reactions to stressors in adult insects.

While more research is necessary to understand the sensory strategies for avoiding or compensating for anthropogenic noise, there are some cases where insects experience a significant fitness advantage. This may happen in a predator-prey or parasitoid-host relationship, when the noise decreases the ability of a parasitoid fly to localize calls of their host crickets (Lee and Mason 2017), or when bats as predators of flying insects are less efficient foragers in the presence of anthropogenic noise (Siemers and Schaub 2011).

monsters, monitors, and bearded dragons) species. Soniferous reptiles include some snakes, alligators, crocodiles, geckos, and freshwater and marine turtles (e.g., Young 1997).

Reptiles are surrounded by anthropogenic noise from traffic (in water, on land, and in air), construction, mineral and hydrocarbon exploration and production, etc. Because many anthropogenic noise sources are low in frequency and thus within the reptilian hearing range, understanding the impact of these sources on behavior and physiology is an important start for reptile conservation.

Little literature exists on the impacts of anthropogenic noise on reptiles, with sea turtles having received recent attention. Simmons and Narins recently reviewed the topic (2018). Currently, little is known about how eggs and juvenile reptiles respond to anthropogenic noise. As a result, this section concentrates on adult sea turtles as a representative of reptiles.

Acoustic signals play an important role in turtle social behavior and reproduction. Turtles make very-low-frequency calls of short duration by swallowing or by forcibly expelling air from their lungs. Galeotti et al. (2005) published a summary of sound occurrence, context, and usage in Cryptodira chelonians—a taxon, which is quite soniferous. In general, turtles call when mating or seeking a mate, when they are sick or in distress, or for other reasons. Male red-footed tortoises (*Chelonoidis carbonaria*) make a clucking sound during mounting, Greek tortoises (*Testudo graeca*) whistle during combat, and young big-headed turtles (*Platysternon megacephalum*) squeal when disturbed (Galeotti et al. 2005). Nesting female leatherback sea turtles (*Dermochelys coriacea*) make a belching sound (Cook and Forrest 2005; Mrosovsky 1972), and the sounds from leatherback sea turtle eggs are believed to help coordinate hatching (Ferrara et al. 2014).

13.6 Noise Effects on Reptiles

Reptiles have both aquatic (sea turtles, alligators, and crocodiles) and terrestrial (geckos, snakes, iguana, whiptails, geckos, chameleons, gila

13.6.1 Reptile Hearing

Not all reptiles produce sound for communication. Most reptiles can detect substrate-borne vibrations (e.g., Barnett et al. 1999; Christensen

et al. 2012). The auditory anatomy of most reptile species includes a tympanic membrane near the rear of the head, a middle ear with a stapes, and a fluid-filled inner ear housing the lagena and its sound-sensing cells (Wever 1978). Brittan-Powell et al. (2010) indicated that reptile hearing is similar in frequency range to hearing in birds and amphibians. The most sensitive lizards have similar absolute sensitivities to birds. Ridgway et al. (1969) used electrophysiological methods to test hearing abilities of the green sea turtle (*Chelonia mydas)* and found peak sensitivity between 300 and 400 Hz, with the best hearing range from 60 to 1000 Hz. In general, the best frequency range of hearing in chelonids (turtles, tortoises, and terrapins) is 50–1500 Hz (Popper et al. 2014).

13.6.2 Behavioral Responses to Noise

Sea turtles may be exposed to acute and chronic noise. The soundscape of the Peconic Bay Estuary, Long Island, NY, USA, a major coastal foraging area for juvenile sea turtles, was recorded during sea turtle season. There was considerable boating and recreational activity, especially between early July and early September. Samuel et al. (2005) suggested that increasing and chronic exposure to high levels of anthropogenic noise could affect sea turtle behavior and ecology. Indeed, loggerhead sea turtles have been shown to dive when exposed to seismic airgun noise—perhaps as a means of avoidance (DeRuiter and Larbi Doukara 2012). In the terrestrial world, desert tortoises (*Gopherus agassizii*) exposed to simulated jet overflights did not show a startle response or increased heart rate, but they froze; and in response to simulated sonic booms, they exhibited brief periods of alertness (Bowles et al. 1999).

Unfortunately, there is a complete lack of data on masking of biologically important signals in sea turtles and other reptiles by anthropogenic noise (Popper et al. 2014). Similarly, there has been little research on physiological effects of noise in reptiles.

13.7 Noise Effects on Amphibians

Frogs rely heavily on acoustic communication for mating. Noise has been shown to alter both the production and perception of frog vocalizations. This can have serious implications for reproduction in these animals. Males that do not call as often will not attract females to their locations along a pond edge. Females that do not hear the advertisement calls from the males will not be able to localize or approach them. Further, they will not be able to sample multiple males for selection of the most attractive one. Studies have been conducted in both the laboratory and the field to determine the effects of noise on acoustic communication in frogs, for both vocal production and auditory perception.

13.7.1 Frog Hearing

The amphibian ear consists of a tympanic membrane on the outside through which sound enters the ear, a middle ear containing a columella, similar to the mammalian stapes, that provides mechanical lever action, and an inner ear in which sound is converted to neural signals (Wever 1985). The inner ear contains two papillae, known as the amphibian papilla, which responds to lower frequencies, and the basilar papilla, which responds to higher frequencies. Audiograms show good sensitivity between 100 Hz and a few kHz (e.g., Megela-Simmons et al. 1985). Some species, however, exhibit sensitivity also to ultrasound (Narins et al. 2014), and others to infrasound (Lewis and Narins 1985).

13.7.2 Behavioral Responses to Noise

Some species of frogs, like other animals, are known to avoid roads and highways, possibly to avoid both traffic mortality and a reduced transmission of vocal signals (reviewed by Cunnington and Fahrig 2010). Several studies, however, failed to document behavioral avoidance of noise by frogs or did not find reduced

frog abundance near continuous noise sources such as highways (Herrera-Montes and Aide 2011).

Nonetheless, noise does affect the perception of acoustic signals by frogs. Bee and Swanson (2007) investigated the potential of noise from road traffic to interfere with the perception of male gray treefrog (*Dryophytes chrysoscelis*) signals by females. Using a phonotaxis assay, they presented females with a male advertisement call at various signal levels (37–85 dB re 20 μPa) in three masking conditions: (1) no masking noise, (2) a moderately dense breeding chorus, and (3) road traffic noise recorded in wetlands near major roads. In both the chorus and traffic noise maskers, female response latency increased, orientation behavior toward the signal decreased, and response thresholds increased by about 20–25 dB. The authors concluded that realistic levels of traffic noise could limit the active space, or the maximum transmission distance, of male treefrog advertisement calls. Another treefrog (*Dendropsophus ebraccatus*) tested in a laboratory to compare the effects of dominant frequency and signal-to-noise ratio on call perception showed a low-frequency call preference in quiet conditions (usually correlated with larger, more attractive males), but no preference at higher signal-to-noise ratios (Wollerman and Wiley 2002). These results indicate that females listening to males in a noisy environment will likely make errors in mate choice.

Sun and Narins (2005) examined the effects of fly-by noise from airplanes and played back low-frequency sound from motorcycles to an assemblage of frog species in Thailand. Three of the most acoustically active species (*Microhyla butleri, Sylvirana nigrovittata,* and *Kaloula pulchra*) decreased their calling rate and the overall intensity of the assemblage calls decreased. However, calls from another frog (*Hylarana taipehensis*) seemed to persist. The authors suggested that the anthropogenic noise suppressed the calling rate of some species, but seemed to stimulate calling behavior in *H. taipenhensis*. Another study found that the vocalization rate of European treefrog (*Hyla arborea*) decreased in traffic noise (Lengagne

2008). Barber et al. (2010) believed that these frogs were unable to adjust the frequency or duration of their calls to increase signal transmission. Penna et al. (2005) found a similar decrease in call rate in leptodactylid frogs (*Eupsophus calcaratus*) exposed to recordings of natural noise in the wild.

An effective way to increase the likelihood that acoustic signals will be received is by increasing the intensity of those signals (Lombard effect). Love and Bee (2010) measured the intensities of vocalizations produced in the laboratory by Cope's gray treefrog (*Dryophytes chrysoscelis*) in the midst of different levels of background noise, similar to a frog chorus. They found no evidence for the existence of the Lombard effect in their frogs. Frogs produced calls at a level of 92–93 dB re 20 μPa, regardless of noise level. Similar to findings from other frogs, Cope's gray treefrogs increased call duration and decreased call rate with increasing noise levels. However, they appeared to be maximizing their call amplitudes in every calling situation, which does not allow them to increase their call intensities further when needed. On the contrary, túngara frogs (*Engystomops pustulosus*) and rhacophorid treefrogs (*Kurixalus chaseni*) did increase their call levels in noise (Halfwerk et al. 2016; Yi and Sheridan 2019).

Another possible way for a frog to increase communication efficacy would be to increase the frequencies of their calls to be above the frequency of the masking noise. Parris et al. (2009) found that two species of frogs (southern brown treefrog, *Litoria ewingii*, and common eastern froglet, *Crinia signifera*) called at a higher frequency in traffic noise (e.g., 4.1 Hz/dB for *L. ewingii*), and suggested this was an adaptation to be heard over the noisy environmental conditions. An extreme form of this frequency-increasing behavior has been discovered in concave-eared torrent frogs (*Odorrana tormota*) in China (Feng and Narins 2008). These frogs live near extremely loud streams and waterfalls (58–76 dB re 20 μPa, up to 16 kHz), which should make vocalizations difficult for other frogs to hear, at least at the lowest frequencies. The calls from these frogs are quite different from the
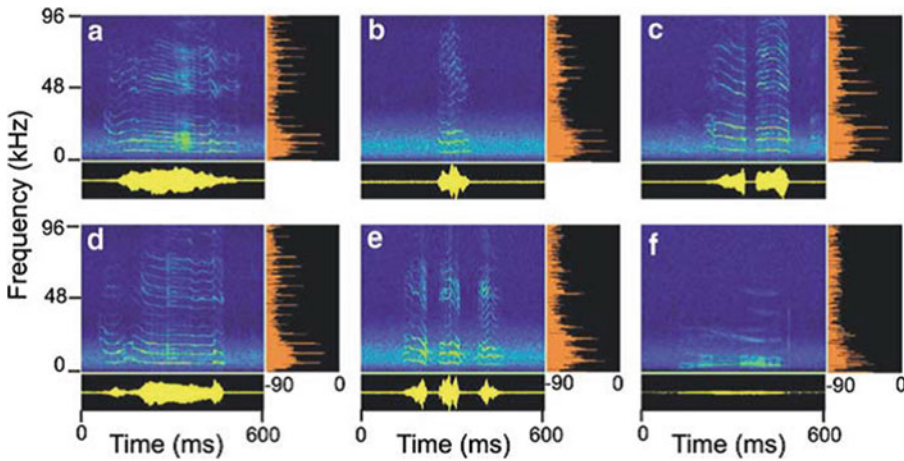
Fig. 13.8 Spectrograms, waveforms, and call spectra from six vocalizations from the *O. tormota* frog (Feng and Narins 2008). Reprinted by permission from Springer Nature. A. S. Feng and Narins, P. M. Ultrasonic communication in concave-eared torrent frogs (*Amolops tormotus*). Journal of Comparative Physiology A, 194(2), 159–167; https://link.springer.com/article/10.1007/s00359-007-0267-1. © Springer Nature, 2008. All rights reserved

vocalizations of other frogs, however. These torrent frogs produce numerous vocalizations with energy in the ultrasonic frequency range (Fig. 13.8). A phonotaxis study found that female torrent frogs actually preferred synthetic male calls embedded in higher-amplitude stream noise than those embedded in lower-amplitude stream noise (Zhao et al. 2017). These ultrasonic signals are both produced and perceived by males and females, suggesting that they are not just a by-product of vocal production, and are instead an adaptation to avoid signal masking in a very noisy environment (Shen et al. 2008).

Some species of frogs are known to use visual signals when conditions are noisy, in an effort to improve communication. Grafe et al. (2012) recorded acoustic and visual communication strategies in noisy conditions by the Bornean rock frog (*Staurois parvus*). These frogs modified the amplitude, frequency, repetition rate, and duration of their calls in response to noise, but in addition engaged in visual foot-flagging and foot-touching behaviors. In a noisy world and with limited flexibility in vocal production capabilities, adding a visual component to an acoustic signal may be one of the only ways these animals are able to adapt.

13.7.3 Physiological Responses to Noise

Spatially separating a signal from a masker is one way to improve signal detectability. Spatial release from masking has been demonstrated in frogs behaviorally as well as physiologically. Ratnam and Feng (1998) recorded from single units in the inferior colliculus of northern leopard frogs (*Lithobates pipiens*) and found improvements in signal detection thresholds with spatially separated signals and noise maskers relative to spatially coincident signals and maskers. This has been shown in laboratory studies with awake behaving animals, when female Cope's gray treefrogs approached a target signal (male calling frog) more readily when it was spatially separated (by 90°) from a noise source (Bee 2007). This spatial release from masking, in the range of 6–12 dB, is similar to what is seen in other animals such as budgerigars (*Melopsittacus undulatus*; Dent et al. 1997) and killer whales (Bain and Dahlheim 1994).

Finally, increased levels of corticosterone, which correlated with impaired female mobility, have been shown in high traffic noise conditions in female wood frogs (*Lithobates sylvaticus*)

(Tennessen et al. 2014), although a recent study suggests that eggs taken from high traffic noise conditions yielded frogs that were less affected by noise exposure than frogs from eggs taken from low traffic noise environments, suggesting adaptations are possible (Tennessen et al. 2018). Whether it is from the stress or the masking of the acoustic signals, anthropogenic noise has been shown to have negative consequences.

13.8   Noise Effects on Fish

All fish species studied to date can detect sound. Hundreds of species are known to emit sound with the most prominent display of sound production in fishes being their choruses on spawning grounds (Slabbekoorn et al. 2010). Adult, juvenile, and larval-stage fishes actively use environmental sound to orientate and settle (Jeffrey et al. 2002; Simpson et al. 2005, 2007). Herring (*Clupea harengus*) have shown avoidance behavior to playbacks of sounds of killer whales, one of their predators (Doksaeter et al. 2009). Underwater anthropogenic noise can have a variety of effects on fish, ranging from behavioral changes, masking, stress, and temporary threshold shifts, to tissue and organ damage, and death in extreme cases (Hawkins and Popper 2018; Normandeau Associates 2012; Popper and Hastings 2009). Mortality can also result from an increased risk of predation in noisy environments (Simpson et al. 2016). Despite the growing amount of literature, our understanding of the cumulative effects of multiple exposures and the fitness implications to wild fish is limited.

13.8.1   Fish Hearing

Fish have two systems detecting sound and vibration: the inner ear and the lateral line system. The inner ear of fish resembles an accelerometer. It contains otoliths, which are bones of approximately three times the water density. Waterborne acoustic waves therefore result in differential motion between the otoliths and the fish's body, thus bending hair cells coupled to the

otoliths of the inner ear, which sends neural signals to the brain. The inner ear is sensitive to particle motion. Fish with swim bladders close to or even connected to the ears are also sensitive to acoustic pressure. This is because the sound pressure excites the gas bladder, which reradiates an acoustic wave that drives the otolith. Particle motion then creates differential movement between the otoliths and the rest of the ear. The lateral line system involves neuromasts that detect water flow and acoustic particle motion. Due to variability in otolith anatomy and the absence or presence and variable connectivity of swim bladders, fish hearing varies greatly with species in terms of sensitivity and bandwidth, with most species sensitive to somewhere between 30 and 1000 Hz, but some species detecting infrasound, and others ultrasound up to 180 kHz (Popper and Fay 1993, 2011; Tavolga 1976). Hearing in noise has been studied and parameters such as the critical ratio (signal-to-noise ratio for sound detection, see Chap. 10) have been measured (Fay and Popper 2012; Tavolga et al. 2012); however, the significance of acoustic masking to fish fitness and survival remains poorly understood.

13.8.2   Behavioral Responses to Noise

The schooling behavior of fish has been observed to change in response to an approaching airgun with fish swimming faster, deeper in the water column, and in tighter schools (Davidsen et al. 2019; Fewtrell and McCauley 2012; Neo et al. 2015; Pearson et al. 1992). Caged fish had compacted near the center of the cage floor at received levels of 145–150 dB re 1 $\mu Pa^2 s$ and swimming behavior returned to normal after 11–31 min (Fewtrell and McCauley 2012). A startle response was noted when the airgun was discharged at close range (Pearson et al. 1992), but not when the received level was ramped up by approaching from a longer range; also, the startle response diminished over time (Fewtrell and McCauley 2012). Wild pelagic and mesopelagic species dove deeper and their abundance increased at long range from the airgun array (Slotte et al. 2004). There are a few studies
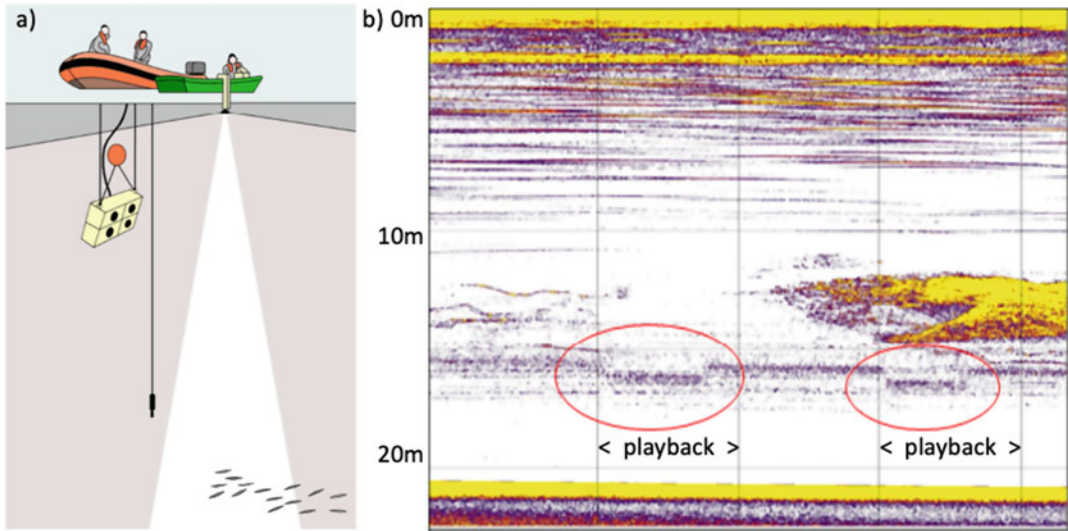
Fig. 13.9 (**a**) Experimental setup to study fish responses to playbacks of pile driving sound. (**b**) Echogram of zooplankton dropping in depth below sea surface during playback of pile driving sound (red ellipses). Time is along the x-axis; playback started at the 1st vertical black line, stopped at the 2nd line, restarted at the 3rd line, and stopped at the 4th line (modified from Hawkins et al. 2014). © Acoustical Society of America, 2014. All rights reserved

documenting a drop in catch rates of pelagic fish after seismic surveying (Engas and Løkkeborg 2002; Engås et al. 1996; Slotte et al. 2004), believed to be due to behavioral responses.

Hawkins et al. (2014) played pile driving noise to wild zooplankton and fish. A loudspeaker was deployed from one boat for sound transmission, while an echosounder and side-scan sonar were deployed from a second boat for animal observation (Fig. 13.9a). Zooplankton dropped in depth below the sea surface after playback onset as shown by the echogram in Fig. 13.9b. Wild sprat (*Sprattus sprattus*) and mackerel (*Scomber scombrus*) exhibited a diversity of responses including break-up of aggregations and reforming of much denser aggregations in deeper water. The sprat is sensitive to sound pressure, however the mackerel lacks a swim bladder and is sensitive to the particle motion. The occurrence of behavioral responses increased with the received level. The 50% response thresholds were 163.2 and 163.3 dB re 1 μPa pk-pk and 135.0 and 142.0 dB re 1 μPa^{2}s (single-strike exposure) for sprat and mackerel, respectively (Hawkins et al. 2014; Fig. 13.10).

13.8.3 Effects of Noise on the Auditory and other Systems

After exposure to intense pulsed sound from airguns, extensive hearing damage in the form of ablated or missing hair cells was found in pink snapper (*Pagrus auratus*) (McCauley et al. 2003a, b). Other studies have found only limited or no hearing damage or threshold shift in various species of fish from airgun exposure (Hastings and Miksis-Olds 2012; Popper et al. 2005; Song et al. 2008). Apart from the typical differences in experimental setup, exposure regime, and species tested, a factor influencing the degree of noise impact might be the direction from which sound is received (specifically, vertical versus horizontal incidence; McCauley et al. 2003a). Fish ears are not symmetrical and many anthropogenic sound sources have a strong vertical directionality under water due to their near-surface deployment leading to a dipole sound field.

Halvorsen et al. (2012, Fig. 13.11) looked for tissue and organ damage in Chinook salmon (*Oncorhynchus tshawytscha*) that were placed inside a standing-wave test tube (High-Intensity
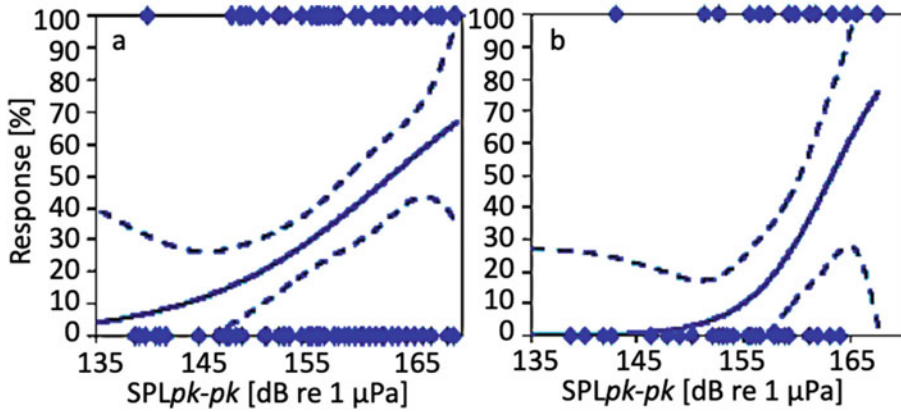
Fig. 13.10 Dose-response curves (solid lines) and 95% confidence intervals (dashed lines) of (a) sprat and (b) mackerel to peak-to-peak sound pressure levels from pile driving (modified from Hawkins et al. 2014). © Acoustical Society of America, 2014. All rights reserved
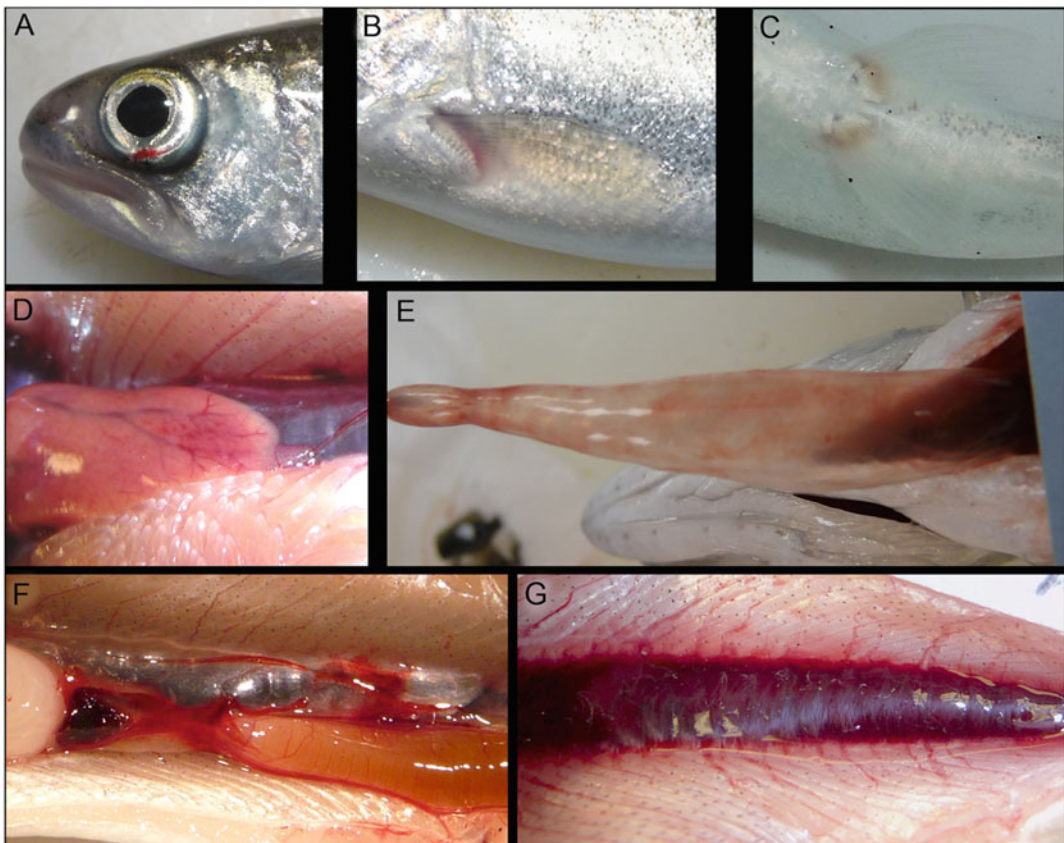

Fig. 13.11 Chinook salmon injuries from noise exposure. Mild: (**a**) eye hemorrhage, (**b**, **c**) fin hematoma. Moderate: (**d**) liver hemorrhage and (**e**) bruised swim bladder. Mortal: (**f**) intestinal hemorrhage and (**g**) kidney hemorrhage (Halvorsen et al. 2012). © Halvorsen et al.; https://journals.plos.org/plosone/article?id=10.1371/journal.pone.0038968; licensed under CC BY 4.0; https://creativecommons.org/licenses/by/4.0/

Controlled Impedance Fluid-filled wave Tube, HICI-FT) in which pressure and particle motion could be controlled. Physical injury commenced at 211 dB re 1 μPa^2s cumulative sound exposure resembling 1920 strikes of a pile driver at 177 dB re 1 μPa^2s each.

Yelverton (1975) conducted studies of the gross effects of sounds generated from underwater explosive blasts on fish. He found three important factors that influenced the degree of damage: the size of the fish relative to the wavelength of the sound, the species' anatomy, and the location of the fish in the water column relative to the sound source.

13.9   Noise Effects on Birds

Birds rely heavily on acoustic communication for life functions such as warning others about predators, finding and assessing the quality of mates, defending territories, and discerning which youngster to feed (Bradbury and Vehrencamp 2011). When environmental noise levels are high, such functions become difficult or impossible, unless the birds can make temporary or permanent adjustments to their signal, posture, or location. There have been several studies on the effects of noise on survival and communication in birds in the field as well as the laboratory, and on the ways that birds adjust their communication signals and/or lifestyles to adapt to the noisy modern world.

13.9.1   Bird Hearing

The avian ear has three main parts: an outer, middle, and inner ear. The outer ear is typically hidden by feathers, but consists of a small external meatus. A tympanic membrane separates the outer and middle ear. The middle ear contains the columella that mechanically transmits sound to the inner ear, and a connected interaural canal to aid in directional hearing. The basilar papilla in the inner ear converts sound into neural signals. Most birds hear between 50 Hz and 10 kHz, with

some species' hearing extending into the infrasonic range (Dooling et al. 2000).

13.9.2   Behavioral Responses to Noise

Several studies have demonstrated that some birds are affected by low-frequency (<3 kHz) anthropogenic noise from roadways and that long-term exposure can lead to lower species diversity or lower breeding densities in an area (reviewed by Goodwin and Shriver 2011; Reijnen and Foppen 2006). Urban noise is known to affect reproduction and mating behaviors of birds in several ways. Urban noise can mask acoustic components of the lekking display by male greater sage grouse (*Centrocercus urophasianus*; Blickley and Patricelli 2012). It also disrupts female preference for low-frequency songs sung by male canaries (des Aunay et al. 2014) and great tits (Halfwerk et al. 2011). Females of these (and other) species prefer males that sing lower-frequency songs over those that sing higher-frequency songs because the low-frequency songs are sung by males of higher quality (e.g., Gil and Gahr 2002). When low-frequency urban noise masks the low-frequency components of calls and songs, females either cannot detect or find the males that are singing or cannot discriminate between the high-quality males singing at low frequencies and the poorer-quality males singing at higher frequencies.
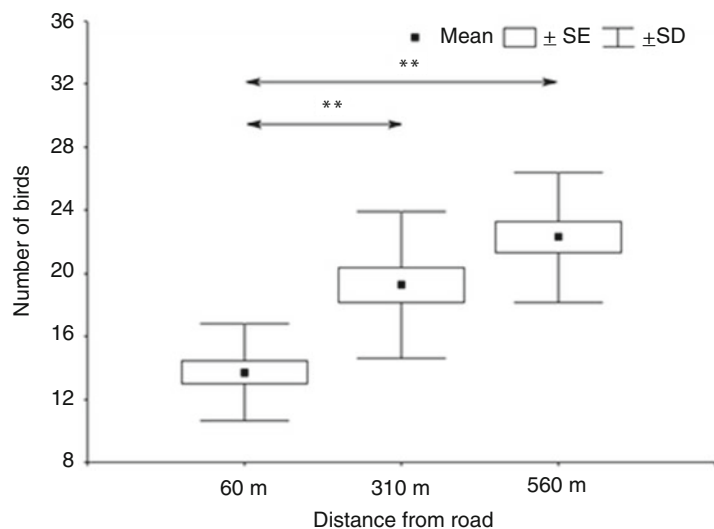
Urban noise also has influences on where birds choose to live and breed, often resulting in consequences for choosing less favorable habitats. For instance, Eastern bluebirds (*Sialia sialis*) living in noisier environments were found to have reduced reproductive productivity and brood size compared to those living in quieter habitats (Kight et al. 2012). The presence and absence of construction and highways often changes the distribution of birds. Foppen and Deuzeman (2007) compared the distribution of reed warbler (*Acrocephalus arundinaceus*) pairs in the Netherlands before a highway was built through a nesting area and after the highway was present. When the highway was present

there were fewer nesting pairs, meaning that some birds were avoiding preferred habitats to avoid traffic noise. The road was temporarily closed and the number of nesting pairs increased; however, once the road reopened the number of nesting pairs again decreased. A more extensive study conducted in the Netherlands found that 26 of 43 (60%) woodland bird species showed reduced numbers near roads (Reijnen et al. 1995). Another count of birds near and far from roads showed that even when habitats were similar to one another, but either near to or far from a highway, the number of birds in each area increased with increasing distance from the road (Fig. 13.12), correlating with noise levels (Polak et al. 2013). That is, both abundance and diversity of birds increased as noise levels decreased. Other studies have confirmed that birds with higher-frequency calls were less likely to avoid the roadways than birds with lower-frequency calls (Rheindt 2003), again pointing to the challenges that many birds have when communicating in low-frequency urban noise, and highlighting the difficult choice that birds must face: Do the costs of choosing a less favorable habitat outweigh the benefits of living in quieter environments? The answer to this question clearly differs across both individual birds and species.

When birds do choose to nest in noisier environments, there could be consequences for mating and reproductive success. Nestling white-crowned sparrows (*Zonotrichia leucophrys*) tutored with songs embedded in anthropogenic noise later sung songs at higher frequencies and with lower vocal performance than those tutored with non-noisy control songs (Moseley et al. 2018). As another example, when alarm calls were presented to tree swallow (*Tachycineta bicolor*) nestlings, the tree swallows in quiet environments crouched more often (hiding from predators) while the nestlings in noisy environments produced longer calls and did not crouch (McIntyre et al. 2014). Nestling tree swallows living in noisier environments produced narrower-bandwidth and higher-frequency calls than those from quieter nests (Leonard and Horn 2008), although hearing of noise-reared nestlings does not differ from that of quiet-reared nestlings (Horn et al. 2020). These studies indicate that noise could affect how well offspring hear predators and how well parents hear begging calls. It also could influence the rate of feeding nestlings and could even have long-lasting effects on call structure, which could influence breeding success of those nestlings as adults. In a laboratory study looking at the effects of noise on reproduction, high levels of environmental noise eroded pair preferences in zebra finches (Swaddle and Page 2007). Paired females chose non-partner males over their partners when moderate to high

Fig. 13.12 Relationship between bird abundance at point-count locations and distance from the road. Arrows show significant differences between points (Polak et al. 2013). © Springer Nature, 2013; https://link.springer.com/article/10.1007/s10342-013-0732-z/figures/5. Licensed under CC BY; https://creativecommons.org/licenses/

levels of white noise were presented in a preference test. These results have implications for noisy environments altering the population's breeding styles and eventually the evolutionary trajectory of the species (Swaddle and Page 2007).

13.9.3 Communication Masking

To know exactly how noise affects acoustic communication in birds, playback or perceptual experiments must be conducted to measure auditory acuity in a controlled environment. Experiments would use either pure tones and white noise or more complex and natural signals that birds use for communication purposes. Controlled laboratory studies measuring the ability to detect simple pure tones in broadband noise have been conducted in over a dozen bird species (reviewed by Dooling et al. 2000) using operant conditioning techniques. These studies have shown that as the frequency of the tone increases, it must be incrementally louder to hear it in a noisy background. This is not unlike the trend seen in other animals, suggesting a preserved evolutionary mechanism for hearing in noise.

Other laboratory studies measuring the detection and discrimination of calls and songs embedded in various types of noise can reveal more about the exact nature of the active space for the natural acoustic signals used for communication by social birds. Psychoacoustic studies often test the abilities of birds to detect, discriminate, or identify songs or calls that are embedded in a chorus of other songs or different types of noise (e.g., urban or woodland). Operant conditioning experiments on zebra finches, European starlings (*Sturnus vulgaris*), canaries (*Serinus canaria*), great tits (*Parus major*), and budgerigars all show that birds have excellent acuity for detecting or discriminating communication signals relative to pure tones, possibly due to the ecological relevance of these signals (Appeltants et al. 2005; Dent et al. 2009; Hulse et al. 1997; Lohr et al. 2003; Narayan et al. 2007; Pohl et al. 2009). In a field test of call discrimination, juvenile king penguins in a noisy colony were able to discriminate the calls of their parents from calls of other adults at a negative signal-to-noise ratio, suggesting that the enhanced detectability of natural vocal signals found in the laboratory actually translates to excellent acuity in the wild (Aubin and Jouventin 1998).

All of the above-mentioned studies reveal that songs and calls are more or less discriminable or detectable when they are presented within different masker types. For instance, great tits have better thresholds for detecting song elements embedded in woodland noise than urban noise (Fig. 13.13a; Pohl et al. 2009). Interestingly, detection of song elements in the dawn chorus was the most difficult condition for the great tits compared to the other noise types, suggesting that birds are not necessarily listening to one another in the mornings while they are singing. Canaries trained to identify canary songs embedded in one to four other distractor canary songs found it more difficult when there were more songs present, similar to conditions of the dawn chorus where many birds are singing overlapping songs (Fig. 13.13b; Appelants et al. 2005). Another laboratory study determined birds' abilities to discriminate auditory distance, a task crucially important for territorial birds. Pohl et al. (2015) trained great tits to discriminate between virtual birdsongs at near and far distances, presented in quiet or embedded in a noisy dawn chorus. The birds accurately discriminated between distances, although this was much harder in noisy than in quiet conditions. In summary, these experiments and others demonstrate that hearing in noise is possible, and that factors such as the spectro-temporal make-up of signals, noise type, and noise level all have an influence on hearing signals in noise.

As a whole, results from the laboratory and field experiments suggest that bird communication is more successful in quiet, rather than noisy environments, that the type of noise matters for communication, and that if noise is present, adjustments need to be made to the calls or songs of signalers for those signals to be detected, discriminated, and localized by the receivers. One such adjustment that has shown to be effective is changing the position of the signal relative to the
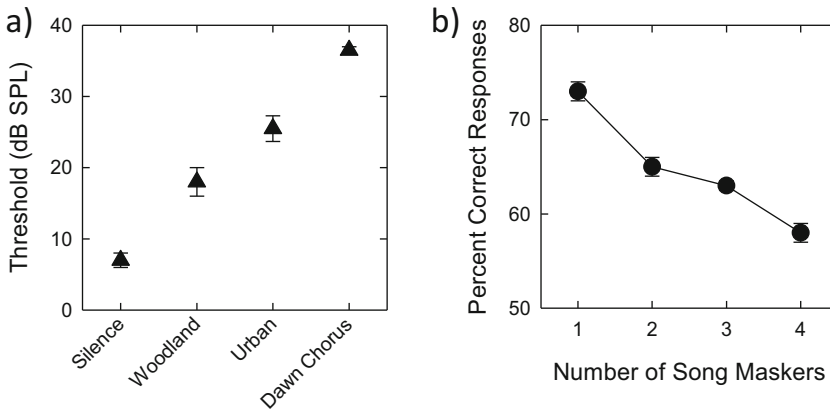
Fig. 13.13 (**a**) Masked thresholds for great tits detecting a synthetic song element embedded in silence, woodland noise, urban noise, or dawn chorus noise (adapted from Pohl et al. 2009). Performance is best for quiet conditions, worst for the chorus conditions. Thresholds are higher for urban noise than woodland noise. (**b**) Performance for canaries discriminating song elements embedded in 1–4 other songs (adapted from Appeltants et al. 2005). As the number of maskers increases, performance decreases

masker. Dent et al. (1997) found that thresholds for budgerigars detecting a pure tone in white noise were 11 dB lower when the signal and noise were separated by 90° in space than when they were co-located (i.e., spatial release from masking). A follow-up study showed an even greater advantage when the spatially separated signal was zebra finch song and the masker was a zebra finch chorus (Fig. 13.14; Dent et al. 2009). Thus, when birds are trying to communicate with one another in noisy environments, changing their position or even simply moving their heads will increase communication efficiency in similar ways as humans attempting to speak to one another in a noisy cocktail party will often move their head toward a speaker.
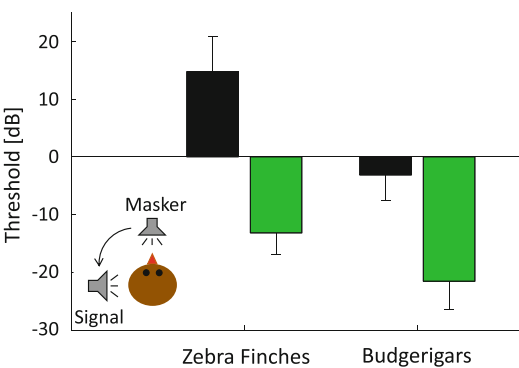
Another adjustment made by many birds is to shift the frequency content of songs to a higher range, as documented for European blackbirds (*Turdus merula*; Slabbekoorn and Ripmeester 2008), plumbeous vireos (*Vireo plumbeus*; Francis et al. 2011), gray vireos (*Vireo vicinior*; Francis et al. 2011), European robins (McMullen et al. 2014), chaffinches (Verzijden et al. 2010), black-capped chickadees (*Poecile atricapillus*; Proppe et al. 2011), and a number of tropical birds (de Magalhães Tolentino et al. 2018). Whether this is a true adaptation attempting to increase the lowest frequencies of songs above the highest frequencies of the noise, whether it is simply easier for the birds to make high frequencies louder, or whether urban birds live in denser environments and want to distinguish their songs from those of other birds is still being debated (e.g., Nemeth et al. 2013).

Pohl et al. (2012) tested the consequences of such shifts on perception in the laboratory. These authors trained great tits to detect or discriminate

Fig. 13.14 Signal-to-noise ratio thresholds for detecting a zebra finch song are higher (worse) when a chorus masker is co-located with the song (black boxes) than when the song is spatially separated from the masker (green boxes), in both budgerigars and zebra finches. Adapted from Dent et al. (2009)

between song phrases embedded in urban or woodland noises. In the urban noise background, it was easier for the tits to detect the high-frequency phrases than the low-frequency phrases. There was no difference in the woodland noise for detection of the different song types. For birds attempting to discriminate high- or low-frequency songs embedded in woodland or urban noises, the researchers found that the high-frequency elements were more useful in urban conditions, while the whole song was used for discrimination in woodland noise. Thus, birds that are changing their calls and songs into higher-frequency ranges for improved communication in noisy urban environments are doing so adaptively.

Other vocal adjustments made by birds in response to noise are to sing more during the quiet night than during the noisy day (as in European robins; Fuller et al. 2007), to shift the initiation of the dawn chorus by as much as 5 h to compensate for traffic noise (as in European blackbirds; Nordt and Klenke 2013), and to increase the intensity of vocalizations (Lombard effect). Black-capped chickadees modify the structure and frequencies of their alarm calls in response to noise (Courter et al. 2020), while house wrens (*Troglodytes aedon*) reduce the size of their song repertoires in addition to changing their song frequencies (Juárez et al. 2021). In a field study on noisy miners (*Manorina melanocephala*), Lowry et al. (2012) found that individuals at noisier locations produced louder alarm calls than those at quieter locations. The Lombard effect has also been demonstrated in the laboratory in Japanese quail (*Coturnix japonica*; Potash 1972), budgerigars (Manabe et al. 1998), chickens (*Gallus gallus domesticus*; Brumm et al. 2009), nightingales (*Luscinia megarhynchos*; Brumm and Todt 2002), white-rumped munia (*Lonchura striata*; Kobayasi and Okanoya 2003), and zebra finches (Cynx et al. 1998). A recent experiment measuring songs of the white-crowned sparrows in urban San Francisco during the 2020 COVID-19 shutdown showed that the birds responded to the decrease in noise levels with a return to decades-old song frequencies (Derryberry et al. 2020), suggesting that they have an almost-immediate ability to re-occupy an acoustic niche within a soundscape.

13.9.4 Physiological Effects

One major advantage birds possess, compared to humans, is the ability to regenerate auditory sensory cells lost during exposure to very loud sounds (Ryals and Rubel 1988), therefore birds experience no hearing loss over time from either aging or noisy environments. Birds do, however, experience stress from noise (Blickley et al. 2012; Strasser and Heath 2013).

Acoustic communication in birds is vital for survival, and understanding how noise affects sound production and perception is important for conservation efforts. Birds are clearly affected by the increasing levels of urban noise in their environments, but many adjust their calling and singing styles or locations to overcome problems of communicating in noise. Certainly, there are both limits to and consequences of those adjustments.

13.10 Noise Effects on Terrestrial Mammals

Anthropogenic noise affects mammals in a variety of ways changing their behavior, physiology, and ultimately ability to succeed in what otherwise might be considered optimal habitat. Terrestrial mammals show responses that range from ignoring or tolerating to avoiding noise, with potential impacts ranging from negligible to severe (Slabbekoorn et al. 2018b).

13.10.1 Terrestrial Mammal Hearing

Among terrestrial mammals, humans (*Homo sapiens*) are the most studied species with prevalent research addressing hearing physiology and psychology, hearing loss, and restoration. The mammalian ear consists of mechanical structures (incus, malleus, and stapes) evolutionarily derived from elements of the jaw that function

to translate sound from acoustic waves to nerve signals in the cochlea and auditory nerve. Though very effective, the ear can sustain damage and it degrades with age. Hearing loss results in reduced auditory acuity and limited information for the mammal to use. Loss can be caused by sudden exposure to high-intensity sound (e.g., from an explosion or gunfire) or by repeated or prolonged noise exposure (e.g., at industrial workplaces, at rock concerts, or from personal media players).

While the general structure of the mammalian ear is shared amongst terrestrial mammal species, there is great diversity in the sounds mammals can perceive, in the sounds they produce, and in their responses to sound. While human hearing ranges from about 20 Hz to 20 kHz, elephants use infrasound (sounds extending below the human hearing range, i.e., below 20 Hz; Herbst et al. 2012; Payne et al. 1986) and bats use ultrasound (sounds extending above the human hearing range, i.e., above 20 kHz, with some species hearing and emitting sound up to 220 kHz; Fenton et al. 2016). Rodents are known to be quite diverse, with subterranean species having excellent low-frequency hearing and terrestrial rodents having excellent ultrasonic hearing (reviewed by Dent et al. 2018). Mammals can thus be expected to display a diversity of responses to noise.

13.10.2 Behavioral Responses to Noise

One of the most frequently studied sources of noise in terrestrial mammal habitats is traffic noise from cars, trains, or aircraft. The most frequently reported response is animal movement away from the noise source. For example, Sonoran pronghorn (*Antilocapra americana sonoriensis*) increased their use of areas with lower levels of noise over areas with higher levels of noise from military aircraft (Landon et al. 2003). In the case of mountain sheep (*Ovis canadensis mexicana*), 19% showed disturbance to low-flying aircraft (Krausman and Hervert 1983). Prairie dogs (*Cynomys ludovicianus*) were exposed to playback of highway noise in an experimental prairie-dog town that was previously absent of anthropogenic noise. The treatment area had fewer prairie dogs above ground. Those that were above ground spent less time foraging and much more time exhibiting vigilant behavior (Shannon et al. 2014) leading to earlier predator detection and earlier flight response (Shannon et al. 2016).

A major concern regarding these behavioral responses by wildlife to traffic corridors is habitat fragmentation together with limited connectivity. Noisy areas may displace wildlife and form barriers to migration and dispersal (Barber et al. 2011; Fig. 13.15). Roads also fragment bat
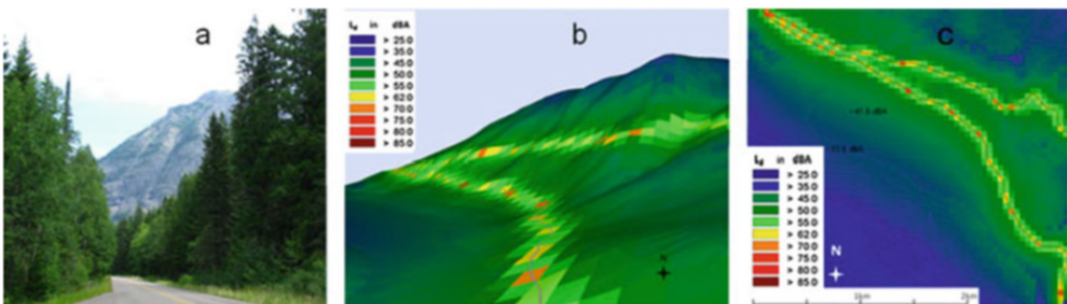

Fig. 13.15 (**a**) Photo of the Going-to-the-Sun road in Glacier National Park, USA. (**b**) 3D plot of 24-h traffic noise. (**c**) 2D plot of 24-h traffic noise (Barber et al. 2011). Road noise may form a barrier to wildlife migration. Reprinted by permission from Springer Nature. Barber, J. R., Burdett, C. L., Reed, S. E., Warner, K. A., Formichella, C., Crooks, K. R., Theobald, D. M., and Fristrup, K. M. Anthropogenic noise exposure in protected natural areas: estimating the scale of ecological consequences. Landscape Ecology, 26(9), 1281; https://link.springer.com/article/10.1007/s10980-011-9646-7.

habitat, although many species cross roadways or fly through underpasses (Kerth and Melber 2009).

Animals may adapt temporal behavioral patterns around noise exposure. Black-tufted marmosets (*Callithrix penicillata*) living in an urban park in Brazil stayed in quieter, central (i.e., away from road noise) areas during the day, and only utilized the park edges at night or weekends (Duarte et al. 2011). Forest elephants (*Loxodonta cyclotis*) became more nocturnal in areas of industrial activity; and while the study found no direct link to noise intensity, concern about natural biorhythms near noisy industrial sites was raised (Wrege et al. 2010).

Noise may affect foraging behavior. Woodland caribou stopped feeding when exposed to noise from petroleum exploration (Bradshaw et al. 1997). Reduced food intake in noise slowed growth in rats, pigs, and dogs (Alario et al. 1987; Gue et al. 1987; Otten et al. 2004). Gleaning bats (*Myotis myotis*) displayed reduced hunting efficiency during road noise playbacks (Schaub et al. 2008; Siemers and Schaub 2011). Similarly, Brazilian free-tailed bats (*Tadarida brasiliensis*) were less active and produced fewer echolocation bursts near a noisy gas compression station (Bunkley et al. 2015). Peromyscus mice, on the other hand, were more successful collecting pine seeds (a major food source) near noisy gas-extraction sites because competing, seed-collecting jays (*Aphelocoma californica*) abandoned the site (Francis et al. 2012). Additionally, predators of the mice, like owls, avoided the noisier sites, which may result in reduced predation of the mice (Mason et al. 2016). Finally, some animals may associate noise with reinforcement, such as food sources, and learn to approach sounds. Badgers (*Meles meles*) quickly learned to approach an acoustic deterrent device baited with food (dinner bell effect; Ward et al. 2008).

One pathway by which noise disrupts animal behavior is by acoustic masking. Piglets use vocalization bouts to coordinate nursing with sows and noise disrupted this communication leading to reduced milk ingestion and increased energetic costs for the piglets attempting to elicit milk (Algers and Jensen 1985). Some animals can adjust their calls to reduce masking (Lombard

effect). Cats increased the amplitude of calls in noise (Nonaka et al. 1997). Common marmosets (*Callithrix jacchus*) and cotton-top tamarins (*Saguinus oedipus*) increased both amplitude and duration of calls in noise (Brumm et al. 2004; Roian Egnor and Hauser 2006). Cotton-top tamarins timed their calls to avoid overlap with periodic noise (Egnor et al. 2007). Horseshoe bats (*Rhinolophidae*) increased echolocation amplitudes and shifted echolocation frequency in noise (Hage et al. 2013).

13.10.3 Physiological Responses to Noise

Human studies have shown that noise exposure can lead to a variety of health effects ranging from a feeling of annoyance to disturbed sleep, emotional stress, decreased job performance, higher chance of developing cardiovascular disease, and decreased learning in schoolchildren (Basner et al. 2014). We can only begin to understand the effects of noise on the health of other mammalian species.

Studies on elk (*Cervus canadensis*) and wolves (*Canis lupus*) in Yellowstone National Park, USA, had elevated levels of glucocorticoid enzymes (a blood hormone that indicates stress) when snowmobiles were allowed in the park. After banning snowmobiling, enzyme levels returned to normal, although a direct link to noise exposure was not made (Creel et al. 2002). After ongoing zoo visitor noise, giant pandas (*Ailuropoda melanoleuca*) exhibited increased glucocorticoids, negatively impacting reproduction efforts (Owen et al. 2004). In male rats exposed to chronic noise, testosterone decreased (Ruffoli et al. 2006). Pregnant mice exposed to 85–95 dB re 20 μPa alarm bells had pups with lower serum IgG levels, indicating impaired immune responses (Sobrian et al. 1997). Chronic noise exposure in rats affected calcium regulation leading to detrimental changes at cellular level (Gesi et al. 2002). Desert mule deer (*Odocoileus hemionus crooki*) and mountain sheep had increased heart rates relative to increased levels of aircraft noise playback. Heart rate returned to

normal within 60–180 s and responses decreased over time potentially indicating a form of habituation (Weisenberger et al. 1996).

13.10.4 Effects of Noise on the Auditory System

The physiological impact of noise is well documented in several mammalian species, particularly laboratory animals, due to the ability to systematically expose and test individuals. Systematic research has shown that several sound features (such as sound frequency, duration, intensity, amplitude rise time, continuous versus temporary exposure, etc.) impact how an animal's auditory system is affected by noise exposure. For example, chinchillas experienced TTS from exposure to the sound of a hammer hitting a nail repeatedly (Dunn et al. 1991). While some of the chinchillas were exposed to repeated hammering (a series of separate sound events), others were exposed to continuous noise of the same spectrum as nail hammering (one single sound event). While all chinchillas showed a decrease in hearing sensitivity, the chinchillas exposed to the repeated hammering had more hearing loss (Dunn et al. 1991).

NIHL can occur from mechanical damage and/or from metabolic disruption of acoustic structures (Hu 2012). Mechanical damage occurs during the sound exposure due to excessive movement caused by sound waves. Depending on the level of the sound, loud noise can damage structures at the cellular level. Metabolic damage occurs due to a cascade of changes at the cellular level from mechanical damage and can continue for weeks after sound exposure.

In TTS, damage may occur to the synapses and stereocilia, while in PTS, damage is more extensive, including outer hair cell death and fibrocyte loss. For example, the audiograms of four species of Old-World monkeys (*Macaca nemestrina, M. mulatta, M. fascicularis*, and *Papio papio*) were compared before and after exposure to octave-band noise (between 0.5 and 8 kHz at levels of 120 dB re 20 μPa) for 8 h daily for 20 days. Loss of both inner and outer hair cells at the basal end of the organ of Corti and hence PTS were produced (Hawkins et al. 1976). The difference in noise exposure when an individual transitions from having temporary to permanent damage varies by species as well as depending on several individual factors such as past sound exposure, age, genetics, etc. (Hu 2012).

Exposure to continuous, high-level (>100 dB re 20 μPa) sounds has been shown to damage or destroy hair cells in multiple species, such as rats, rabbits, and guinea pigs (Borg et al. 1995; Chen and Fechter 2003; Hu et al. 2000). Recently, exposure to lower-amplitude sounds over long periods of time has also been shown to cause permanent damage. Mice exposed to 70 dB re 20 μPa continuous white noise for 8 h a day over the course of up to 3 months showed increased hearing thresholds and decreased auditory response amplitudes (Feng et al. 2020). Notably, the mice also showed aggravated age-related hearing loss in relatively young mice (mice were 8 weeks old at the start of exposure) (Feng et al. 2020).

Some animals can mitigate the impact of noise on the auditory system using a stapedial reflex to close the auditory meatus. When exposed to a loud sound, the contraction of the stapedial muscle causes a decrease in auditory sensitivity by closing the auditory meatus, thus negating some potential damage. This reflex is well documented in humans and appears to primarily play a role in sudden, unexpected sounds with sharp rise times. The reflex is thought to function similarly in most terrestrial mammals, for example in rabbits. Rabbits exposed to sound in normal conditions had very little threshold shifts, but when their stapedial reflex was inactivated (by blocking the nerve) during noise exposure, PTS was observed at otherwise not NIHL inducing levels (Borg et al. 1983). In cats, this reflex functions even under anesthesia (McCue and Guinan 1994). However, damage to the auditory nerve connections (synaptopathy) can also damage auditory reflexes; for example, in mice, synaptopathy was directly correlated to the function of the middle ear muscle reflex (Valero et al. 2018).

Synaptopathy not only occurs from noise exposure, but also at old age or from exposure to ototoxins (Valero et al. 2018).

13.11 Noise Effects on Marine Mammals

As with terrestrial animals, the potential effects of noise exposure on marine mammals may include a range of physical effects on auditory and other systems, as well as behavioral responses, and interference with sound communication systems (Erbe et al. 2018; Southall 2018). Several reviews have recently been completed, for specific noise sources (such as shipping, Erbe et al. 2019b; dredging, Todd et al. 2015; and wind farms, Madsen et al. 2006), and specific geographic regions (such as Antarctica; Erbe et al. 2019a). Current knowledge is summarized here, ranging from issues that are likely most experienced, but less severe, to effects that may more rarely occur but are increasingly severe. Events of the latter category, such as mass strandings and mortalities of marine mammals associated with strong acute anthropogenic sounds (notably certain military active sonar systems or explosives), have historically driven and dominated the awareness, interest, and research on the potential effects of noise on marine mammals (e.g., Filadelfo et al. 2009). However, there is increasing concern over sub-lethal, yet potentially more widespread, effects (notably behavioral influences) of more chronic noise sources and their consequences for individual fitness and ultimately population parameters (e.g., New et al. 2014; Ocean Studies Board 2016). Southall et al. (2007) reviewed the available literature at that time and made specific recommendations regarding effects of anthropogenic noise on hearing and behavior in marine mammals. Substantial additional research and synthesis of available data has expanded on their assessment, improving the empirical basis for these evaluations and expanding consideration to other important areas discussed here (e.g., masking and auditory impact thresholds; Erbe et al. 2016a; Finneran 2015). And so the Southall

et al. (2007) criteria were updated in 2019 (Southall et al. 2019b).

13.11.1 Marine Mammal Hearing

In most situations of noise exposure, marine mammals might merely detect a sound without a specific adverse effect. Furthermore, animals arguably have to be able to detect signals in order for most of the effects described here to potentially occur. Hearing capabilities and specializations vary widely in marine mammals. Some species, such as pinnipeds, have adaptations to facilitate both aerial and underwater hearing (Reichmuth et al. 2013). Other species, including the odontocete cetaceans, have very wide frequency ranges of underwater hearing extending well into ultrasonic ranges to facilitate echolocation (Mooney et al. 2012). For other key species, including many of the endangered mysticete cetaceans, virtually no direct data are available regarding hearing, which is instead estimated from anatomical and sound production parameters.

Southall et al. (2007) developed the concept of functional marine mammal hearing groups. Each group was assigned a frequency-specific auditory filter (called weighting function) to account for known and presumed differences in hearing sensitivity within marine mammals (Fig. 13.16). Using additional direct data, these hearing groups and weighting functions were substantially improved and modified (Finneran 2016). These weighting functions are applied to the noise spectrum in order to estimate the likelihood of NIHL, by comparison to published TTS and PTS onset thresholds expressed as weighted cumulative sound exposure levels (National Marine Fisheries Service 2018).

Understanding and directly accounting for the frequency-specific parameters of noise and how they interact with background noise and marine mammal-specific hearing is important in considering the contextual aspects of potential behavioral responses (Ellison et al. 2012), auditory masking (Erbe et al. 2016a), and hearing impairment and damage (e.g., Finneran 2015).
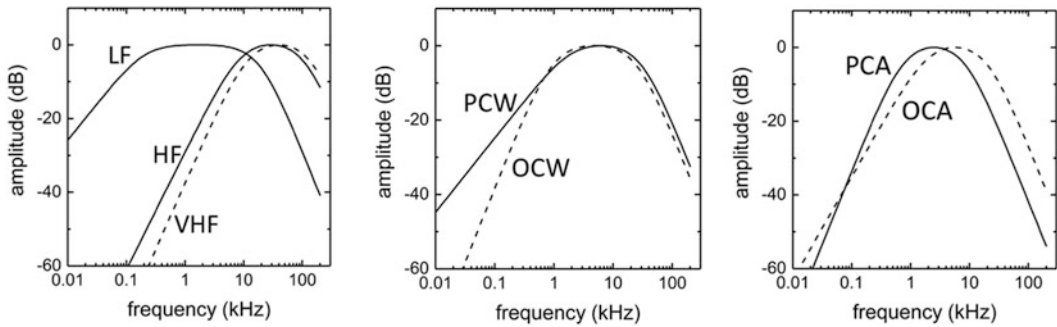
Fig. 13.16 Auditory weighting functions for marine mammal functional hearing groups; LF: low-frequency cetaceans, HF: high-frequency cetaceans, VHF: very-high-frequency cetaceans, PCW: phocid carnivores in water, OCW: other carnivores in water, PCA: phocid carnivores in air, OCA: other carnivores in air (Southall et al. 2019b)

13.11.2 Behavioral Responses to Noise

Noise exposure may lead to a variety of behavioral responses (and severity) in marine mammals, ranging from minor changes in orientation to separation of mothers and dependent offspring, or mass mortality. Southall et al. (2007) reviewed these responses and proposed a qualitative relative severity scaling that takes into account the relative duration and potential impacts on biologically meaningful activities. This approach has been applied and modified in quantifying behavioral responses in the context of exposure-response risk functions (e.g., Miller et al. 2012; Southall et al. 2019a). While sound exposure level is an important aspect of determining the relative probability of a response, other contextual factors of exposure also may be critically important, including animal behavioral state (e.g., Goldbogen et al. 2013), spatial proximity to the noise (e.g., Ellison et al. 2012), sensitization to noise exposure (Kastelein et al. 2011), or nearby vessel noise (Dunlop et al. 2020). A variety of experimental and observational methods have been applied in evaluating noise exposure and behavioral responses, resulting in a large volume of scientific literature on this subject that is reviewed generally here.

Behavioral responses to noise have been studied in both field and laboratory. The advantage of field studies is the observation of animals in their natural environment, but it can be challenging to observe individuals and determine exposure levels and responses with sufficient resolution and sample size. Field studies of large sample size include observations of changes in whale distribution in response to industrial noise and seismic surveys (see Richardson et al. 1995 for an overview), recordings of vocal behavior of whales exposed to military sonar (Fristrup et al. 2003; Miller et al. 2000), and a recent series of experiments exposing migrating humpback whales to 20, 440, and 3300-in^3 seismic airgun arrays (Dunlop et al. 2016, 2017a, 2020). Many recent experimental field studies have considered potential effects of active sonar on cetaceans (Southall et al. 2016). Among the many broad results and conclusions are dose-response curves for exposure level and response probability in killer whales (Miller et al. 2014) and humpback whales (Dunlop et al. 2017b, 2018), behavioral state-dependent responses in blue whales (*Balaenoptera musculus*; Goldbogen et al. 2013) and humpback whales (Dunlop et al. 2017a, 2020), and changes in social behavior following noise exposure in pilot whales (*Globicephala* sp.; Visser et al. 2016) and humpback whales (Dunlop et al. 2020). For instance, Goldbogen et al. (2013) showed that deep-feeding blue whales are much more likely to change diving behavior and body orientation in response to noise than those in shallow-feeding or non-feeding states
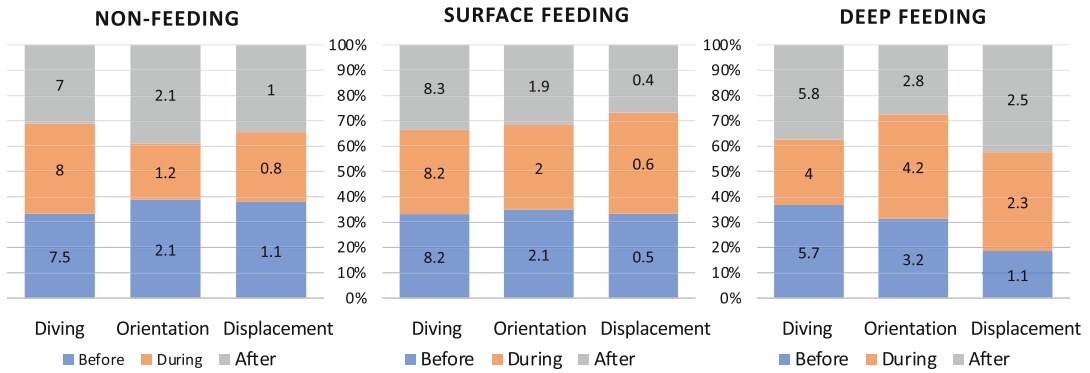
Fig. 13.17 Relative response differences in various aspects of blue whale behavior between non-feeding, surface-feeding, and deep-feeding individuals (adapted from Goldbogen et al. 2013). Response magnitude was quantified using generalized additive mixed models for behavioral parameters relevant to each behavioral state and potential responses in terms of diving, orientation, and displacement

(Fig. 13.17). This finding has been replicated and expanded with individual blue whales, demonstrating the same context-dependency in response probability as well as potential dependence in response probability based on horizontal range from the sound source even for the same received levels (Southall et al. 2019a).

Some species such as long-finned pilot whales appear behaviorally tolerant of noise exposure (e.g., Antunes et al. 2014), whereas beaked whales (Family Ziphiidae) are clearly among the more sensitive species behaviorally (DeRuiter et al. 2013; Miller et al. 2015; Stimpert et al. 2014; Tyack et al. 2011). The analysis of multivariate behavioral data to determine changes in behavior, including potentially subtle but important changes, is statistically challenging, although recent substantial progress in analytical methods has been made as well (Harris et al. 2016).

Experimental laboratory approaches have the advantage of greater control and precision on multivariate aspects of exposure and response, but lack the contextual reality in which free-ranging animals experience noise. Studies that evaluated noise exposure and response probability in captive harbor porpoises (e.g., Kastelein et al. 2011, 2013) demonstrated a particular sensitivity of this species, which matched field observations. Studies with captive bottlenose dolphins (*Tursiops truncatus*) and California sea lions (*Zalophus californianus*) have included large sample sizes and repeated exposures to demonstrate species, age, and experiential differences in response probability to military sonar signals (Houser et al. 2013a, b).

Observational methods (visual and acoustic) have provided complementary data to assess both acute and chronic noise exposure. Passive acoustic monitoring over large areas and time periods demonstrated changes in acoustic behavior and inferred movement of beaked whales in response to military sonar signals (e.g., McCarthy et al. 2011) resulting in dose-response curves (Moretti et al. 2014). Similarly, large-scale monitoring linked cetacean distribution and behavior to seismic surveys (e.g., Pirotta et al. 2014; Thompson et al. 2013), impact pile driving (e.g., Dähne et al. 2013; Thompson et al. 2010; Tougaard et al. 2009), and acoustic harassment devices (e.g., Johnston 2002).

Such observational studies lack experimental control, resolution to the individual level, detail on fine-scale responses, and ability to differentiate short-term responses to noise from those to other stimuli, but offer information on broad-scale spatio-temporal changes in habitat use and behavior. Ideally, experimental approaches would be combined with broad-scale observational methods to discover potential population-level effects (see Southall et al. 2016).

13.11.3 Communication Masking

Noise can interfere with or "mask" acoustic communication by marine mammals (Erbe et al. 2016a). Masking is due to the simultaneous presence of signal and noise energy within the same frequency bands. Masking reduces the range over which a signal may be detected. Or, in other words, the signal must be louder, for it to be detected in the presence of noise (Fig. 13.18).

The area over which an animal call can be detected by its intended recipients (i.e., the active space or communication space) fluctuates in space and time. Models have been developed to quantify lost communication space and applied to mysticetes communicating near busy shipping lanes (Fig. 13.19; Clark et al. 2009; Hatch et al. 2012).

The Lombard effect has been demonstrated in marine mammals as an increase in vocalization source levels (e.g., Helble et al. 2020; Holt et al. 2009; Thode et al. 2020), duration (Miller et al. 2000), or repetition (Thode et al. 2020). Additionally, marine mammals have demonstrated increased detection capabilities based on angular separation between signal and noise sources,
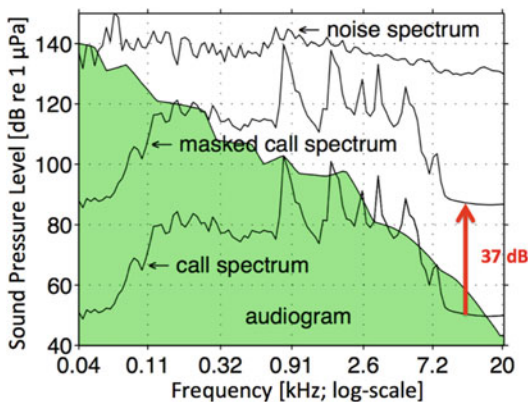
termed a spatial release from masking (e.g., Turnbull 1994), or based on wide-band amplitude-modulation patterns in the noise, termed a comodulation masking release (e.g., Branstetter et al. 2013). These compensatory and signal processing capabilities reduce the masking potential of noise.

13.11.4 Effects of Noise on the Auditory and Other Systems

While behavioral responses and auditory masking may occur relatively far from sound sources, impacts to the auditory system are expected at higher levels hence shorter ranges. As with masking, the frequency of noise exposure is important in terms of the potential for NIHL, and noise at frequencies where animals are more sensitive has a greater potential for inducing such effects in marine mammals (Finneran 2015). Furthermore, the temporal pattern of noise matters substantially in terms of the potential for NIHL. Impulsive signals with rapid rise times are more likely to cause NIHL (see Finneran 2015). The risk and severity of NIHL increases with repeated and longer exposures, but simple energy-based models integrating exposure level over time cannot fully predict potential NIHL.

Despite substantial recent research, our understanding of NIHL in marine mammals remains limited. TTS has been studied in fewer than ten species, and not in any mysticete. Controlled exposure experiments that would produce a PTS are infeasible due to animal ethics considerations. Nonetheless, TTS studies in odontocetes and pinnipeds produced TTS-onset levels and information on frequency-dependence (reviewed by Finneran 2015). Recent experiments produced frequency-weighted TTS-onset levels higher than the original exposure criteria compiled by Southall et al. (2007). However, some studies (e.g., Kastelein et al. 2012; Lucke et al. 2009) demonstrated much lower TTS-onset levels, specifically in harbor porpoises.

Noise may further cause non-auditory physiological impacts that may not be immediately apparent. Noise has increased stress hormones in
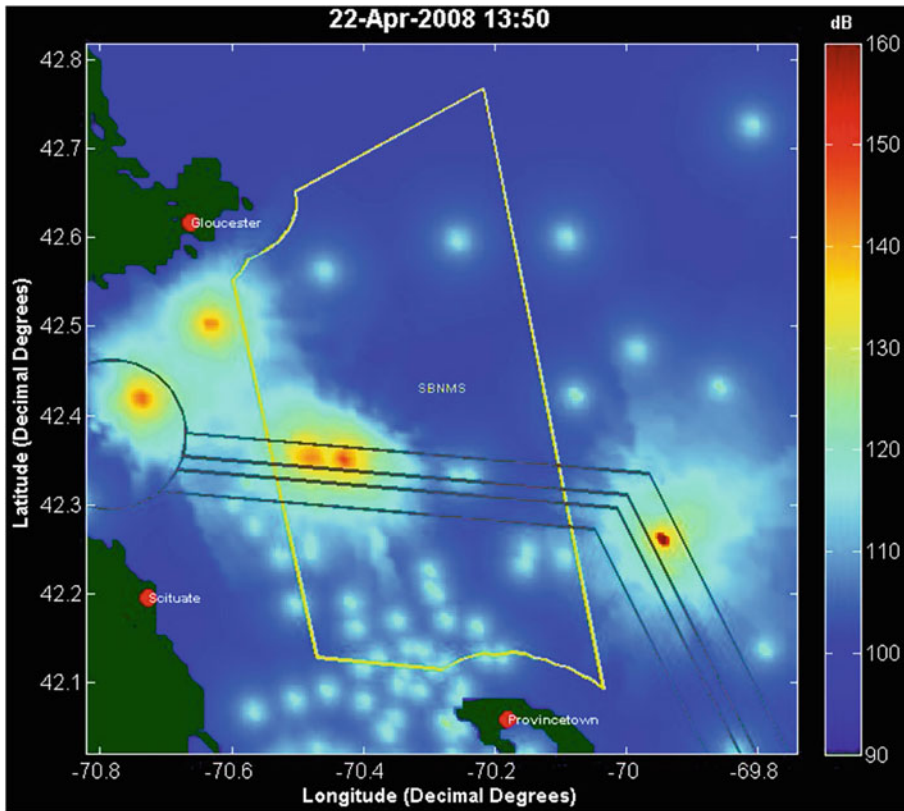

Fig. 13.18 Beluga whale (*Delphinapterus leucas*) audiogram (shaded green), spectrum of a call at detection threshold (measured behaviorally) in the absence of noise, spectrum of an icebreaker's bubbler noise, and the masked call spectrum in the presence of bubbler noise. The spectra are shown as band levels, with the bandwidths aiming to represent the auditory filters. The upwards shift of the call spectrum equals the amount of masking: 37 dB (Erbe 2000)

Fig. 13.19 Chart of acoustic footprints of North Atlantic right whales (*Eubalaena glacialis*; light blue dots) and ships (larger footprints with red centers) off Cape Cod, Massachusetts Bay, USA. The larger and stronger ship noise footprints can easily engulf (i.e., mask) the right whale calls. Stellwagen Bank National Marine Sanctuary outlined in yellow. Figure courtesy of Chris Clark

the blood of captive marine mammals (e.g., Romano et al. 2004). In the wild, stress hormones in right whales decreased when ambient noise from shipping was lower (Rolland et al. 2012). Such measurements of noise-induced stress in marine mammals are comparable to studies with other vertebrates (Romero and Butler 2007). However, information is lacking on how stress scales with noise exposure and on the long-term health impacts of prolonged stress.

Finally, beaked whales that stranded after exposure to military sonar exhibited lesions and gas or fat emboli (Fernandez et al. 2005; Jepson et al. 2003). While some form of decompression sickness has been hypothesized, the physiological mechanisms for such emboli to occur are poorly understood. These physiological effects may have

been secondarily caused or exacerbated by the animals' behavioral responses to sonar.

13.12 Summary

This chapter presented examples of the variety of effects noise can have on animals in terrestrial and aquatic habitats. Studies on the hearing in noise and on behavioral and physiological responses to noise have concentrated on fish, frogs, birds, terrestrial mammals, and marine mammals. Clearly, more research is needed for invertebrates, reptiles, and all groups of freshwater species. In addition, more studies on the metabolic costs of these responses are needed.

Animals demonstrate a hierarchy of behavioral and physiological responses to noise. Behavioral reactions to anthropogenic noise include a startle response, change in movement and direction, freezing in place, cessation of vocal behavior, and change in behavioral budgets. Animals can also modify their signals to counteract the effects of noise and improve communication. Such modifications include changes in amplitude, duration, and frequency. Some animals also increase the redundancy of their signals by repeating them more often. Physiological reactions to anthropogenic noise are indicated by increased cortisol levels (indication of stress), temporary or permanent hearing loss, and physical damage to tissues and organs such as lungs and swim bladders.

The effects of anthropogenic noise on individual animals can escalate to the population level. Ultimately, species-richness and biodiversity could be affected. However, methods and models to address these topics are in their infancy.

There is the potential to mitigate any negative impacts of anthropogenic noise by modifying the noise source characteristics and operation schedules, finding alternative means to obtain operational goals of the noise source, and protecting critical habitats. Effective management of habitats should include noise assessment. Further research is needed to understand the ecological consequences of chronic noise in terrestrial and aquatic environments.

Remote wilderness areas are not immune to the effects of anthropogenic noise, because sound travels very well (with little loss over long ranges) in many terrestrial and aquatic habitats. Resource managers should continue to be vigilant in monitoring and mitigating the effects of anthropogenic noise on animals.

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