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Aquatic Noise Pollution: Implications for Individuals, Populations and Ecosystems

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Anthropogenically driven environmental changes affect our planet at an unprecedented scale, and are considered to be a key threat to biodiversity. According to the World Health Organisation, anthropogenic noise is one of the most hazardous forms of anthropogenically driven environmental change and is recognised as a major global pollutant. However, crucial advances in the rapidly emerging research on noise pollution focus exclusively on single aspects of noise pollution, e.g. on behaviour, physiology, terrestrial ecosystems or by focusing on certain taxa. Given that more than two thirds of our planet is covered with water, there is a pressing need to get a holistic understanding of the effects of anthropogenic noise in aquatic ecosystems. We found experimental evidence for negative effects of anthropogenic noise on an individual's development, physiology, and/or behaviour in both invertebrates and vertebrates. We also found that species differ in their response to noise, and highlight the potential underlying mechanisms for these differences. Finally, we point out challenges in the study of aquatic noise pollution and provide directions for future research, which will enhance our understanding of this globally present pollutant.

1. Background

Many species are currently experiencing anthropogenically driven environmental changes, which can negatively affect the persistence of populations or species [1,2]. One form of anthropogenically driven environmental change is the change in the acoustic environment through anthropogenic noise pollution. According to the World Health Organisation, anthropogenic noise is one of the most hazardous forms of pollution and has become omnipresent within terrestrial and aquatic ecosystems [3,4]. Anthropogenic noise is any unwanted or disturbing sound. In aquatic ecosystems, noise is intentionally produced for seismic exploration, harassment devices or sonar, or an unintentional by-product such as industry, shipping and recreational boating [5].

Sound is the propagation of a mechanical disturbance through a medium, such as air or water, taking the form of acoustic waves [6]. Underwater sound has both a pressure and a particle motion component, and hearing can be defined as the relative contribution of each of these sound components to auditory detection [7]. Therefore, hearing may involve the detection of pressure, and/or particle motion. Particle motion perception differs from pressure perception by limiting the detectable frequency range to a few hundred Hertz, by restricting the detectable sound intensities to higher levels, and also by shortening distances over which sounds can be perceived [8].

In recent years, a number of excellent reviews focusing on single aspects of noise pollution have been published, e.g. behaviour [9]; physiology [10]; conservation: [11-14], terrestrial ecosystems [15,16] or by focusing on certain taxa e.g.[17-25]. Given that more than two thirds of our planet is covered with water, there is a pressing need to specifically understand the effects of anthropogenic noise in aquatic ecosystems. To close this gap, we review how noise pollution in the aquatic environment affects species across the taxonomic scale by looking how noise affects an individuals' development, physiology and/or behaviour. Then, we discuss why species may differ in their susceptibility to anthropogenic noise and critically evaluate challenges in the study of aquatic noise pollution; finally, we provide directions for future studies, which will enhance our understanding of this important global pollutant.

2. Effects of anthropogenic noise

Anthropogenic noise can affect an individual's anatomy, physiology, and/or behaviour in several ways [26]: (i) hearing damage, including permanent threshold shifts, and other non-auditory tissue damage from exposure to very loud sounds; (ii) temporary threshold shifts from acoustic overexposure; (iii) masking of sounds hindering the perception of acoustic information [27]; (iv) changing hormone levels, leading to stress responses and lack of sleep. At least for the first three of these, direct auditory effects strongly depend on the level and duration of noise exposure, which often correlates with the proximity of the individual to the noise source [25]. There is evidence that intense and impulsive sounds can damage tissues and potentially result in mortal effects when animals are close to a noise source, but far more individuals are likely to be exposed to sounds at some distance from the noise source where the intensity is lower, with effects being more likely to be behavioural rather than physical [25,26]. Thus, the effects of anthropogenic noise can range from small, short-term behavioural adjustments to large behavioural or physiological changes resulting in death (figure 1).

(a) Development

Noise can affect both the anatomy and the morphology of an organism, by mechanically damaging single cells as well as entire organs. For example, noise can damage statocysts in invertebrates, ears and/or swim bladders in fish, and auditory organs in marine mammals [28,29]. Such noise induced damages can negatively affect perception and orientation, and/or buoyancy control, which may result in mass strandings in both invertebrates and vertebrates (e.g., [28,29]).

Noise can also affect organisms during various stages of ontogeny. While early life stages may be able to tolerate natural environmental fluctuations, anthropogenically induced environmental changes can reach beyond the natural range. Consequently, anthropogenic noise can lead to morphological malformations [30], reduce the successful embryonic development and increase larvae mortality [31]. This suggest that noise may affect developmental instablity, i.e. the inability of the genome to buffer developmental processes against disturbances [32] and canalisation, i.e. the ability of a population to express the same phenotype regardless of variablity of its environment or genotype [33]. Such changes early in life will result in fitness cost and may impact on population dynamics and resilience, with potential implications for community structure and function (figure 1).

However, not all species are affected by noise during early life stages: whilst anthropogenic noise did not affect crab larvae survival [34] it increased mortality in some fish larvae ([35], but see [36]). One explanation for these contrasting results is that the fry of some species rely on detection of reef noise for habitat selection [37], which may explain why embryonic coral reef fish respond to noise [38]. On the other hand, the lack of an effect on early life stages in other species may be explained by embryos and fry developing hearing capacity to detect sounds later during ontogeny [36].

(b) Physiology

One of the changes in response to noise that links anatomy, morphology and physiology is the impact on hearing. Noise exposure can change hearing capabilities by increasing the auditory threshold level [39,40]. Following noise exposure, several regions of saccules can exhibit significant loss of hair bundles demonstrating damage caused by noise, but with the potential of recovery [41], depending on both the duration of noise exposure and the frequency [39]. Anthropogenic noise can also influence the endocrine system, leading to an increase in secretion of the stress hormone cortisol in fish ([40,42] but see [43]) and mammals [44]. Although the exact mechanism remains unclear, physiological stress caused by noise is a likely source for developmental delays and growth abnormalities [30,31,35] but also may hamper reproduction, growth and immunity [45].

Anthropogenic noise can also affect the metabolism of both invertebrates and vertebrates. Crustaceans exposed to ship-noise consumed more oxygen than those exposed to ambient harbour noise [46]. In Perciformes, anthropogenic noise elicited a rise in cardiac output [47] and increased lactate and haematocrit levels reflecting increased muscle metabolism [48]. Since muscle activity can be a large part of the fish energy budget, noise may thus result in an increase of metabolic costs [49]. Thus, noise can affect various aspects of an individual’s physiology, that are negatively associated with metabolism, immune responses, survival and recruitment as well as affecting development [10].

(c) Behaviour

Initial responses of individuals to changes in the environment are often behavioural [50]. Consequently, noise pollution can induce a variety of behavioural changes by (i) overlapping with the hearing range of species (figure 2), (ii) overlapping with the bandwidth of acoustic information (figure 2), i.e. the acoustic information is masked, (iii) distracting individuals [51] even if acoustic information is not energetically masked [52], and (iv) affecting behaviour across sensory modalities: cuttlefish, for example, changed their visual signals when exposed to anthropogenic noise [53], and aquatic mammals may alter the use of their primary communication channel [54].

Broadly speaking, species can use sound to provide or extract information by actively producing sound, e.g. in communication and/or echolocation, and passively by extracting information from environmental cues. Mitigating the effects of anthropogenic noise during communication is crucial because noise reduces the range at which a signal can be detected and processed. Ship noise, for example, reduces communication range of Ziphiidae by a factor of more than five [55]. One of the most common behavioural responses mitigating increasing noise levels is the adjustment of acoustic signals [56] to maintain their detection and efficiency [57]. In addition to communication, some species produce sound such as echolocation to gather information about their environment. In Delphinidae, noise decreased the accuracy to detect objects with sonar and increasing noise levels ceased the production of sonar clicks due to a decrease in effectiveness [58]. Thus, acoustic information used in navigation and prey location is disrupted by noise, individuals will have difficulties locating indispensable resources, e.g. suitable habitats and food.

Noise can affect the perception of environmental cues which many species use to gather information about the environment [59]. Acoustic cues play an important role for larval orientation and settlement decisions, e.g. in reef fish and crustaceans, because these cues can indicate both the presence and suitability of particular habitat types [60-62]. Furthermore, noise may affect predator-prey interactions: fish can use sound generated by prey to hunt efficiently [63], and prey, on the other hand, may suppress acoustic behaviour in response to predator sounds [64-67]. Moreover, noise can increase the risk of predation or affect anti-predator behaviour by reducing anti-predator defence in both invertebrates and vertebrates ([68,69] but see [70]).

Foraging might not only be affected through masking of cues that are important to detect prey (see above). When experimentally exposed to noise, fish showed increased handling errors and decreased discrimination between food and non-food items [71] or ceased feeding [72], whereas shore crabs disrupted their feeding [69]. Thus, anthropogenic noise can lead to significant impacts on an individual's foraging and feeding efficiency in both invertebrates and vertebrates. Noise pollution can also alter small scale movements leading to avoidance of noise, e.g. fish and squid which alter their position in the water column in response to anthropogenic noise [73,74], whereas large scale movements can lead to the abandonment of habitats [75].

Noise may also negatively affect the social structure between pairs and groups, leading to weakened social bonds and instability in group cohesion by increasing the aggression between individuals [68]. Such behavioural changes can impede defence against predators of eggs and fry [68], reduce the ability to maintain territories [76], or alter the reproductive behaviour and output of individuals by negatively influencing mate choice, courtship and parental care [17]. An increase in agonistic behaviours, including the quantity and quality of contests between individuals, may increase the amount of energy used or the likelihood of injury or death [68].

3. Challenges and directions for future studies

There are a few challenges in the study of aquatic noise pollution, which fall into four broad categories: (a) linking proximate and ultimate individual responses to ecological effects; (b) interactions among multiple environmental stressors; (c) species-specific responses; and (d) study design, i.e. experiments with suitable controls and replicates. Only by addressing these issues we will be able to get a better understanding of the effects of noise pollution and set the right conservation actions.

(a) Bridging the gap: linking proximate and ultimate individual responses to ecological effects

Due to the complexity of ecosystem processes, we currently have only little understanding of how proximate and ultimate individual responses may translate into ecological effects (figure 1). While we have found experimental evidence of how noise affects behaviour, development and physiology, we have only little experimental data how these changes may translate into individual fitness and population-level consequences. One example illustrating how increasing noise may affect ultimate individual responses is the effect of noise on predator-prey interactions: acoustic disturbance can impair anti-predator responses in fish, which directly affects the likelihood of survival [77]. Whether these ultimate individual responses translate into ecological effects in the wild remains to be shown.

(b) Interactions among multiple environmental stressors

Anthropogenic stressors, such as noise pollution, have an ever increasing effect on the environment, but these stressors rarely act in isolation [78]. Often organisms are exposed to several environmental stressors and the resulting interactions among them simultaneously. For example, the impact of anthropogenic noise in the marine environment may be amplified by ocean acidification and/or an increase in water temperature both affecting transmission of sound in water. Ocean acidification has led to a decrease in pH, which reduces the absorption of sound in oceans, making them noisier by decreasing sound absorbing abilities for low frequencies [79,80]. Increasing temperatures, on the other hand, lead to a decrease of speed at which sound travels. Carefully planned experiments are needed to investigate the complexity of such multifaceted interactions of environmental stressors.

(c) Species specific responses

Anthropogenic noise affects a wide range of aquatic invertebrates and vertebrates and responses to noise can differ between species (figure 2). Non-mutually exclusive explanations why species respond differently to anthropogenic noise are: Firstly, differences in auditory capabilities and sensitivities to detect sound pressure and/or particle motion (e.g. [81-83]). Notably, the role that particle motion plays in the biology and ecology of species is still largely unknown [84]. The detection of pressure is well described in mammals and certain fish with morphological specialisations that use the swimbladder as a pressure-to-particle motion converter [7]. In contrast, the detection of particle motion is found in cartilaginous and some teleost fish that do not have specialised adaptations to detect or process sound pressure [8,85]. At least a third of all teleost species developed structures for sound pressure detection where air-filled cavities within the body, e.g. the swim bladder, undergo volume changes because air is more compressible than fluids in a sound field [8]. These changes will result in oscillations transmitted to the inner ear improving hearing capabilities, functioning as pressure-to-particle motion transducers [8]. However, if a noise source is more than a few metres away from an organism, noise may have less impact on species relying on particle motion, because it can only be detected over short distances, in a small frequency range and at sound intensities at higher levels (see above). In contrast, species relying on sound pressure detection will detect sound pressure changes over large distances and thus may be more vulnerable to increasing noise levels than species relying on particle motion alone. Hence, aquatic mammals and fish species able to detect sound pressure may be more vulnerable to increasing noise than species relying on particle motion alone. Due to the variety of perception modes among species, more work is needed to understand the interplay between a species' sound detection mechanisms and its vulnerability to increasing noise levels. To unravel the link between hearing mechanisms and vulnerability to anthropogenic noise is particularly important for conservation and species management.

Secondly, species might also respond differently to different types of noise, e.g. whether it is chronic or not, and/or has daily fluctuations. To assess the effects of different types of anthropogenic noise in aquatic environments it is necessary to quantify the distinctive characteristics of individual noise sources because aquatic environments can be complex in their characteristics [19]. Some of the noise produced by human activities is impulsive and intense, particularly close to the sound source (e.g. explosions, seismic air guns, impact pile driving), whereas other human noises are less pronounced but are chronic (e.g. wind farms, vessels). This added complexity, i.e. differences in response to different noise sources, is seen in both behavioural and physiological responses to noise. For example, Balaenopteridae reacted differently to ship noise and noise generated by air guns, with the latter causing avoidance behaviour and changes to communication, whilst the former only affected communication [86]. These differences in response could be related to temporal differences (e.g. [87]) or structural differences in the characteristics of the noise stimuli. Therefore, caution must be taken when extrapolating results from one species or noise type to another [25].

The importance of noise pollution has been recognised in conservation in both aquatic and terrestrial ecosystems [11-14]. Often, the aim of conservation is to protect entire ecosystems, but conservation can only be successful if we understand how and why species are affected by environmental changes, as individual changes can have population consequences [88]. While there are some attempts to understand why terrestrial species differ in their response [e.g. [89,90] and the how noise affects species composition [91,92], we still need such formal comparison for aquatic species. To fill this knowledge gap is important, because the effects of noise have often been oversimplified, by suggesting that species are either sensitive and abandon an area or are not and remain [14]. However, as our review shows there is compelling evidence that the effects of noise can be quite subtle by affecting developmental and physiological processes in species quite differently (see above).

(d) Demonstrating cause and effect relationships

A major challenge in understanding how anthropogenically induced environmental changes affect organisms is establishing cause and effect relationships. Only carefully designed experiments can control for potentially confounding factors [93], which allow to draw robust conclusions about the effects of noise. Noise exposure experiments in free ranging aquatic animals are difficult to conduct, therefore, tank-based experiments have been successfully used as an alternative (e.g. [77,94,95]), and alternative approaches in semi-open settings are starting to emerge (e.g. [96,97]).

There is an ongoing debate on how efficacious tank-based experiments can be [98]: Firstly, the sound field produced in small tanks is complex and is dominated by the particle velocity element of the sound field [99]. Thus, the noise animals are exposed to in a tank-based setup may differ from real world conditions e.g. [70,77]. Secondly, loud speakers do not have a linear response and thus change the spectral quality of the sounds played, resulting in a different balance between the sound pressure and particle velocity components of sound [100]. Thus, the particle motion generated from tank-based playback experiments may not closely mimic real-world situations. However, tank-based experiments also have some major advantages. Firstly, tank-based experiments mimic common ecological circumstances faced by many species where individuals cannot avoid noise polluted areas [72]. Secondly, in some situations only experiments carried out under controlled laboratory conditions allow us to understand the underlying mechanisms that lead to an animals' response, which is the basis for successful conservation [12]. Finally, most noise exposure experiments have been short-term, and there is only very little known about long-term effects of noise. To understand the long-term effects of noise pollution the repeated or long-term exposure of the same individuals to noise is necessary. This may prove particularly difficult in the field, but could be achieved in laboratory settings. Work of this nature will highlight whether species habituate to noise over time, or become sensitised to the noise stimulus.

4. Conclusions

Anthropogenic noise is rapidly becoming omnipresent in both aquatic and terrestrial environments. We found comprehensive evidence that noise affects an individual's development, physiology, and/or behaviour. As aquatic and terrestrial habitats differ in their sound propagation properties [6], i.e. sound in water travels faster and greater distances, and attenuates less than sound in air, noise pollution in aquatic ecosystems may be more far-reaching than in terrestrial ecosystems by covering larger areas. The interplay with other environmental stressors may also intensify the problems for species inhabiting noise-polluted aquatic habitats. The patterns highlighted here illustrate how noise in aquatic ecosystems causes major changes and potentially impacts a wide range of species. Given the mixed results from studies investigating the impact of aquatic noise pollution on different species and life history stages, care must be taken when extrapolating results between species. As many invertebrates and fish are sensitive to particle motion, rather than sound pressure, it is crucial to monitor particle motion along with sound pressure. However, as this field continues to grow, and research questions become more fine-tuned, we see that the impact noise has on aquatic species involves complexities, such as hearing abilities and noise types. These complexities will affect the nature of responses, and thus should be highlighted and examined if we are to develop effective noise mitigation strategies to conserve and protect the world's aquatic wildlife more efficiently.

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Figure 1. The effects of anthropogenic noise on individuals' anatomy, physiology and behaviour. Changes in the acoustic environment through increasing noise levels can lead to immediate proximate responses, resulting in variety of emergent responses. Anthropogenic noise can have non-mutually exclusive interrelated effects on proximate and ultimate individuals responses leading to large scale ecological effects.

Figure 2. (a) Examples of hearing and signal production ranges of different taxa that can be affected by anthropogenic noise (modified and extended from [17]). We used the minimum and maximum value reported in the literature (hearing range: dark blue bars, signal production range: light blue). Note: fish have a huge diversity in hearing and production mechanisms [7]; therefore, examples were chosen to illustrate the variety of their hearing and perception. The noise ranges (shown in grey) indicate where the majority of sound sources have most of their energy [5]. Data obtained from various studies (for details see supplementary material ESM 1). (b) The effect of noise pollution across taxa. The majority of studies published found a relationship with noise. Dark grey bars indicate the number of cases that did find a significant effect and light grey bars those that did not (for details see supplementary material ESM 2).

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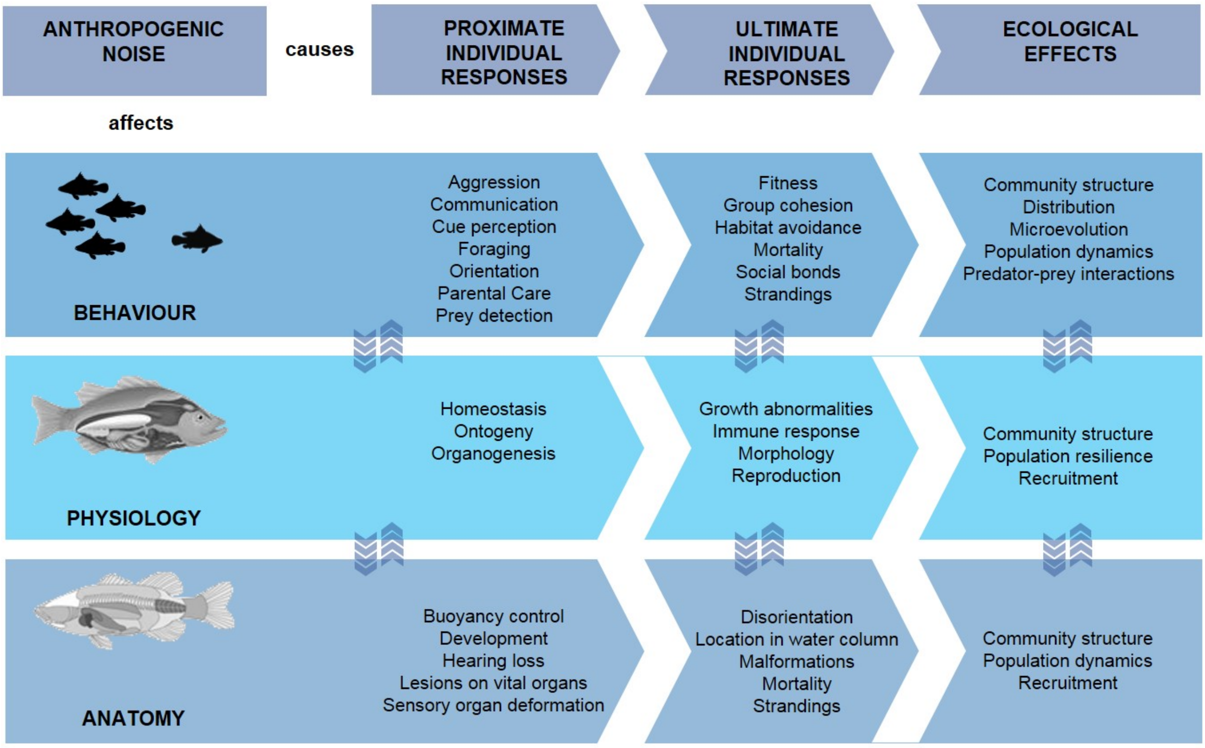
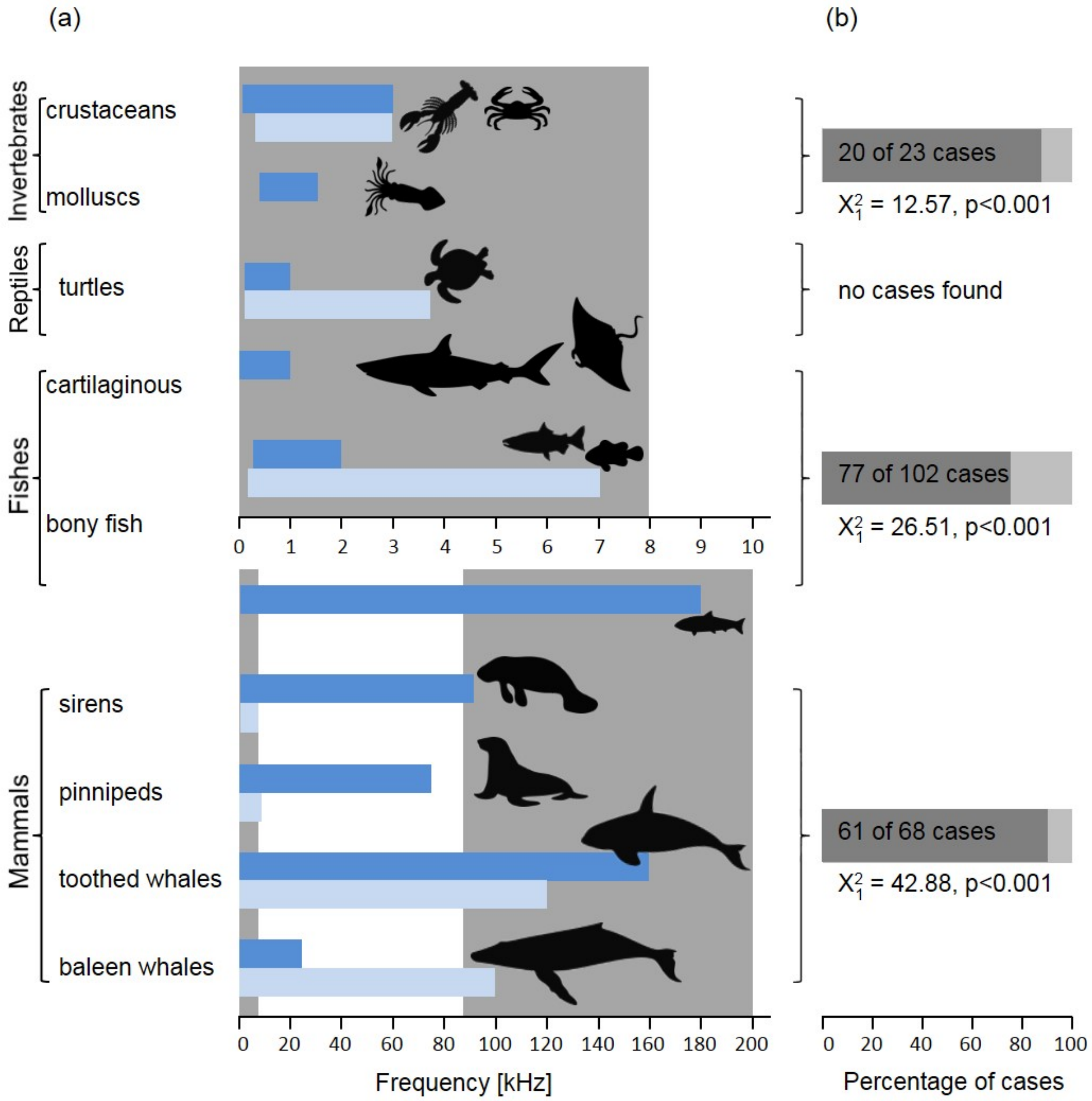

ANTHROPOGENIC NOISE
causes
PROXIMATE INDIVIDUAL RESPONSES
ULTIMATE INDIVIDUAL RESPONSES
ECOLOGICAL EFFECTS
affects
BEHAVIOUR
Aggression
Communication
Cue perception
Foraging
Orientation
Parental Care
Prey detection
Fitness
Group cohesion
Habitat avoidance
Mortality
Social bonds
Strandings
Community structure
Distribution
Microevolution
Population dynamics
Predator-prey interactions
PHYSIOLOGY
Homeostasis
Ontogeny
Organogenesis
Growth abnormalities
Immune response
Morphology
Reproduction
Community structure
Population resilience
Recruitment
ANATOMY
Buoyancy control
Development
Hearing loss
Lesions on vital organs
Sensory organ deformation
Disorientation
Location in water column
Malformations
Mortality
Strandings
Community structure
Population dynamics
Recruitment


(a)
(b)
Invertebrates
crustaceans
molluscs
Reptiles
turtles
Fishes
cartilaginous
bony fish
Mammals
sirens
pinnipeds
toothed whales
baleen whales
0 1 2 3 4 5 6 7 8 9 10
0 20 40 60 80 100 120 140 160 180 200
Frequency [kHz]
20 of 23 cases
X_1^2 = 12.57, p<0.001
no cases found
77 of 102 cases
X_1^2 = 26.51, p<0.001
61 of 68 cases
X_1^2 = 42.88, p<0.001
0 20 40 60 80 100
Percentage of cases