Zooplankton as a model to study the effects of anthropogenic sounds on aquatic ecosystems

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This article has been peer-reviewed and published in
Science of the Total Environment, 928: 172489 (2024)
https://doi.org/10.1016/j.scitotenv.2024.172489

RESEARCH ARTICLE

Open Access

Associate Editor:
Daniel A. Wunderlin

Reviewers:
Three anonymous reviewers

Cite as: Prosnier L. (2024). Zooplankton as a model to study the effects of anthropogenic sounds on aquatic ecosystems. Science of the Total Environment, 928: 172489 https://doi.org/10.1016/j.scitotenv.2024.172489

ABSTRACT

There is a growing interest in the impact of acoustic pollution on aquatic ecosystems. Currently, research has primarily focused on hearing species, particularly fishes and mammals. However, species from lower trophic levels, including many invertebrates, are less studied despite their ecological significance. Among these taxa, studies examining the effects of sound on holozooplankton are extremely rare. This literature review examines the effects of sound on both marine and freshwater zooplankton. It highlights two differences: the few used organisms and the types of sound source. Marine studies focus on the effects of very intense acute sound on copepods, while freshwater studies focus on less intense chronic sound on cladocerans. But, in both, various negative effects are reported. The effects of sound remain largely unknown, although previous studies have shown that zooplankton can detect vibrations using mechanoreceptors. The perception of their environment can be affected by sounds, potentially causing stress. Limited research suggests that sound may affect the physiology, behaviour, and fitness of zooplankton. Following this review, I highlight the potential to use methods from ecology, ecotoxicology, and parasitology to study the effects of sound at the individual level, including changes in physiology, development, survival, and behaviour. Responses to sound, which could alter species interactions and population dynamics, are expected to have larger-scale implications with bottom-up effects, such as changes in food web dynamics and ecosystem functioning. To improve the study of the effect of sound, to better use zooplankton as biological models and as bioindicators, researchers need to better understand how they perceive their acoustic environment. Consequently, an important challenge is the measurement of particle motion to establish useable dose-response relationships and particle motion soundscapes.

Keyword: Holozooplankton, Acoustic pollution, Aquatic ecosystems, Individual, Community, Particle motion soundscape.

Introduction

Anthropogenic underwater sounds are a well-established pollutant for marine ecosystems (Hildebrand, 2009), leading to international policies aimed at reducing their impact (Colbert, 2020). Human activities, such as seismic surveys, shipping, and operational wind farms, affect soundscapes by increasing ambient background levels over minutes to years and over meters to thousands of kilometres (Duarte et al., 2021). These sounds are considered to be part of the soundscape, along with other biotic (biophony) and abiotic (geophony) sounds. They are commonly known as noise (Hildebrand, 2009; Francis & Barber, 2013; Hawkins & Popper, 2017; Slabbekoorn, 2019; Duarte et al., 2021; Solé, Kaifu, et al., 2023), defined as 'the aggregate of sounds occurring in a particular place or at a particular time' or 'a sound of any kind' (Oxford English Dictionary). This noise now constitutes the majority of ambient noise (Wenz, 1962; Frisk, 2012; Duarte et al., 2021) with maximal intensity in low frequencies (Wenz, 1962; Wysocki et al., 2007; Hildebrand, 2009; Vračar & Mijić, 2011; Sertlek et al., 2019). For instance, anthropogenic activities in the Northeast Pacific have led to a 40 dB increase in ambient low-frequency noise (Frisk, 2012). This increase in noise has been found to have a significant impact on aquatic organisms, both directly by inducing stress and indirectly by altering communication and detection of clues (Radford et al., 2014; Williams et al., 2015; Erbe et al., 2016; Lecchini et al., 2018; Solé, Kaifu, et al., 2023). Noise is a highly diverse phenomenon, varying in intensity, structural spectrum, and temporal pattern due to various sources, such as airguns and shipping. Noise can be punctual, repeated (regular or random), and continuous (with or without variability). These temporal characteristics make sounds more or less predictable (Francis & Barber, 2013), as suggested by the ability of fish to habituate to chronic noise exposure (Nichols et al., 2015; Rojas et al., 2021). Additionally, noise exposure can be influenced by the behaviour of organisms, such as their ability to escape from noise sources or their natural movement (e.g., diel variation). Sound perception is a vital ability for communication, foraging, reproduction, orientation, and avoiding threatening situations (Montgomery et al., 2006; Erbe et al., 2016; Roca, 2018; Lecchini et al., 2018), explaining why hearing ability are optimised for a naturally-noisy environment (Amoser & Ladich, 2005; Wysocki et al., 2007). More, marine mammals (Erbe et al., 2016), fishes (Radford et al., 2014), crustaceans (Popper et al., 2001), and insects (Aiken, 1985) also produce sounds to communicate or as a by-product of certain activities, such as crustacean displacement (Giguère & Dill, 1979), bivalve valve movements (Di Iorio et al., 2012), or foraging (Hyacinthe et al., 2019). These sounds act as a cue for prey (Plachta & Popper, 2003), predators (Giguère & Dill, 1979; Holt & Johnston, 2011), competitors, and conspecifics (Putland et al., 2016).

Extensive research has been conducted on the effects of noise on marine fish and mammals, as they possess hearing organs and are sensitive to sound pressure levels (Erbe et al., 2016; Weilgart, 2018; Cox et al., 2018; de Jong et al., 2020). However, there are very few studies on the response of aquatic invertebrates to noise (Sordello et al., 2020) even they can perceived sound and are considered to be non-hearing organisms (lack identified auditory organs), despite their biodiversity (Wale et al., 2021; Vereide & Kühn, 2023; Solé, Kaifu, et al., 2023). It is worth noting that there is a limited number of studies on terrestrial invertebrates' response to noise, as reviewed by Raboin & Elias (2019). Here, I focus on holozooplanktonic species, which are zooplanktonic throughout their entire life cycle. These species play a crucial role in transferring energy between primary resources and higher trophic levels, as noted by numerous studies (Porter, 1973; Stoecker & Capuzzo, 1990; Frederiksen et al., 2006; Heneghan et al., 2016; Ratnarajah et al., 2023). Any effects on zooplankton could have significant repercussions on ecosystem functioning, including the carbon cycle, as highlighted by the Marine Zooplankton Colloquium (2001), Richardson (2008), and Steinberg & Landry (2017). For example, Rohr et al. (2023) analysed models showing that a 5% change in grazing rate can affect export and secondary productivity by more than 1 $PgC.yr^{-1}$ (i.e., more than 1 billion tons of carbon). Therefore, it is essential to understand the responses of zooplanktonic species to noise to prevent human impacts (Pinel-Alloul et al., 2021; Declerck & de Senerpont Domis, 2023; De Meester et al., 2023).

Research conducted in the 1990s revealed that small crustaceans, which make up zooplankton, are able to respond to environmental vibrations. Yen et al. (1992) and Gassie et al. (1993) demonstrated that calanoid copepods use mechanoreceptors in their first antennae to detect environmental vibrations. Consequently, the main sound feature important for invertebrates is particle motion rather than pressure level (Nedelec et al., 2016; Rogers et al., 2021; Solé, Kaifu, et al., 2023). Studies have shown that noise can have a negative effect on the response of crustaceans, molluscs, and cnidarian species. For example, it can impair larvae development, affect oxygen consumption and predatory behaviour in adults (André et al., 2011; Edmonds et al., 2016; Solé et al., 2016). These effects are caused by damages to sensory hair cells of statocysts. Buskey et al. (2002) showed that copepods (*Acartia* spp.) exhibit behavioural responses by increasing their speed a few milliseconds after exposure to vibration stimuli. The responses to noise vibration have raised questions about the effects of anthropogenic activities, in particular seismic airguns and boat noise, on zooplankton. Previous studies have shown that vertebrates are impacted by anthropogenic noise, resulting in effects on their survival and behaviour (McCauley et al., 2003; Fewtrell & McCauley, 2012), however Solé, Kaifu, et al. (2023) found that only two out of approximately 90 studies on marine invertebrates involved holozooplanktonic arthropods (McCauley et al., 2017; Fields et al., 2019). The majority of the other zooplanktonic organisms studied (see the marine review by Vereide & Kühn, 2023) are larvae of bivalves (Aguilar de Soto et al., 2013), cephalopods (Solé et al., 2018), crustaceans (Stenton et al., 2022), and, more rarely, other taxa such as bryozoans (Stocks et al., 2012).

This review is the first to provide an overview of how noise affects marine and freshwater holozooplankton. I searched articles referenced by Google Scholar using terms related to noise (such as noise, sound, acoustic, boat noise, airgun, anthropogenic, and pollution), organisms (including zooplankton, invertebrates, arthropods, crustaceans, molluscs, cnidarians, medusae, copepods, and daphnia), and habitat (aquatic, marine, and freshwater). I then expanded my search by adding references from the initially identified publications, as well as papers citing them, to reduce the risk of missing relevant articles. Only holozooplankton organisms were considered, excluding meroplankton such as planktonic larvae (e.g., decapods, bivalves, fishes) and planktonic adults (e.g., cnidarians). The sources used for this study included peer-reviewed articles, but also book chapters, meeting proceedings, and preprints, as there are limited peer-reviewed studies available. Sixteen articles were found that studied the effects of noise, with nine focusing on marine systems and seven on freshwater systems. This highlights the significant gap in research considering zooplanktonic species that are widely used as bioindicators (Parmar et al., 2016; Dahms et al., 2016; Ebert, 2022). To fill this gap, I propose methodologies inspired by ecology, ecotoxicology, and parasitology studies. This text offers a wide range of ideas for exploring the impact of noise on zooplankton. Thus, I highlight that zooplankton should be a good model to study the effects of anthropogenic sounds from physiological effects to community impacts, but that a major recurring problem is the measurement of sound in terms of particle motion.

Noise effects on zooplankton species: a review

Responses from marine species

Studies in marine systems have primarily demonstrated the adverse effects of acute noise (150-180 dB SEL Re 1µPa^2.s) on copepod survival. In *in situ* experiments, McCauley et al., (2017) observed increased mortality of various zooplankton crustaceans, such as small copepods, cladocerans, and krill larvae, when exposed to a seismic survey. The authors hypothesized that this mortality, observed the day after noise exposure, resulted from damage to the crustaceans' mechanoreceptors. This explanation may be limited for their mortality observed one day after noise exposure, but suggest long-term effects. However, no measurements were taken on subsequent days. Fields et al. (2019) demonstrated a less intense effect of the airgun, resulting in a small increase in copepod mortality and no impact on their behaviour. The difference in the intensity of the negative effect may be attributed to the size of the plankton species, which varied between the two studies. Until now, no mechanical explanations have been provided, but it appears that smaller zooplankton species are less affected by noise (Solé, Kaifu, et al., 2023). Vereide et al. (2023) observed increased mortality of the small copepod *A. tonsa* exposed to airguns, supporting this hypothesis. A new study clearly showed a difference of effect of a pressure drop (like airgun) on large and small copepods (Vereide et al., 2024). Additionally, non-lethal effects on copepods were reported by Tremblay et al. (2019), Fields et al. (2019) and Kühn et al. (2023). Fields et al. (2019) also reported altered expression of two unannotated genes, but the consequences for organisms are unknown. Following a 24-h exposure to acute boat noise, two copepod species were studied. The results showed that the feeding behaviour of *A. tonsa* was altered, with a reduction in their ingestion and clearance rate (Kühn et al., 2023). However, the clearance rate of the copepod *Eurytemora herdmani* was not affected (Aspirault et al., 2023). However, chronic exposure to noise only had physiological impacts on copepods (*A. tonsa*) by altering ROS (reactive oxygen species) activities, and did not affect their ingestion rate or O2 consumption (Tremblay et al., 2019). The only study on a non-crustacean taxon, a rotifer, showed a reduction in egg production, with smaller-sized eggs of *Brachionus plicatilis* (Aspirault et al., 2023).

Responses from freshwater species

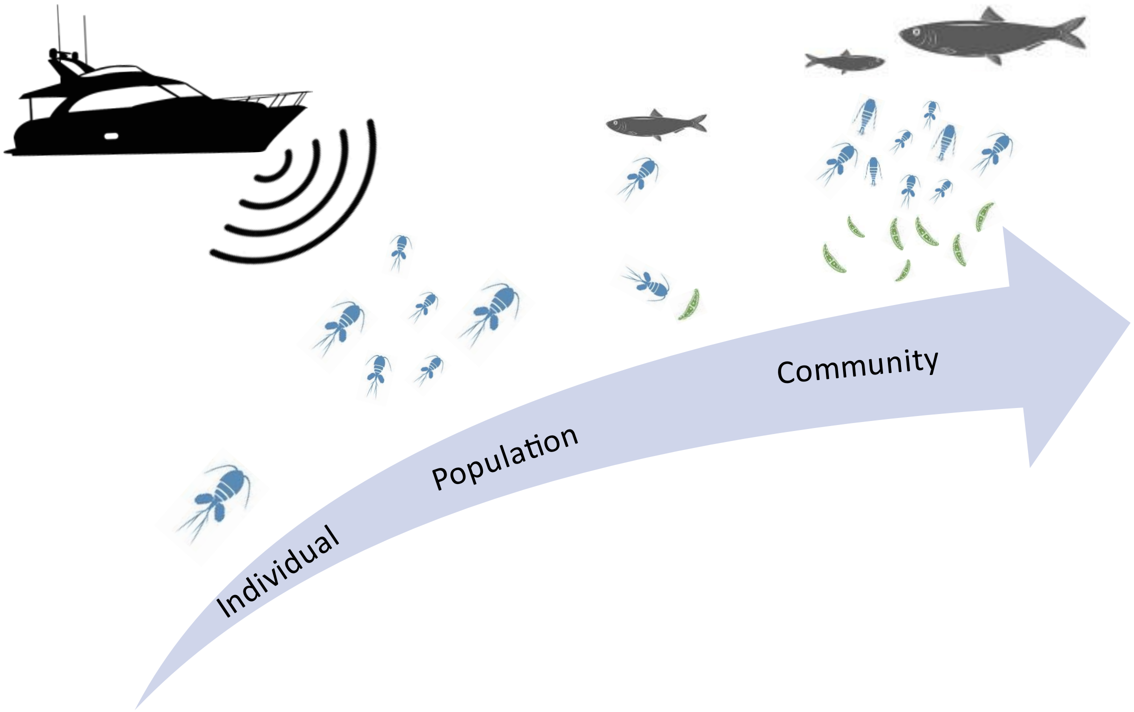
Freshwater ecosystems are threatened by shipping activities that overlap with frequencies used by aquatic animals (Mickle & Higgs, 2018). Studies have focused on the effects of chronic or acute noise (100-150 dB RMS Re 1µPa^2) on daphniid behaviour, survival, and communities. Sabet et al. (2019) investigated the short-term effects of motorboat noise on the mobility of the cladoceran (Crustacean) *Daphnia magna*. The study found no change in the swimming behaviour of *D. magna*, which is consistent with a previous study that examined the effects of regular and intermittent noise (Sabet et al., 2015). This result was also confirmed in a study with another *Daphnia* species, where the mobility of *D. pulex* was not affected by exposure to motorboat noise for the first time (Rojas, Prosnier, et al., 2023). The boat noises did not have any impact on the survival or fecundity of chronically exposed *D. magna*, as reported by Prosnier, Rojas, et al. (2023). However, chronic exposure to broadband noise resulted in a decrease in their velocity, but an increase in their survival and fecundity, according to Prosnier et al. (2022). Two studies have demonstrated the effect of boat noise on the community scale. Rojas, Desjonquères, et al. (2023) and Rojas, Gouret, et al. (2023) highlighted that noise can have a greater impact on the zooplanktonic community, specifically on the proportions of *Bosminidae* and *Daphniidae*, in the absence of fish predators compared to their presence. This suggests that noise can affect aquatic communities in ways beyond the influence of vertebrates. Therefore, motorboat noise, which is the least intense but of longer duration than airgun noise, may affect zooplanktonic arthropods but appears to have contrasting behavioural effects among species, making it difficult to generalize effects.

Noise effects on zooplankton species: conclusions

From these sixteen articles on the effects of noise on zooplankton, we can draw some conclusions about both the results and the research itself. It is evident that all studied aspects show physiological marker alterations (such as an increase in ROS activity), developmental alterations leading to reduced size, lower survival and fecundity, lower speed and ingestion rate, and an alteration of the community composition. The variation in results (alteration vs non-alteration) could be attributed to the lack of standardization in the emitted sounds (Solé, Kaifu, et al., 2023). Another important finding is that the studies mainly focused on two taxa, copepods in marine environments and daphniids in freshwater ones, raising questions about the generalisability of the results to the wider zooplankton diversity (De Meester et al., 2023). The final lesson concerns the difference in aims between marine and freshwater studies. Freshwater studies concentrate on the chronic effects of noise on fitness, behaviour, and community, while marine studies focus on the acute effects of noise on physiology, survival, and feeding. As a result, marine and freshwater studies are currently mainly complementary, and comparisons between them are limited to drawing general theories.

Future perspectives: zooplankton as a model

Recent studies have highlighted the various ways in which sounds affects zooplankton. I have identified five research areas in which zooplanktonic species could be good models, that require further exploration (Fig. 1). The first four axes focus on isolated individuals, while the fifth considers a more holistic approach. It is important to note that papers often focus on only one aspect, and therefore, methodologies may differ significantly. (1) Neurology: it is important to identify the frequencies and intensity of sound that can affect organisms. A wide variety of noises have been investigated, ranging from realistic (such as airgun and boat noises) to artificial (such as broadband noises). Standardization of research methods would allow for better comparison between studies. (2) Physiology: it is necessary to assess how noise-induced stress directly affects an individual's metabolism, including gene expression and energetic cost. (3) Fitness: This section discusses the impact of noise on the population's fitness, including survival and fecundity rates, as well as changes in development, such as effects on morphology. The effects on fitness are primarily a result of the energetic cost of stress, which can reduce survival rates. Additionally, indirect effects from other factors may also impact fitness. (4) Behaviour: Noise can damage hearing and mask environmental cues, leading to changes in perception. Physiological stress caused by noise can also affect various behaviours. Additionally, noise can impact energy requirements, which in turn can affect predation, fecundity, and physiology. This axis examines the impact of noise on behaviour, which is closely linked to the previous axes. The predator-prey relationship is also considered in this axis, as behaviour plays a crucial role in predicting vulnerability



Neurology	Physiology		Fitness		Behaviour		Community
Noise perception	Genetic expression	ROS, Composition	Development	Survival, Fecundity	Mobility	Predation Feeding	Composition, dynamic

Figure 1. Summary of the main objectives, i.e., the five axes I have distinguished, to study noise effects on zooplankton. See table 1 for the detailed literature following the lower part of this figure.

to predation and ability to prey. Finally (5) Community: the effect of noise refers to the repercussions of alterations in an individual's survival, fecundity, and behaviour. Most research on the effect of noise on zooplankton focuses on the first four axes, while the last one is the aim explained by the others to answer the crucial question. How does anthropogenic noise affect aquatic food webs? It is important to consider the different effects of acute and chronic exposure, as well as short-term and long-term effects. It is crucial to maintain a balanced and objective approach when discussing these transversal aspects. The long-term effects of chronic exposure raise questions about the ability of aquatic organisms to habituate to noise and the importance of noise predictability. To answer these questions, previous work in related fields, such as fundamental ecology, ecotoxicology, and parasitology, has provided a wealth of methodological knowledge. In the following sections, I present several methodologies to address gaps in each of these areas. It is worth noting that in many cases, only one study has been conducted (either in a freshwater or marine system, with only one species studied, and only one type of noise) (Table 1).

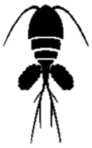
Zooplankton: overview of existing methodologies

Neurology: Noise detection

Before exploring how sounds affect organisms, it is important to understand how they detect it. Zooplankton species lack a hearing system and rely solely on external mechanoreceptors, such as those found on the first antennae of copepods (Yen et al., 1992; Gassie et al., 1993). They are not capable of detecting pressure levels (measured in µPa), but rather particle motion (measured in m/s) (Nedelec et al., 2016; Rogers et al., 2021). Therefore, it is now recognised that measuring particle motion is essential to understand zooplankton reactions to noise (André et al., 2016; Popper & Hawkins, 2018) and, consequently, to characterise various sources of noise, such as airguns and shipping. Given this information, it would be interesting to conduct electrophysiological experiments, as previously done (Gassie et al., 1993; Hartline et al., 1997). Other methods, such as behavioural methods, provide information on which sounds are detectable by organisms (Buskey et al., 2002). Currently, there is limited data available on non-zooplanktonic crustaceans. The existing research indicates that these crustaceans have a strong ability to detect low frequency noise below 3000 Hz (Duarte et al., 2021; Solé, Kaifu, et al., 2023). Lovell et al. (2005) demonstrated, using electrophysiology methods, that the common prawn (*Palaemon serratus*) has a frequency range of 100-3000 Hz. Similar studies on zooplanktonic species are necessary to determine their frequency range and ideally create a spectrogram. This will allow for comparison and prediction of the impact of anthropogenic noise, such as airguns (10-300 Hz) and boats (10-20000 Hz) (Duarte et al., 2021). The only neurophysiology study conducted on a zooplanktonic copepod detected a frequency range of 40 to 1000Hz (Yen et al., 1992). Other studies have also investigated the effects of sound frequency on copepods, with literature suggesting a noise effect for a range of 0.7-500Hz (Fields et al., 2019), 100-3 000Hz (Kühn et al., 2023), on rotifer for a noise of 100-10 000Hz (Aspirault et al., 2023), and on daphnia for a noise of 100-20 000Hz (Prosnier et al., 2022). It is important to note that these findings are based on objective evaluations and are not influenced by subjective opinions. However, some studies either show no effect or do not provide a frequency range of noise exposure.

Furthermore, the lack of behavioural or neuronal response may be attributed to damage to mechanoreceptors caused by high levels of noise. This phenomenon has been observed in two species of Mediterranean *Scyphozoan medusa* (Solé et al., 2016) and the sea louse *Lepeophtheirus salmonis*, a parasitic copepod (Solé, Lenoir, Fortuño, et al., 2021), and can be visually detected using microscopy. These methods can help determine noise thresholds in terms of intensity, frequency, and particle motion for both detection and damage. Similar to ecotoxicological methods, Tyack & Thomas (2019) proposed a dose-response method, allowing us to link the intensity of noise and its impacts, but it would be mandatory to consider intensity in term of particle motion and per frequency.

Table 1: Relevant studies on noise impacts on marine and freshwater holozooplankton species. Significant effects are in bold. The figures in the first column illustrate that there are mainly two taxa: copepods in marine studies and cladocerans in freshwater studies.

				Neurology	Physiology		Fitness		Behaviour		Community
	Study[1]	**Sound (source) (dB [2])**	**Duration**	**Noise perception**	**Genetic**	**ROS, Composition**	**Development**	**Survival, Fecundity**	**Mobility**	**Predation, Feeding**	**Composition, dynamic**
Marine 	(Gassie et al., 1993)	Acute (vibrations)	Short-term (direct)	**↗ Neuronal activity**							
	(Buskey et al., 2002)	Acute (vibrations)	Short-term (direct)						**↗ Speed Direction change**		
	(McCauley et al., 2017)	Acute (airgun) (156 SEL)	Short-term (1 day)					**↘ Survival**			
	(Fields et al., 2019)	Acute (airgun) (183-221 SEL)	Short-term (1 day) Long-term (7 days)		**Genetic expression**			**↘ Survival**	Speed Escape		
	(Tremblay et al., 2019)	Chronic (motor noise)	?			O_2 consumption **↗ ROS activity**				Ingestion rate	
	(Vereide et al., 2023)	Acute (airgun) (166-180 SEL)	Long-term (6 days)				**↘ Size** **Delayed stage**	**↘ Survival (immediate and delayed)**			
	(Kühn et al., 2023)	Chronic (boat noise) (174 SEL)	Short-term (2-4 days)							**↘ Ingestion rate** **↘ Clearance rate** Handling time	
	(Aspirault et al., 2023)	Chronic (boat noise) (129 RMS)	Short-term (1 day)				Size	**↘ Fecundity (egg production and size)**		Clearance rate	
	(Vereide et al., 2024)	Acute (airgun) (226 peak)	Short-term (5 h)					**↘ Survival**	**↘ Speed**		
Freshwater 	(Sabet et al., 2015)	Acute (regular and intermittent) (122 RMS)	Short-term (direct)						Speed Depth		
	(Sabet et al., 2019)	Acute (boat noise)	Short-term (direct)						Speed Hops Depth		
	(Prosnier et al., 2022)	Chronic (broadband noise) (128 RMS)	Long-term (+30 days)				Size	**↗ Survival** **↗ Fecundity**	**↘ Speed**		
	(Prosnier et al., 2023)	Chronic (boat noise) (103-150 RMS)	Long-term (+30 days)					Survival Fecundity			
	(Rojas, Prosnier, et al., 2023)	Acute (boat noise) (100-122 RMS)	Short-term (direct)						Speed		
	(Rojas, Gouret, et al., 2023)	Chronic (boat noise) (100-122 RMS)	Long-term (44 days)								**Sp. abundance**
	(Rojas, Desjonquères, et al., 2023)	Chronic (boat noise) (105-110 RMS)	Long-term (42 days)								**Sp. abundance**

1. Peer-reviewed articles are underlined
2. SEL: Sound-Exposure Level in dB Re $1\mu Pa^2.s$, RMS: Root-Mean-Square in dB Re $1\mu Pa^2$, peak: Zero-to-Peak in dB Re $1\mu Pa^2$

Physiology: Metabolism measurements

Physiological stress markers can be measured in zooplankton, from individual to natural community levels. Utility has been demonstrated in studies on fish, where cortisol measurements were taken in a noise context (Nichols et al., 2015; de Jong et al., 2020). Several methods have been developed in ecotoxicology for studying copepods, which have become popular biological models (Handy & Depledge, 1999; Raisuddin et al., 2007; Dahms et al., 2016). Similarly, water fleas are commonly used as biological models for freshwater systems (Bownik, 2020; Ebert, 2022). For short- and long-term experiments, it is possible to measure reactive oxygen species (ROS) that cause cellular damage, as well as the organism's composition, such as protein or carbon content, and gene expression. This provides information about the chain reaction's underlying mechanisms (Dahms et al., 2016). In their study, Lee et al. (2019) measured various ROS (reactive oxygen species) levels, including glutathione, GST, glutathione reductase (GR), glutathione peroxidase (GPx), and superoxide dismutase (SOD), to investigate the impact of ocean acidification on the copepods *Tigriopus japonicus*. The authors found that higher concentrations of stress markers were present. In their study, Won et al. (2014) measured the concentration of fatty acids in copepods (*Paracyclopina nana*) after exposure to UV radiation. Prosnier et al. (2024) measured the quantities of carbohydrates, lipids, and proteins in *D. magna* infected with an iridovirus, while Forshay et al. (2008) measured the carbon-to-nitrogen ratio in *D. pulicaria* infected with a chytridiomycete fungus. Oxygen consumption can be measured through respirometry methods, which have been used to study both copepods and daphniids (McAllen & Taylor, 2001; Zitova et al., 2009). These studies demonstrate the potential for using these methodologies in the field of zooplankton bioacoustics. However, pooling small individuals can lead to a loss of individual variability. In a noise context, Tremblay et al. (2019) found no effects on O2 consumption but observed higher levels of ROS (similar to Lee et al., 2019). Fields et al. (2019) reported a higher expression of two genes with unknown effects, indicating the need for further study to uncover any underlying effects. To assess the ability of zooplankton to habituate to noise, measuring physiological markers would be a useful tool to determine whether they return to a basal level after a certain exposure time. These physiological changes may be a direct result of noise stress, as acidification affects ROS (Lee et al., 2019), or they may be a by-product of behavioural changes, such as modifications in mobility (Prosnier et al., 2022) or feeding rate (Kühn et al., 2023), which could affect their energy budget.

Fitness: survival and reproduction measurements

Anthropogenic noise can directly affect zooplankton species through physiological stress or behavioural changes. The most visible effects, with obvious implications for zooplankton populations and communities, are those on fitness, i.e., reproductive success through effects on survival and fecundity. In contrast to studies on vertebrates, it is easier to obtain much information on the fitness of isolated individuals or populations under *in situ* (realistic) or laboratory (controlled) conditions. For zooplankton, it is easy to observe effects on survival, fecundity and development of eggs, juveniles/larvae and adults at each stage (Dahms et al., 2016). In the context of noise, McCauley et al. (2017) and Vereide et al. (2023) studied immediate and delayed mortality in marine zooplankton, while Aspirault et al. (2023) studied rotifer fecundity; Prosnier et al. (2022, 2023) studied both mortality and fecundity in the freshwater water flea *Daphnia magna*. Reduced development in copepods exposed to airgun noise is also being developed using size or stage duration (Vereide et al., 2023), which could have fitness implications over generations. Related to development, Olivier et al. (2023) developed the Larvosonic system to study the effects of noise on small aquatic organisms. In addition, the study of population dynamics, coupled with mathematical modelling, allows us to determine effects on fitness components (such as reproductive rate, generation time and growth rate...). For example, in ecotoxicology, Leung et al. (2007) studied the effects of tributyltin on the snail *Lymnaea stagnalis* using the Euler-Lotka equation (see also Starke et al., 2021; Prosnier et al., 2023).

McCauley et al. (2008) coupled a structured model and controlled experiments to characterise the dynamics of a *Daphnia*-algae system.

Behaviour: individual and predation measurements

Behaviour is certainly one of the most studied aspects of the effects of anthropogenic noise, as noise should affect communication and perception of the environment (Tidau & Briffa, 2016). Zooplankton responses to noise have mainly been studied in freshwater during fish predation experiments to test whether noise alters their behaviour (anti-predator defence, swimming distance, detectability) and thus their vulnerability (Sabet et al., 2015; Rojas et al., 2021; Rojas, Gouret, et al., 2023, see also Fernandez-Declerck et al., 2023 for a small zoobenthic prey). Nevertheless, many other behavioural measurements have been carried out to test if and how a contaminant might affect a zooplanktonic organism. Bownik (2017) suggested measuring swimming speed (see also, in noise experiments, Sabet et al., 2019; Prosnier et al., 2022; Rojas, Prosnier, et al., 2023), swimming time, hopping frequency (used for water fleas but also applicable to copepods, (Elmi et al., 2021)), vertical distribution (important for diel migration, tested myself for noise-exposed *D. magna*, unpublished data), swimming trajectory and sinking rate. Changes in mobility could affect noise exposure, either because diel migration leads to diel exposure, or because mobility could be interpreted as the ability to escape pollutants (Michalec et al., 2013). Note that some morphological and behavioural differences between sexes need to be considered (Holm et al., 2018), and therefore males and females could respond differently to anthropogenic noise. In the case of population studies, it is also possible to measure their spatial distribution and individual spacing, i.e., swarming behaviour (Buskey et al., 1996). These behavioural measurements can also be performed in the context of multiple stimuli, where, for example, noise could affect the response to other stimuli such as olfactory stimuli, known as cross-sensory interference (Halfwerk & Slabbekoorn, 2015) - but none of these effects have been reported for crabs (Hubert et al., 2021; Solé, De Vreese, et al., 2023).

In relation to the vulnerability to predation, a recent study shows that marine copepods produce sounds that are likely to be audible to their predators (Kühn et al., 2022). This sound production has previously been described for freshwater copepods and daphnids in response to predation by Chaoborus larvae (Giguère & Dill, 1979). These sounds may be a by-product of their mobility, probably during escape behaviour. In the context of anthropogenic noise, this raises the question of whether ambient noise is able to mask these sounds, which could be a cue to predators or conspecifics. And, if the sound is not simply a by-product, are organisms able to modify their sound emission in response to environmental noise? Both effects (masking and modulation) are known in marine mammals and fish (Putland et al., 2018) – leading to higher or lower detection by their predator.

Noise should affect predator-prey relationships. Behavioural changes should affect the encounter rate of prey and predators and thus their predation rate or vulnerability to predation (Gerritsen & Strickler, 1977). Noise may also affect the perception of prey and predator (masking effect) and physiology (energy requirements). It is therefore interesting to study the effects of noise on predation by considering a system where zooplankton are either prey or predators. For example, Sabet et al. (2015) and Rojas, Prosnier, et al. (2023) studied the behaviour of *D. magna* because they were fish prey. In parasitism experiments, Prosnier et al. (2024) studied how *Daphnia* infection affected the attack rate and handling time of its predator. As consumers, zooplankton can be herbivores or filter-feeders, such as cladocerans or small copepods, or active predators, such as larger species. Regarding filter feeders, Hong et al. (2012) measured the beating of feeding appendages of *A. tonsa* in an ecotoxicological study. The classic functional response experiments (Holling, 1959a; b) used in the fish experiments cited above could be used for both filter feeders (Porter et al., 1982) and active predators (Krylov, 1988), as was done for larvae of the damselfly *Ischnura elegans* exposed to boat noise, showing an increase in handling time (Villalobos-Jiménez et al., 2017). Note that these behavioural measures are useful to explain results when the species studied is a prey or a predator.

In the context of noise, Tremblay et al. (2019), Kühn et al. (2023), and Aspirault et al. (2023) studied the ingestion rate of copepods. In terms of predation-related behaviour, the body rotation of *Chaoborus* larvae has been studied to explain their susceptibility to predation by fish (Rojas et al., 2021; Rojas, Prosnier, et al., 2023) or their predation rate on cladocerans (Rojas, Desjonquères, et al., 2023).

From individual to community

Experimental approaches

Alteration of key processes such as metabolism, reproduction, survival and predator-prey interactions through behavioural changes will directly affect the population dynamics of species and therefore the community. However, current research has mainly focused on individual responses, which is not sufficient and there is a need to assess complex communities for a global response (Kunc et al., 2016). Recent results suggest that if noise alters developmental rate, survival and/or fecundity, it may also alter competitiveness, as demonstrated by Decaestecker et al. (2015) in the case of water flea infection by a pool of parasites. Therefore, it can be assumed that effects on zooplankton can induce top-down effects through cascading effects and bottom-up effects (Sommer et al., 2001; Banerji et al., 2015; Wollrab & Diehl, 2015). Mesocosm studies have highlighted how changes in biological (community response) and spatial (from microcosm to mesocosm) scales affect dynamics. They have shown that responses are more complex than expected as community complexity increases (Gérard Lacroix, pers. comm. with freshwater experiments). In marine systems, the assessment of other stressors such as acidification has highlighted the utility of plankton community studies coupled with biochemical measurements (Spisla et al., 2021). To study communities, it is possible to study community dynamics, stability and composition. Physiological measurements, such as stable isotopes, are good tools to assess long-term effects on communities (Boisnoir et al., 2020), targeting dietary shifts over time. As a reminder in the noise context, see the community studies by Rojas, Gouret, et al. (2023), with vertebrates, and Rojas, Desjonquères, et al. (2023), without vertebrates. These complex community studies provided indirect effects on organisms that may be less affected by noise, such as phytoplankton (no observed effect on the density of the microalgae *Diacronema lutherie* and *Tetraselmis suecica* after 24 h exposure to boat noise (Aspirault et al., 2023)), i.e., a by-product of changes in herbivory – but one study showed that the seagrass *Posidonia oceanica*, an aquatic plant, could be affected by noise (Solé, Lenoir, Durfort, et al., 2021), suggesting a possible direct effect on phytoplankton.

Theoretical approaches

To date, only experimental approaches have been used to understand how noise affects organisms and communities, despite its recognised importance in understanding observed ecological dynamics (McCauley et al., 2008). An exception is the work of Roca (2018), who modelled predator-prey relationships as a function of ambient noise intensity. Models are useful tools for studying the effects of pollutants (Lamonica et al., 2023), from simple systems (e.g., predator-prey interactions, see Prosnier et al. (2015)) to complex food webs (Clements & Rohr, 2009). Theoretical studies provide a better understanding of the mechanisms by which noise affects community structure and stability (Wollrab & Diehl, 2015). For instance, Hulot et al. (2000) used models to understand the importance of bottom-up and top-down effects in freshwater mesocosms. Similarly, in an infected tri-trophic system, Banerji et al. (2015) used a model to show that trophic changes were driven by host mortality rather than changes in predator behaviour. In addition, a combination of noise propagation models (Barber et al., 2011; Lin et al., 2019; Guibard et al., 2022) and food web models may be useful for developing spatially structured models. These models will allow us to understand the role of zooplankton mobility (diel migration, noise escape, natural flow) in temporally and spatially structured noise pollution.

Enlarging view

I have suggested different measurements of noise effects on zooplankton at different levels (Table 2). However, we must bear in mind that all these levels are interrelated. For example, the effect on mobility should directly affect their survival or fecundity through a change in energy allocation. Prosnier et al. (2022) explained their surprising increase in fitness by the reduced mobility of *D. magna* exposed to noise. The reduced consumption of *A. tonsa* (Kühn et al., 2023) raises the question of its effect on fitness. Prey mobility is generally studied to explain differences in foraging behaviour of predators (Sabet et al., 2015; Rojas et al., 2021; Fernandez-Declerck et al., 2023); therefore, in a community context, noise should indirectly affect the fitness of zooplanktonic organisms. It is also possible to link behaviour and physiology, e.g., activity, predation and O_2 consumption of fish and bivalves (Fernandez Declerck, unpublished data; Turco et al., 2023). Another interesting point is the deleterious effects on mechanoreceptors (Solé et al., 2016). This permanent damage should have long-term effects on their behaviour, their ability to detect prey or predators, and thus on their fitness. These different and generally independent studies presented in the review not only focus on numerous interesting effects of noise, but also highlight mechanisms that could explain how and why noise affects or could affect all these levels.

It is important to note that this paper focuses on holozooplanktonic species (primarily arthropods), although many other groups are part of the zooplankton (the meroplanktonic species) for part of their life cycle. These organisms can be affected by noise – see reviews by Vereide & Kühn (2023) and Solé, Kaifu, et al. (2023) – when they are zooplanktonic in the larval stages (Simpson et al., 2011; Aguilar de Soto et al., 2013; Nedelec et al., 2015) or, more rarely, during their adult stage (cnidarian, Solé et al., 2016). Moreover, they could be affected during their other stages when they are nekton (fish, Nichols et al., 2015), benthic (crabs, Wale et al., 2013), fixed (mussels, Hubert et al., 2022) or parasitic (parasitic copepods, Solé, Lenoir, Fortuño, et al., 2021). Therefore, due to the diversity of zooplankton communities and their ecological roles, the methods presented must be developed for all these organisms (note that the Larvosonic system was initially developed for zooplanktonic larvae of a bivalve (Olivier et al., 2023)). This broader perspective is essential for understanding the impact of anthropogenic noise on aquatic communities, taking into account a diversity of effects (Kunc et al., 2016; De Meester et al., 2023).

Table 2: Summary of methodologies usable to study the effects of noise on zooplankton.

Research axes	Objectives	Measurements/Technics	Example of references
Neurology	Characterization of noise detection (frequency, levels), drawing spectrogram	Electrophysiology (neuronal activities)	(Yen et al., 1992; Gassie et al., 1993; Lovell et al., 2005)
		Behavioural reaction to mechanic stimulations	(Buskey et al., 2002)
		Dose-response	(Tyack & Thomas, 2019)
	Physical damages (e.g., receptor degradations)	Microscopic observation	(Solé et al., 2016; Solé, Lenoir, Fortuño, et al., 2021)
Physiology	Link to genetic	Genetic expression	(Fields et al., 2019)
	Acute and chronic stress characterization	Stress marker (ROS, Cortisol)	(Nichols et al., 2015; Dahms et al., 2016; Lee et al., 2019)
		Energetical content (Lipids, Carbohydrates, Proteins)	(Won et al., 2014; Prosnier et al., 2024)
		C/N ratio	(Forshay et al., 2008)
		Respirometry	(McAllen & Taylor, 2001; Zitova et al., 2009; Tremblay et al., 2019)

Fitness	Mortality	Field	(McCauley et al., 2017; Fields et al., 2019; Vereide et al., 2023)
		Lab	(Prosnier et al., 2022, 2023; Aspirault et al., 2023)
	Fecundity	Lab	(Prosnier et al., 2022, 2023)
	Development	Field	(Vereide et al., 2023)
		Lab	(Olivier et al., 2023)
	All	Population (coupling experimental and modelling approaches)	(Leung et al., 2007; McCauley et al., 2008; Starke et al., 2021; Prosnier et al., 2023)
Behaviour	Individual behaviour	Various individual measurements (speed, hopping, orientation, vertical distribution)	(Bownik, 2017; Sabet et al., 2019; Elmi et al., 2021; Prosnier et al., 2022)
		Sex differences	(Holm et al., 2018)
		Cross-sensory interference	(Halfwerk & Slabbekoorn, 2015; Hubert et al., 2021; Solé, De Vreese, et al., 2023)
	Populational behaviour	Swarming	(Buskey et al., 1996)
	Sound production	Lab and field	(Giguère & Dill, 1979; Kühn et al., 2022)
	Predator-prey interaction	Vulnerability to predation (Functional response, handling time, attack rate)	(Sabet et al., 2015; Rojas, Desjonquères, et al., 2023; Rojas, Prosnier, et al., 2023; Prosnier et al., 2024)
		Predation by zooplankton (functional response, ingestion rate, clearance rate)	(Krylov, 1988; Hong et al., 2012; Villalobos-Jiménez et al., 2017; Tremblay et al., 2019; Kühn et al., 2023; Aspirault et al., 2023)
Community	Competition	Competitor abundances in mesocosms	(Decaestecker et al., 2015)
	Trophic cascade, Top-down and bottom-up effects	Multi-trophic network and food-chain experiments (species abundance)	(Sommer et al., 2001; Banerji et al., 2015; Wollrab & Diehl, 2015; Rojas, Desjonquères, et al., 2023; Rojas, Gouret, et al., 2023)
	Community dynamics	Species abundance and biochemical measurements	(Spisla et al., 2021; Rojas, Desjonquères, et al., 2023; Rojas, Gouret, et al., 2023)
		Stable isotopes	(Boisnoir et al., 2020)
		Mathematical models	(Hulot et al., 2000; McCauley et al., 2008; Clements & Rohr, 2009; Prosnier et al., 2015; Lamonica et al., 2023)

Challenges: the particle motion soundscape

As external mechanoreceptors are responsible for sound detection (Yen et al., 1992; Gassie et al., 1993), the crucial sound characteristic is particle motion (measured as particle displacement, speed, or acceleration) rather than sound pressure level, which was measured in all experiments (Table 1) (Nedelec et al., 2016; Popper & Hawkins, 2018). Considering this perceptible sound, the zooplankton's point of hear or its *Umwelt*, is mandatory to understand and to predict how sound is used by them or affects them.

The challenge with particle motion is how to determine it, and to compare with realistic environments. Two possibilities, either to measure it with an accelerometer (less available than the usual hydrophones), either to calculate it. In fact, it is possible to calculate the particle motion from the pressure level in a large environment (without boundary) and far from the sound source (Nedelec et al., 2016; Dahl & Bonnel, 2022; Dahl & Dall'Osto, 2022; Flamant & Bonnel, 2023). For *in situ* experiments or in large mesocosms (e.g., community experiments), it should be possible to know the intensity of particle motion – for both zooplankton and fish experiments – with accelerometer or calculation. However, researches on isolated small organisms often involves working in microcosms (e.g., 100 or 200 mL), which is advantageous in many respects, but difficult in terms of sound. In general, researchers use an acoustic bain-marie, such as the Larvosonic system (Olivier et al., 2023), which could also be used for small pelagic species like zooplankton, or in Prosnier et al. (2022) or Kühn et al. (2023). Here, the space available to use an accelerometer is reduced and it can affect itself particle motion, there are close boundaries, in various material as glass and plastic, and the acoustic source is close to the organisms. To address this, it is necessary to develop methods for measuring particle motion in small environments. To date, previous studies have been uncertain about the representativeness and comparability of the soundscape in terms of particle motion, despite confidence in the sound frequencies and pressure levels. However, measuring pressure levels could be a good proxy for determining differences in intensity levels, i.e., relative intensity of sound (Jones et al., 2022; Olivier et al., 2023). Consequently, it is mandatory to develop methodologies for determining the particle motion soundscape (PMS), rather than just the pressure level soundscape (PLS). For instance, Jones et al. (2022) measured the PMS in coral reef to conclude that the ambient noise seems in general not detectable by fishes and invertebrates above 100 Hz. It is especially true in microcosms to know if, despite close sound source and boundaries, there are realistic soundscapes, and if not, if it is possible to correct it. Using flexible microcosms, as bags, in large bain-marie, like the sea, as demonstrated in Fields et al. (2019) and Vereide et al. (2023), may enhance the zooplanktonic soundscape.

Therefore, future studies should confirm the detection of environmental sound by zooplanktonic species (Jones et al., 2022). We need to establish a dose-detection particle motion relationship in order to obtain a dose-response relationship (Tyack & Thomas, 2019). It needs also to define what is a dose, because there are various sound measurements, such as total intensities and intensity per frequencies, both in dB RMS for chronic exposure and dB SEL for acute exposure (Madsen, 2005; Popper & Hastings, 2009; Slabbekoorn et al., 2010; van Geel et al., 2022), in pressure level and in particle motion. At least, it should be mandatory to determine threshold values, linking sound intensity and biological parameters measured in various way (Table 2) as previously suggested by (Hawkins et al., 2020)

Conclusion

In this article, I started to review the effects of anthropogenic sound on holozooplankton in both marine and freshwater systems. Despite their ecological importance and the evidence that they can detect environmental sound, they have rarely been considered in sound studies. Nevertheless, a diversity of negative effects has been demonstrated for both acute and chronic noise exposure. Common complementary methodologies are proposed to study the effects of noise on neurology, physiology, fitness, behaviour, and community. The review demonstrated the suitability of zooplankton as a biological model for investigating the effects of sound on aquatic organisms. Additionally, using zooplankton as bioindicators will be improved, both for in lab test and for *in situ* observations. Two models have already been used: copepods in marine studies and cladocerans in freshwater studies, however, other groups should not be forgotten. Additionally, including zooplankton in sound studies is essential for understanding the impact of anthropogenic sound on aquatic ecosystems. However, researchers need to address three challenges. (1) determine the dose-detection relationship, e.g., establishing an audiogram. (2) improve the soundscape by limiting boundary effects. (3) draw the detectable aquatic soundscape: the particle motion soundscape. This knowledge will enable us to determine which sounds (in terms of intensity, frequency, and temporality) can impact zooplankton, their interactions, and evolution, thereby influencing the entire aquatic community through bottom-up effects.

Conflict of Interest

The authors declare that the research was conducted in the absence of any commercial or financial relationship that could be construed as a potential conflict of interest.

Author contributions

LP conceived and wrote this article and approved the submitted version.

Acknowledgement

The author would like to thank his binôme Emilie Rojas :), for the numerous useful discussions and complete peer-reviews, and also Théophile Turco; Marta Solé, for the opportunity to write the first draft, Vincent Médoc, Joël Attia, Marilyn Beauchaud, Wenjing Wang, the ENES team, and the meeting “Effects of noise on aquatic life” 2022 in Berlin for many interesting discussions and feedbacks. The author also thanks the four anonymous reviewers for their useful comments. The author has been hosted throughout the writing process by the ENES Bioacoustics Research Laboratory (CRNL, CNRS, Inserm, University of Saint-Etienne, 42100, Saint-Etienne, France).

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