How could noise affect aquatic ecosystems? A lack of zooplankton studies.

Loïc Prosnier

- ENES Bioacoustics Research Laboratory, CRNL, University of Saint Etienne, CNRS, Inserm, Saint-Etienne, France
- France Travail, Saint-Etienne, France

* Corresponding author. Loïc Prosnier, ENES, Université Jean Monnet - St-Etienne, Campus Métare, Bâtiment K. 21, rue du Dr Paul Michelon 42100 Saint-Etienne, FRANCE. lprosnier@gmail.com

ORCID: 0000-0001-5576-3601

One-sentence summaries: Various effects of noise on zooplankton have been described during the past decade, and many methodologies could be used to fill gaps.

Number of words: 6200

Number of figures: 1

Number of tables: 2

Abstract

There is a growing interest in the effects of noise pollution on aquatic ecosystems. To date, these studies have mainly focused on hearing species, especially fish and mammals. Species from lower trophic levels, including many invertebrate species, are less studied despite their ecological importance. Within these taxa, studies investigating the effects of noise on holozooplankton are very rare. For the first time, I reviewed this literature about noise effects on both marine and freshwater zooplankton and showed that the effects of noise are largely unknown. Previous works demonstrate that they could detect vibrations using mechanoreceptors: noise is susceptible to affect the perception of their environment and to cause stress. The few studies suggest effects on physiology, behaviour, and fitness. After this review, and based on methods from ecology, ecotoxicology, and parasitology, I showed how they can be more used to study noise effects at individual scales, such as modifications of physiology, development, survival, and behaviour. Responses to noise, which could change species interactions and population dynamics, are expected to lead to larger-scale implications (i.e., alterations of food web dynamics and ecosystem functioning). We might expect further development of acoustic studies on zooplankton to better understand how anthropogenic noise affects aquatic environments.

Keywords: Zooplankton, Anthropogenic noise, Aquatic ecosystems, Physiology, Fitness, Behaviour Community

1. Introduction

Anthropogenic underwater noise is an established pollutant for marine ecosystems (Hildebrand, 2009) leading to international policies to reduce impacts (Colbert, 2020). Human activities, such as seismic surveys, shipping, or operational wind farms, affect soundscapes by increasing ambient noise levels in space and time over minutes to years and meters to thousands of kilometres (Duarte et al., 2021). Noises are extremely diverse in their intensity, structural spectrum and temporal pattern due to various sources, such as airgun and shipping; noise exposure could also be affected by the behaviour of organisms, such as their ability to escape to noise sources or their natural movement (e.g., diel variation). Noise could be punctual, repeated (regularly or randomly), and continuous (with or without variability). These characteristics lead them to be more or less predictable (Francis & Barber, 2013), affecting differently organisms, as shown in the ability of fish to habituate to chronic noise exposure (Nichols et al., 2015; Rojas et al., 2021). Sound perception is a crucial ability for communication, foraging or avoiding threatening situations. There is now an extensive body of research on the effects of noise on marine fish and mammals (see reviews of Erbe et al., 2016; Weilgart, 2018; Cox et al., 2018; de Jong et al., 2020), as they are known to have hearing organs and thus to be sensitive to sound pressure levels. However, there is a very limited number of studies on aquatic invertebrate responses to noise (see Raboin & Elias (2019) for a review about terrestrial invertebrates), because they are non-hearing organisms (i.e., without identified auditory organs), despite their biodiversity (Wale et al., 2021; Vereide & Kühn, 2023; Solé, Kaifu, et al., 2023). It includes holozooplanktonic species (i.e., zooplanktonic along their entire life cycle), which represent a crucial link for the transfer of energy between primary resources and higher trophic levels (Heneghan et al., 2016; Ratnarajah et al., 2023). Effects on zooplankton could have large repercussions on ecosystem functioning, such as the carbon cycle (Marine Zooplankton Colloquium, 2001; Richardson, 2008; Steinberg & Landry, 2017). For instance, models analysed by Rohr et al. (2023) showed that 5% of the variation of their grazing rate affects export and secondary productivity by more than 1 PgC.yr^{-1} (i.e., more than 1 billion tons of carbon). Understanding the responses of zooplanktonic species to noise is thus mandatory to prevent human impacts.

In both marine and freshwater environments, there are various sounds (natural and anthropogenic, biotic and abiotic) that could be detected by organisms (Duarte et al., 2021). Abiotic sounds, due to turbulence river, wind, wave, and reef, induce a basal ambient noise in a low-frequency range (Wenz, 1962; Wysocki et al., 2007; Hildebrand, 2009; Vračar & Mijić, 2011; Sertlek et al., 2019). Organisms are adapted to this natural noise (Amoser & Ladich, 2005; Wysocki et al., 2007), in their ability to detect noise, and to communicate despite this noise. Moreover, these noises can be clues for organisms. For instance, fish and coral larvae use reef noise to orient them toward coral reefs (Montgomery et al., 2006; Lecchini et al., 2018). Natural ambient noise is also constituted by biological noise. Sounds could be produced to communicate by marine mammals (Erbe et al., 2016), fishes (Radford et al., 2014) and invertebrates as crustaceans (Popper et al., 2001) and insects (Aiken, 1985), or be a by-product, e.g., during displacement of crustaceans (Giguère & Dill, 1979), valve movements of bivalves (Di Iorio et al., 2012) or foraging activities (Hyacinthe et al., 2019). These sounds act as a clue for prey (Plachta & Popper, 2003), predators (Giguère & Dill, 1979; Holt & Johnston, 2011), competitors and conspecifics (Putland et al., 2016). It is now recognised that all these biotic and abiotic sounds are used by the diversity of aquatic organisms (marine mammals, fishes, molluscs, and crustaceans). Nevertheless, due to anthropogenic activities, such as boats, airguns, sonars, pile-driving, and windfarms, ambient noise is increased with a large overlap with natural noise, in the low frequency range and constitute now the large part of ambient noise (Wenz, 1962; Frisk, 2012; Duarte et al., 2021). For instance, the ambient noise of low frequencies is increased by 40 dB due to anthropogenic activities in the Northeast Pacific (Frisk, 2012). Consequently, it is now well-known that these new noises affect aquatic organisms, directly, by inducing stress, or indirectly, by altering communication and clue detection (Radford et al., 2014; Williams et al., 2015; Erbe et al., 2016; Lecchini et al., 2018; Solé, Kaifu, et al., 2023).

Despite the absence of an earing system, invertebrates can be affected by noise. They can detect sound with their external mechanoreceptors (Solé, Kaifu, et al., 2023). Thus, according to their sensory system, the main sound characteristic for invertebrates is the particle motion instead of the pressure level (Nedelec et al., 2016; Rogers et al., 2021). Studies have shown the reactions of crustaceans, as oxygen consumption and predatory behaviour of adults, and impair larvae development (Edmonds et al., 2016), molluscs (André et al., 2011) and cnidarian species (Solé et al., 2016), through damages to sensory hair cells of statocysts, to noise and are summarized in the recent review of Solé, Kaifu, et al. (2023). An important functional group seems completely understudied: in Solé, Kaifu, et al. (2023), only two out of approximately 90 studies on marine invertebrates concern holozooplanktonic arthropods (McCauley et al., 2017; Fields et al., 2019), lacking a non-peer-reviewed article before (Tremblay et al., 2019), and three others have been published since (Kühn et al., 2023; Vereide et al., 2023; Aspirault et al., 2023). The other zooplanktonic organisms studied (see the marine review by Vereide & Kühn, 2023) are in majority 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), where various effects have been noted as lower survival, impaired development and metamorphosis, and faster settlement. Investigation made in the 1990s demonstrated that small crustaceans, constitutive of zooplankton, were able to react to environmental vibration. Yen et al. (1992) and Gassie et al. (1993) showed that calanoid copepods use mechanoreceptors of their first antennae to detect environmental vibrations. They were followed by Buskey et al. (2002), who demonstrated the behavioural responses of copepods (*Acartia* spp.) to increase their speed a few milliseconds after vibration stimuli. These responses to vibration have raised questions about the effects of anthropogenic activities producing noise (e.g., seismic airguns, boat noise) on zooplankton (Utne-Palm et al., 2022), knowing the impacts found in vertebrates (McCauley et al., 2003; Fewtrell & McCauley, 2012), i.e., mainly effects on survival and behaviour.

In this review, I overview how zooplankton responses to noise could be described. First, I reviewed, for the first time, the literature linking noise and marine and freshwater holozooplankton. For this review, I searched articles referenced by Google Scholar with terms for noise (noise, sound, acoustic, boat noise, airgun, anthropogenic, and pollution), organisms (zooplankton, invertebrates, arthropods, crustacean, mollusc, cnidarian, medusa, copepods, daphnia) and habitat (aquatic, marine, freshwater). From this pool of articles, I added references within these initially identified publications, and papers citing them to limit the risk of missing some articles. I considered only organisms that are zooplanktonic throughout their life (i.e., holozooplankton), excluding meroplankton as planktonic larvae (e.g., decapods, bivalves, fishes) and planktonic adults (e.g., cnidarians). I considered peer-reviewed articles as well as book chapters, meeting proceedings and preprints. I found only thirteen articles studying the effects of noise, six in marine and seven in freshwater systems, highlighting how large the gap is. Following this review, and because zooplankton are widely used as bioindicators (Parmar et al., 2016; Dahms et al., 2016; Ebert, 2022), I propose methodologies inspired by ecology, ecotoxicology, and parasitology studies to fill this gap. It would offer a large panel of ideas to develop this interesting question on how noise affects organisms and aquatic communities.

2. Noise effects on zooplankton species: a review

2.1. Responses from marine species

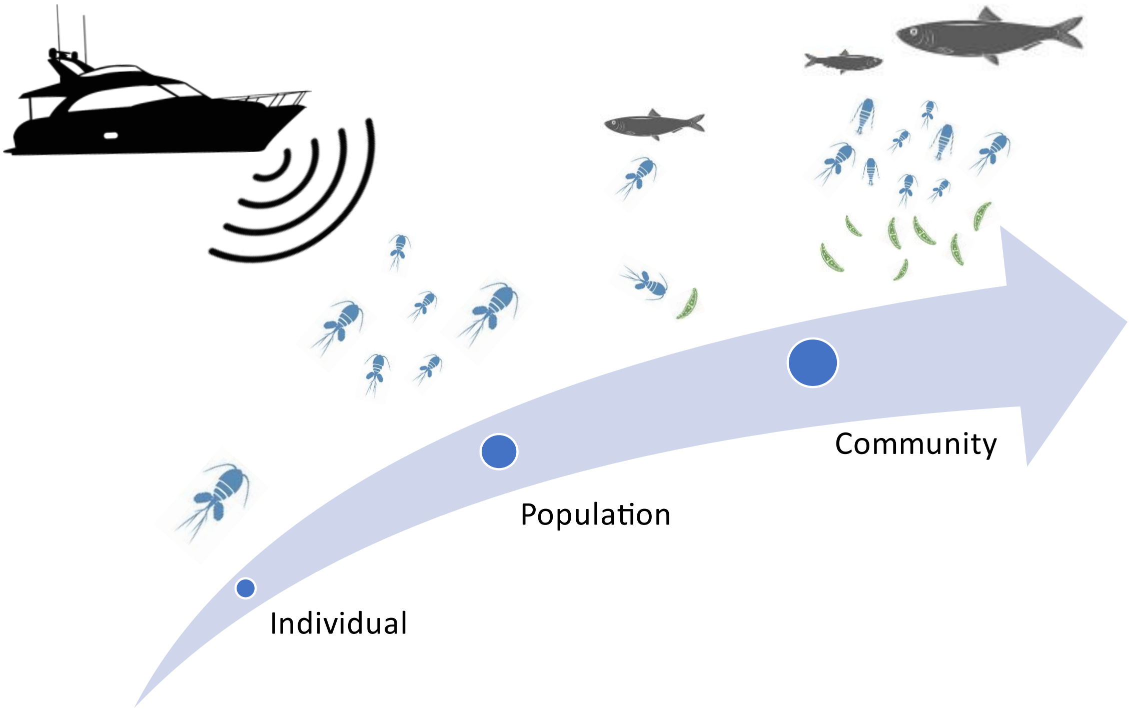
In marine systems, studies have mainly shown the negative effects of acute noise (150-180 dB SEL Re 1µPa^2.s) on copepod survival. In *in situ* experiments, McCauley et al. (2017) observed increased mortality of various zooplankton crustaceans, such as small copepods, cladocerans, and krill larvae exposed to a seismic survey. They hypothesized that this mortality, observed the day after noise exposure, resulted from damage to their mechanoreceptors. This explanation may be limited for their mortality observed one day after noise exposure; however, it suggests that acute exposure to airgun noise could have long-term effects but there were no measurements next days. Fields et al. (2019) showed a less intense effect of the airgun with a small increase in copepod mortality and no effect on their behaviour; these different results, in terms of the intensity of the negative effect, may be explained by the size of the plankton species differing between the two studies. Without mechanical explanations until now, it seems that smaller zooplankton species are less impacted by noise (Solé, Kaifu, et al., 2023). This hypothesis is supported by Vereide et al. (2023), who observed increased mortality of the small copepod *A. tonsa* exposed to airguns. Non-lethal effects on copepods were also reported (Tremblay et al., 2019; Fields et al., 2019; Kühn et al., 2023). Fields et al. (2019) showed altered expression of two unannotated genes, thus consequences for organisms are unknown. After an acute boat noise exposition (i.e., 24h) of two copepod species, the feeding behaviour of *A. tonsa* was altered, with a reduction in their ingestion and clearance rate (Kühn et al., 2023). In contrast, the clearance rate of *Eurytemora herdmani* is not affected (Aspirault et al., 2023). Nevertheless, the only chronic noise exposure on copepods (*A. tonsa*) did not affect the ingestion rate or O_2 consumption but led to physiological impacts with altered ROS (reactive oxygen species) activities (Tremblay et al., 2019). The only study on a non-crustacean taxon, a rotifer, showed reduced egg production (eggs of smaller size) of *Brachionus plicatilis* (Aspirault et al., 2023).

2.2. Responses from freshwater species

Freshwater ecosystems are also threatened by the omnipresence of shipping activities that overlap with prominent frequencies used by aquatic animals (Mickle & Higgs, 2018). Studies are more focused on the effects of less intense chronic or acute noise (100-150 dB RMS Re $1\mu Pa^2$) on daphniid behaviour and survival, and communities. Sabet et al. (2019) tested the short-term effects of motorboat noise on the mobility of the cladoceran (Crustacean) *Daphnia magna* and found no change in their swimming behaviour, as in a previous study with regular and intermittent noise (Sabet et al., 2015). This result was also confirmed in a study with another *Daphnia* species, where the effect of motorboat noise did not affect the mobility of *Daphnia pulex* exposed for the first time (Rojas, Prosnier, et al., 2023). These boat noises also did not affect the survival or fecundity of chronically exposed *D. magna* (Prosnier, Rojas, et al., 2023). However, chronic exposure to broadband noise leads to both a reduction in their velocity and an increase in their survival and fecundity (Prosnier et al., 2022). Two studies enlarged the boat noise effect at the community scale. They highlighted that the effects of noise on the zooplanktonic community – affecting Bosminidae and Daphniidae proportions – could be more important in the absence of fish predators than in their presence (Rojas, Desjonquères, et al., 2023; Rojas, Gouret, et al., 2023), highlighting that aquatic communities could be affected by noise in ways other than by 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.

2.3. *Future perspectives*

All these recent studies highlight that many ways of noise effects on zooplankton are beginning to be explored. About these ways, I distinguished five research axes in which it seems important to continue (Fig. 1); the four firsts are on isolated individuals (or almost). These five axes seem currently distinguished because papers generally focus on one aspect, and the methodology could be greatly different between them. (1) Neurology: the need to identify which frequencies and at which intensity sound can affect organisms. Until now, a wide variety of noises have been investigated, some more realistic (airgun, boat), others more artificial (broadband). A better understanding would allow standardization and lead to comparison between studies. (2) Physiology: there is a need to assess how the stress induced by noise directly affects individual metabolism, i.e., gene expression and energetic cost. (3) Fitness: the

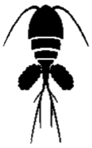


Neurology	Physiology		Fitness		Behaviour		Community
Noise perception	Genetic expression	ROS, Composition	Development	Survival, Fecundity	Mobility	Predation Feeding	Composition, dynamic

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.

effect of noise on the population through fitness measurements, such as survival and fecundity rates, and alterations in development (i.e., effects on morphology). It mainly results from the previous axis (the energetic cost of stress could reduce survival) and could also be affected by the next axis through indirect effects. (4) Behaviour: the effect of noise on behaviour, obviously linked with previous axes – noise damages and masking effects should alter environmental perception, physiological stress should alter various behaviours, energy requirement could affect predation, and energy cost and acquisition could affect fecundity and physiology content. In this axis, I include the predator-prey relationship because behaviour is generally used to explain or predict the ability to prey and vulnerability to predation. Finally, (5) Community: the effect of noise at the community level, that is, the repercussion of alteration of 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 is the aim explained by the other to answer the crucial question: How does anthropogenic noise affect aquatic food webs? Moreover, some transversal aspects need to be considered, such as the different effects due to acute and chronic exposure and the short-term and long-term effects. The long-term effects during chronic exposure raise the question of their ability to habituate to noise and thus the importance of noise predictability. To answer this question, much previous work in other related fields, such as fundamental ecology, ecotoxicology or parasitology, has provided a wealth of methodological knowledge. In the next parts, I present numerous of these methodologies to fill gaps in each of these axes, where rarely more than one study (thus either freshwater or marine system, one species studied, one type of noise) has been conducted (Table 1).

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	**Sound (source) (dB [1])**	**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	
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, Rojas, et al., 2023)	Chronic (boat noise) (103-150 RMS)	Long-term (+30 days)					Survival Fecundity			
	(Prosnier et al., 2022)	Chronic (broadband noise) (128 RMS)	Long-term (+30 days)				Size	**↗ Survival ↗ Fecundity**	**↘ Speed**		
	(Rojas, Gouret, et al., 2023)	Chronic (boat noise) (100-122 RMS)	Long-term (44 days)								**Sp. abundance**
	(Rojas, Prosnier, et al., 2023)	Acute (boat noise) (100-122 RMS)	Short-term (direct)						Speed		
	(Rojas, Desjonquères, et al., 2023)	Chronic (boat noise) (105-110 RMS)	Long-term (42 days)								**Sp. abundance**

1. SEL: Sound-Exposure Level in dB Re 1µPa^2.s, RMS: Root-Mean-Square in dB Re 1µPa^2

3. Zooplankton: overview of existing methodologies

3.1. Neurology: Noise detection

Before asking how organisms are affected by noise, it seems important to understand how they could detect noise. Because zooplankton species have not developed a hearing system, they use only external mechanoreceptors, e.g., on the first antennae of copepods (Yen et al., 1992; Gassie et al., 1993); they are not able to detect the pressure level (i.e., the classical measure in µPa) but the particle motion (i.e., the tidal velocity in m/s) (Nedelec et al., 2016; Rogers et al., 2021). Therefore, it is now recognized that measuring particle motion is mandatory to understand zooplankton reactions to noise (André et al., 2016; Popper & Hawkins, 2018) and consequently to characterize the various noises (airgun, shipping, etc.). Considering this information, electrophysiological experiments as previously done (Gassie et al., 1993; Hartline et al., 1997) would be interesting. Other methods, such as behavioural methods, offer, with lower precision, information on which sounds are detectable by organisms (Buskey et al., 2002). This step is mandatory to determine the frequency range of sound detection by organisms. Until now, the few data, about non-zooplanktonic crustaceans, show a sound detection of low frequency noise below 3000 Hz (Duarte et al., 2021; Solé, Kaifu, et al., 2023). For instance, Lovell et al. (2005) showed, using electrophysiology methods, that the common prawn (*Palaemon serratus*) has a frequency range of 100-3000 Hz. Similar studies on zooplanktonic species are mandatory to, at least, determine a frequency range, and ideally to draw a spectrogram, allowing comparison, and thus prediction, with the frequency of anthropogenic noise, as airgun, 10-300Hz, and boat, 10-20000Hz (Duarte et al., 2021). The only neurophysiology study on a zooplanktonic copepod shows a detection for a frequency range of 40 to 1000Hz (Yen et al., 1992). Other clues of sound frequency effects are available in literature: it suggests a noise effect on copepods for a noise 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). Other studies either show no effect or do not provide a frequency range of noise exposure.

Moreover, the absence of behavioural or neuronal response could be explained by damage to mechanoreceptors due to high noise, as 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 visually detectable with microscopy. These methods could allow us to know noise thresholds (both in terms of intensity, frequency, and particle motion) for 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.

3.2. Physiology: Metabolism measurements

Many physiological markers of stress can be measured on zooplankton, from the individual to the natural community, as has been done, in a noise context, for fish with cortisol measurements (Nichols et al., 2015; de Jong et al., 2020). Several methods have been developed in ecotoxicology (Handy & Depledge, 1999), especially for copepods, which now seem to be popular biological models (Raisuddin et al., 2007; Dahms et al., 2016), as water fleas are for freshwater systems (Bownik, 2020; Ebert, 2022). For instance, for both short- and long-term experiments, it is possible to measure reactive oxygen species (ROS) that involve cellular damage, the organisms' composition, such as protein or carbon content, and gene expression, providing information regarding the basis of the chain reaction (Dahms et al., 2016). Lee et al. (2019) used various ROS measurements (glutathione, GST, glutathione reductase, GR, glutathione peroxidase, GPx, superoxide dismutase, SOD) to determine how ocean acidification affected *T. japonicus* with higher concentrations of stress markers. Won et al. (2014) measured fatty acid concentration in copepods (*Paracyclopina nana*) following UV exposure, whereas

(Prosnier, Loeuille, et al., 2023) measured the quantity of carbohydrates, lipids and protein of *D. magna* infected by an iridovirus; and Forshay et al. (2008) measured the carbon to nitrogen ratio of *D. pulicaria* infected by a chytridiomycete (fungus). Another measurement is oxygen consumption, through respirometry methods, which has already been performed for both copepods and daphniids (McAllen & Taylor, 2001; Zitova et al., 2009). The results of these studies show methodologies that can be used in the field of zooplankton bioacoustics but highlight the constraint of pooling small individuals, leading to a loss of individual variability. In a noise context, Tremblay et al. (2019) showed no effects on O_2 consumption but higher ROS (similar to Lee et al., 2019), and Fields et al. (2019) showed a higher expression of two genes of unknown effects, showing that the issue needs to be studied, as there may be underlying effects. Measurements of physiological markers would be a good tool to obtain information on the ability of zooplankton to habituate to noise, i.e., whether they return to a basal level after a certain time of exposure. These physiological alterations could directly result from noise stress, as acidification directly affects ROS (Lee et al., 2019), or be a by-product of behaviour modifications, as the modification of their mobility (Prosnier et al., 2022) or their feeding rate (Kühn et al., 2023) could affect their energy budget.

3.3. Fitness: survival and reproduction measurements

Due to physiological stress or behavioural changes, anthropogenic noise can directly affect zooplankton species. These most visible effects, which have obvious implications for zooplankton populations and communities, are the effects on fitness, i.e., reproductive success through effects on survival and fecundity. Contrary to the studies on vertebrates, it is easier to obtain much information about fitness on isolated individuals or populations under *in situ* (realistic) or laboratory (controlled) conditions. Zooplankton allows us to easily observe the effects on eggs, juveniles/larvae, and adult survival, fecundity, and development of each stage (Dahms et al., 2016). In a noise context, McCauley et al. (2017) and Vereide et al. (2023)

assessed instantaneous and delayed mortality in marine zooplankton, whereas Aspirault et al., (2023) studied rotifer fecundity; Prosnier et al. (2022) and Prosnier, Rojas, et al. (2023) studied both mortality and fecundity in the freshwater water flea *Daphnia magna*. Reduced development is also being developed with the use of size or stage duration for copepods exposed to airgun noise (Vereide et al., 2023), which could have repercussions on fitness over generations. Linked to development, Olivier et al. (2023) developed the larvosonic, to study the effects of noise on small aquatic organisms. Moreover, the study of population dynamics, coupled with mathematical models, allows us to determine effects on fitness and fitness components (such as reproductive rate, generation time, and growth rate …). For instance, 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, Rojas, et al., 2023). McCauley et al. (2008) coupled a structured model and controlled experimentation to characterize the dynamic of a *Daphnia*-algae system.

3.4. Behaviour: individual and predation measurements

Behaviour is certainly one of the main studied aspects of the impact of anthropogenic noise, as noise should affect communication and perception of the environment (Tidau & Briffa, 2016). Zooplankton responses to noise have been studied primarily in freshwater during fish predation experiments to test whether noise altered their behaviour (anti-predator defence, swimming distance, detectability) and thereby their vulnerability (Sabet et al., 2015; Rojas et al., 2021, 2023; see also Fernandez Declerck et al., 2022 for a small zoobenthic prey). Nevertheless, many other behavioural measurements were performed to test if and how a pollutant could affect a zooplanktonic organism. Bownik (2017) proposed 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 usable for copepods, Elmi et al. (2021)), vertical distribution (important for diel migration, tested myself for *D. magna* exposed to noise, unpublished data), swimming trajectory, and sinking rate. Alteration of mobility could affect noise exposure, either because diel migration leads to diel exposure or because mobility could be interpreted as an ability to escape pollutants (Michalec et al., 2013). Note that some morphological and behavioural differences between sexes need to be taken into account (Holm et al., 2018), and thus, males and females could react differently to anthropogenic noise. In the case of population studies, it is also possible to measure their spatial distribution and their individual distance, i.e., swarming behaviour (Buskey et al., 1996). These behavioural measurements can also be performed in the context of multi-stimuli, where, for instance, noise could affect reaction to other stimuli like 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).

Linked to their vulnerability to predation, a recent study shows that marine copepods produce sounds, likely hearable by their predators (Kühn et al., 2022). This sound production has been previously described for freshwater copepods and daphnids about predation by *Chaoborus* larvae (Giguère & Dill, 1979). These sounds are maybe a by-product of their mobility, likely during escape behaviour. In the context of anthropogenic noise, it raises a question: is noise able to mask these sounds, that could be a clue for predators or conspecifics. And, if the sound is not simply a by-product, are organisms able to modify their sound emission in reaction to environmental noise. The two effects (masking and modulation) are known in marine mammals and fishes (Putland et al., 2018) – leading to higher or lower detection by their predator.

Noise should affect predator-prey relationships. Behaviour alteration should affect the encounter rate of prey and predators and thus their predation rate or vulnerability to predation (Gerritsen & Strickler, 1977). Noise can also affect the perception of prey and predator (masking effect) and physiology (energy needs). Thus, it is interesting to study the effects of noise on predation, by considering a system where zooplankton is either a prey or a predator. For instance, Sabet et al. (2015) and Rojas et al., (2023) studied *D. magna* behaviour because they were fish prey. In parasitism experiments, Prosnier, Loeuille, et al. (2023) studied how *Daphnia* infection affects the attack rate and handling time of its predator. As a consumer, zooplankton can be herbivores or filterers, such as cladocerans or small copepods, or active predators, such as larger species. Regarding the filterer, Hong et al. (2012), in an ecotoxicology study, measured the feeding appendage beating of *A. tonsa*. The classical functional response experiments (Holling, 1959a; b) used during the previously cited fish experiments could be used both for filterers (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 measurements are useful to explain results when the studied species is a prey or a predator. In the noise context, Tremblay et al., (2019), Kühn et al. (2023), and Aspirault et al. (2023) studied the ingestion rate of copepods. Regarding behaviour linked to predation, the body rotation of the insect *Chaoborus* larvae was studied to explain its vulnerability to predation by fish (Rojas et al., 2021; Rojas, Prosnier, et al., 2023) or its predation rate on cladocerans (Rojas, Desjonquères, et al., 2023).

4. From individual to community

4.1. Experimental approaches

Modification 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 that of the community. However, current research has focused mainly 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 the developmental rate, survival and/or fecundity, it may also alter competitiveness, as Decaestecker et al. (2015) demonstrated in the case of water flea infection by a pool of parasites. Therefore, it is possible to assume that effects on zooplankton could 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 when community complexity is increased (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, as stable isotopes, are a good tool to assess long-term effects on communities (Boisnoir et al., 2020), which target dietary shifts over time. To remind us in the noise context, see the community studies of 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 impacted 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 herbivore alterations – 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.

4.2. Theoretical approaches

To date, only experimental approaches have been conducted to understand how noise affects organisms and communities, despite their recognized importance in understanding the observed ecological dynamics (McCauley et al., 2008). One 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 will provide a better understanding of the mechanisms by which noise affects community structure and stability (Wollrab & Diehl, 2015). For example, 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) showed, with a model, that trophic alterations were driven by host mortality rather than by alterations in predator behaviours. In addition, a combination of noise propagation models (Barber et al., 2011; Lin et al., 2019; Guibard et al., 2022) and food web models could be useful for developing spatially structured models. These models allow us to understand the role of zooplankton mobility (diel migration, noise escape, natural current) in temporally and spatially structured noise pollution.

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

Research axes	**Objectives**	**Measurements/Technics**	**Example of references**
Neurology	Characterisation 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, Loeuille, et al., 2023)
		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; Prosnier, Rojas, et al., 2023; Aspirault et al., 2023)
	Fecundity	Lab	(Prosnier et al., 2022; Prosnier, Rojas, et al., 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, Rojas, 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; Prosnier, Loeuille, et al., 2023; Rojas, Desjonquères, et al., 2023; Rojas, Prosnier, et al., 2023)
		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)

5. Discussion

I proposed various measurements of noise effects on zooplankton in several aspects (Table 2). However, we need to keep in mind that all these levels are interconnected. For instance, the effect on mobility should directly affect their survival or their fecundity through an alteration of energy allocation. Prosnier, Rojas, et al. (2022) explained their surprising increase in fitness by the lower mobility of *D. magna* exposed to noise. The lower consumption of *A. tonsa* (Kühn et al., 2023) ask for repercussions on their fitness. Prey mobility is generally studied to explain differences in predator foraging (Sabet et al., 2015; Rojas et al., 2021; Fernandez-Declerck et al., 2023); thus, 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 mussels (Fernandez Declerck, unpublished data; Turco et al., in prep.). Another interesting point is the deleterious effects on mechanoreceptors (Solé et al., 2016). These permanent damages should lead to long-term effects on their behaviour, on their ability to detect prey or predators, and thus on their fitness. These various, and generally independent, studies presented in the review not only focus on numerous interesting impacts of noise but also highlight mechanisms that could explain how and why noise affects, or could affect, all these levels.

Over the past decade, there has been increasing interest in how anthropogenic noise affects ecosystems, particularly marine mammal and fish species. The current perspective highlights that few studies on zooplankton responses in marine and freshwater systems have examined all aspects from individuals to communities. However, there are still huge gaps in knowledge that could be filled by methodologies developed in ecology, ecotoxicology and parasitology studies. Three important areas should be investigated: (1) determining what noise (spectrum, temporality), studied in terms of particle movement, might affect zooplankton diversity, (2) using few model organisms to understand whether noise impacts physiology, fitness and behaviour to a greater or lesser extent, i.e., to understand mechanisms, then enlarging the number of models to assess whether generalizations are possible, and (3) understanding, through experiments and models, how noise affects the structure and stability of zooplankton communities. Consequently, zooplankton species seem to be good models for studying many effects of noise from physiology to community, from the short term to the long term, including multigenerational experiments allowing evolution (Ebert, 2022). A difficulty could be in the experimental design to obtain a correct noise exposition, particularly about the noise spectrum that is greatly affected by the setup and necessitates correction (e.g., Prosnier, Rojas, et al., 2023). Olivier et al. (2023) designed a *larvosonic* system to study the effects of noise on larvae, but this system should also be useful for all zooplanktonic studies.

It is important to consider that this perspective paper focuses on holozooplanktonic species (primarily arthropods), although many other groups are, in part of their cycle life, constituents of zooplankton (the meroplanktonic species). These organisms can be affected by noise – see the reviews of Solé, Kaifu, et al. (2023) and Vereide & Kühn (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 of 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 how anthropogenic noise affects aquatic communities.

Conflict of Interest

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

Author contributions

LP thought and wrote this perspective article and approved the submitted version.

Acknowledgement

The author would like to thank his binôme Emilie Rojas :), for the numerous useful discussions and a complete review, and Théophile Turco too; Marta Solé, for the opportunity to write this article, Vincent Médoc, Joël Attia, Marilyn Beauchaud, Wenjing Wang, the ENES team, the meeting “Effects of noise on aquatic life” 2022 in Berlin, and a NTNU team for many interesting discussions and feedbacks. The author also thanks the three anonymous reviewers for their useful comments.

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