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

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Running title: How anthropogenic noise affect zooplankton?

Number of words: 4800

Number of figures: 1

Number of tables: 1

Abstract

There is a growing interest in the effects of noise pollution on aquatic ecosystems. To date, these works mainly focus on hearing species, especially fish and mammals. Species from lower trophic level, 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 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 induce stress. The few studies suggest effects on physiology, behavior, and fitness. After this review, and based on methods from ecology, ecotoxicology, and parasitology, I showed how they can be more used to study the noise effects at individual scales, as modifications of physiology, development, survival, and behavior. Responses to noise, that could change species interactions and population dynamics, are expected to lead to larger scale implications (i.e., alterations of food webs dynamics and ecosystem functioning). We might expect further development of acoustic studies on zooplankton, in order to better apprehend how anthropogenic noise affects aquatic environments.

Keyword: Zooplankton, Anthropogenic noise, Aquatic ecosystems, Physiology, Fitness, Behavior, Community

1. Introduction

Anthropogenic underwater noise is an established pollutant for marine ecosystems (Hildebrand, 2009). Human activities, such as seismic survey, shipping, or operational wind farms, affect soundscapes by increasing ambient noise levels in space and time over minutes to years and over meters to thousands of kilometers (Duarte et al., 2021). Noises are extremely diverse in their intensity, in their structural spectrum and in their temporal pattern, due to various sources as airgun and shipping; noise exposure could also by affected by the behavior of organisms, as their ability to escape to noise source 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 more or less predictable (Francis & Barber, 2013) affecting differently organisms, as showed in the ability of fish to habituate to chronic noise exposition (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 organ, thus to be sensitive to sound pressure level.

However, it exists a very limited number of research on invertebrate responses to noise, despite their biodiversity (Wale et al., 2021; Vereide & Kühn, 2023; Solé, Kaifu, et al., 2023), and especially holozooplanktonic species (i.e., zooplanktonic along all their life cycle). These non-hearing organisms (i.e., without identified auditory organs) represent a crucial link for the transfer of energy between primary resource and higher trophic levels (Heneghan et al., 2016; Ratnarajah et al., 2023). Cases shown reaction of crustaceans (Edmonds et al., 2016), mollusks (André et al., 2011) and cnidarian species (Solé et al., 2016) 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 around 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 were 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), and crustaceans (Stenton et al., 2022), and more rarely other taxa as bryozoans (Stocks et al., 2012). Investigation made in the 90s 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 had been followed by Buskey et al. (2002) that demonstrated the behavioral responses of the copepods (*Acartia* spp.) to increase their speed few milliseconds after vibration stimuli. These responses to vibration have raised questions about the effect 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). The importance of zooplankton in aquatic ecosystem could be illustrated by their role in the carbon cycle (Steinberg & Landry, 2017). Therefore, all anthropogenic perturbations should greatly affect ecosystem functioning (Marine Zooplankton Colloquium, 2001; Richardson, 2008), and noise would not except. Understanding responses of zooplanktonic species to noise is thus mandatory to prevent human impacts.

In this Perspective paper, I overview how zooplankton responses to noise could be described. Firstly, 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), for organisms (zooplankton, invertebrates, arthropods, crustacean, mollusk, cnidarian, medusa, copepods, daphnia) and the habitat (aquatic, marine, freshwater). From this pool of articles, I added cited and citing literature. I considered only organisms that are zooplanktonic along all their life (i.e., holozooplankton), excluding meroplankton as planktonic larvae (e.g., decapods, bivalves, fishes) and planktonic adult (e.g., cnidarians). Note that only one article published in 2021, on *Daphnia* exposed to 432 Hz and 440 Hz, have been excluded due to some personal doubt on its quality – thus not cited here but easily findable with these details. I considered peer-reviewed articles as well as book chapters, meeting proceedings and preprints. I found only thirteen articles studying effects of noise, six in marine and seven in freshwater systems, highlighting how large is the gap. 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 from 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

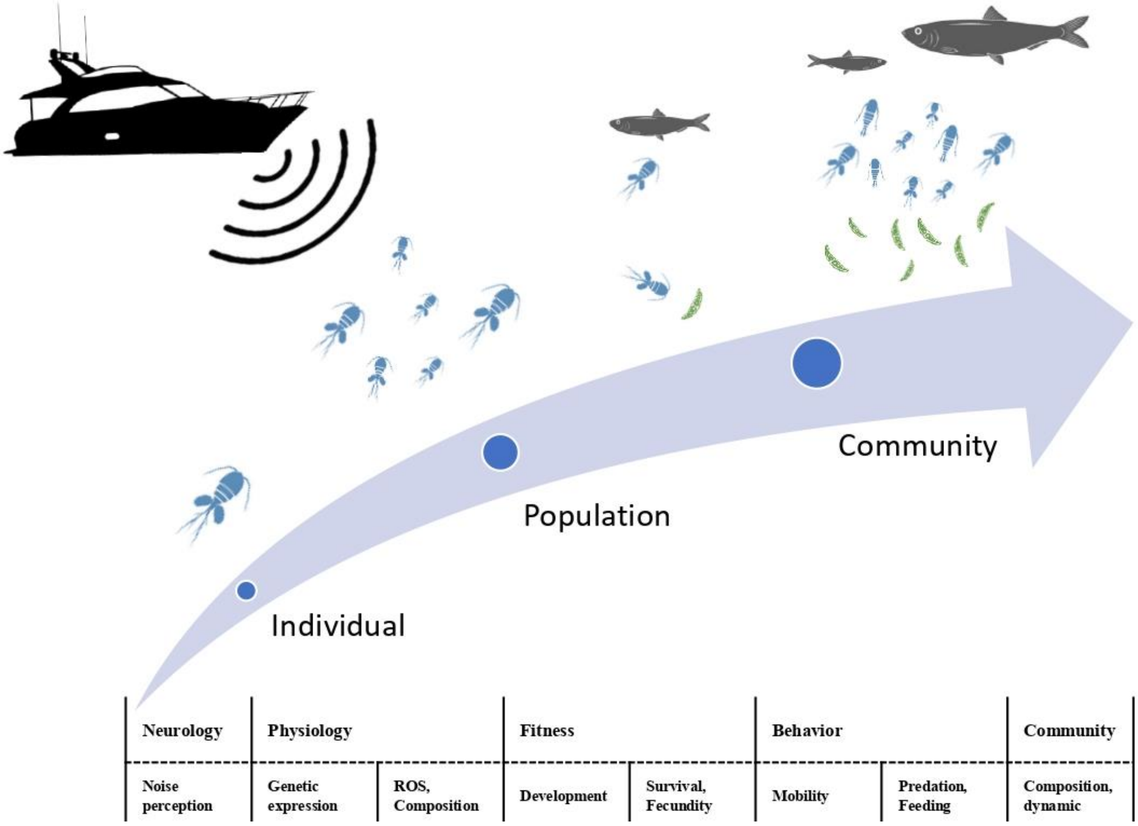
In marine system, studies mainly showed negative effects of acute noise (150-180 dB SEL Re 1µPa^2) on copepods' survival. In *in situ* experiments, McCauley et al. (2017) observed increased of mortality of various zooplankton crustaceans, such as small copepods, cladocerans, and krill larvae exposed 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 a one-day mortality; however, it suggests that an acute exposure to airgun noise could have long-term effects. Fields et al. (2019) showed a more limited effect of the airgun with a small increase in copepods' mortality, and no effect on their behavior; these contrary results may be explained by the size of the plankton species differing between the two studies (Solé, Kaifu, et al., 2023). This explanation is supported by Vereide et al. (2023) that observed increased mortality of the small copepods *A. tonsa*, exposed to airgun. Non-lethal effects on copepods were also reported (Tremblay et al., 2019; Fields et al., 2019; Kühn et al., 2023). Fields et al. (2019) suggest altered gene expression without knowing the effects of these genes on the organisms. Feeding behavior of *A. tonsa* were altered with a reduction of their filtration rate during 24h-exposure to boat noise (Kühn et al., 2023), contrary to the copepods *Eurytemora herdmani* (Aspirault et al., 2023). Nevertheless, the only chronic noise exposure, on copepods (*A. tonsa*), did not affect ingestion rate or O_2 consumption, but lead to physiological impacts with altered ROS (Reactive Oxygen Species) activities (Tremblay et al., 2019). The only study on a non-crustacean taxa, a rotifer, showed a reduced egg production (eggs of smaller size) of *Brachionus plicatilis* (Aspirault et al., 2023).

2.2. Responses from freshwater species

Freshwaters 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 effects of less intense chronic or acute noise (100-150 dB RMS Re 1µPa) on daphniids behavior and survival, and communities. Sabet et al. (2019) tested the short-term effects of motorboat noise on the mobility of the cladocera (Crustacean) *Daphnia magna* and found no change in their swimming behavior, as in a previous study with regular and intermittent noise (Sabet et al., 2015). This result 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 not affect survival or fecundity of *D. magna* chronically exposed (Prosnier et al., 2023). Whereas, a chronic exposition to broadband noise leads both to a reduction of their velocity and an increase of their survival and their fecundity (Prosnier, Rojas, et al., 2022). Two studies enlarged boat noise effect at the community scale. They highlighted that the effects of noise on zooplanktonic community – affecting Bosminidae and Daphniidae proportions – could be more important in the absence of fish predator than in their presence (Rojas et al., 2022; Rojas, Desjonquères, et al., 2023), highlighting that aquatic communities could be affected by noise through others ways 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 behavioral effects among species, making it difficult to generalize effects.

2.3. Future perspectives

All these recent studies highlight that many interesting questions are beginning to be explored. I distinguished five 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 paper generally focus on one aspect, and methodology could be greatly different between them. (1) Neurology: the need to identify which sounds are able of affecting organisms. Until now, a wide variety of noise have been investigated, some more realistic (airgun, boat),

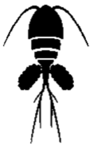


Neurology	Physiology		Fitness		Behavior		Community
Noise perception	Genetic expression	ROS, Composition	Development	Survival, Fecundity	Mobility	Predation, Feeding	Composition, dynamic

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.

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 affects directly individual metabolism, i.e., genes expression and energetical cost. (3) Fitness: the effect of noise on population through fitness measurement such as survival and fecundity rate, and also alteration in development (i.e., effects on morphology). It mainly results from the previous axis (energetical cost of stress could reduce survival), and could also be affected by the next axis through indirect effects. (4) Behavior: the effect of noise on behavior, obviously linked with previous axes (energy requirement could affect predation, and energy acquisition could affect fecundity). In this axis, I include predator-prey relationship, because behavior is generally used to explain or to predict the ability to prey and the vulnerability to predation. Finally, (5) Community: the effect of noise at the community level, that is the repercussion of alteration of individual’s survival, fecundity, and behavior. 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 to the crucial question: How anthropogenic noise affect aquatic food webs? Moreover, some transversal aspects need to be considered as the different effects due to acute and chronic exposition, and the short-term and long-term effects. The long-term effects during chronic exposition raises the question of their ability to habituate to noise, and thus the importance of noise predictability. To answer it, much previous work in other related fields, such as fundamental ecology, ecotoxicology or parasitology provides 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 interested in (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**		**Behavior**		**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**							
	(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** **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 et al., 2023)	Chronic (boat noise) (103-150 RMS)	Long-term (+30 days)					Survival Fecundity			
	(Prosnier, Rojas, et al., 2022)	Chronic (broadband noise) (128 RMS)	Long-term (+30 days)				Size	**Survival** **Fecundity**	**Speed**		
	(Rojas et al., 2022)	Chronic (boat noise) (100-122 RMS)	Long-term (44 days)								**Composition**
	(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)								**Composition**

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

3. Zooplankton: overview of existing methodologies

3.1. Noise detection

Before asking how organisms are affected by noise, it seems important to understand how they could detect the 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). So, it is now recognized that measuring the 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 …). Considering this information, electrophysiological experiments as previously done (Gassie et al., 1993) would be interesting. Other methods, such as the behavioral one, offer, with a lower precision, information on which sounds are detectable by organisms (Buskey et al., 2002). But the lack of response could be explained by damages to mechanoreceptors due to high noise, as it was observed on two species of Mediterranean Scyphozoan medusa (Solé et al., 2016) and the sea lice *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 damages. Like ecotoxicological methods, Tyack & Thomas (2019) proposed a dose-response method, allowing to link intensity of noise and its impacts. A supplementary point should be considered: because mechanoreceptors and chemoreceptors are closely related in their position, in their structure and, maybe, in their genes (Hartline et al., 1997), noise could be “detected” by zooplankton through their chemoreceptors. Studies on crabs showed no effect on their ability to find food with their chemoreceptors during boat noise or sweep exposure (Hubert et al., 2021; Solé, De Vreese, et al., 2023) but it is not yet tested on zooplankton species.

3.2. 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 the 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, Superoxyde Dismutase, SOD) to determine how ocean acidification affected *T. japonicus* with higher concentration of the stress markers. Won et al. (2014) measured fatty acid concentration in copepods (*Paracyclopina nana*) following UV exposure, whereas (Prosnier, Loeuille, et al., 2022) 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 the oxygen consumption, through respirometry methods, already done 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 to pool the small individuals, leading to a loss of individual variability. To reminder, 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 exposition. These physiological alterations could directly result from the noise stress, as acidification directly affect ROS (Lee et al., 2019), or be a by-product of behavior modifications, as the modification of their mobility (Prosnier, Rojas, 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 the physiological stress or behavioral changes, anthropogenic noise can directly affect zooplankton species. These most visible effects, which have obvious implication for zooplankton populations and communities, are the effects on fitness, i.e., the reproductive success through effects on survival and fecundity. One of the great interest of zooplankton species is the possibility to obtain a lot of information on isolated individuals or population, and in *in situ* (realistic) or laboratory (controlled) conditions. Zooplankton allows to easily observe 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 delay mortality on marine zooplankton whereas Aspirault et al., (2023) studied rotifer fecundity; Prosnier, Rojas, et al. (2022) and Prosnier et al. (2023) studied both mortality and fecundity on the freshwater water fleas *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), that could have repercussion on fitness along generations.

3.4. Behavior and predation measurements

Behavior is certainly one of the main studied aspects of the impact of anthropogenic noise, as noise should affects 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 behavior (anti-predator defense, 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 behavioral measurements were done to test if and how a pollutant could affect a zooplanktonic organism. Bownik (2017) proposed to measure swimming speed (see also, in noise experiments, Sabet et al., 2019; Prosnier, Rojas, et al., 2022; Rojas 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 lead to diel exposure, or either because mobility could be interpreted as an ability to escape to pollutant (Michalec et al., 2013). Note that there is some morphological and behavioral difference between sex that need to be taken into account (Holm et al., 2018), and thus male and female could react differently to anthropogenic noise. In case of population studies, it is also possible to measure their spatial distribution and their individual distance, i.e., the swarming behavior (Buskey et al., 1996). Linked to their vulnerability to predation, a recent study shows a new behavior of zooplanktonic arthropods: they produce sounds, likely hearable by their predators (Kühn et al., 2022). In a context of anthropogenic noise, it raises two questions: is noise could mask these sounds, or are organisms able to modify their sound emission in reaction to environmental noise – because the two effects are known in marine mammals and fish (Putland et al., 2018) –, leading to higher or lower detection by their predator.

Many of these behaviors should affect the encounter rate of prey and predator, thus their predation rate and vulnerability (Gerritsen & Strickler, 1977). More, noise can also affect perception of the environment (prey and predator detection through masking effect) and physiology (energy needs) that are also involved in predation. On this aspect, it is mandatory to consider zooplanktonic organisms as prey and as predators. For instance, Sabet et al. (2015) and

Rojas et al., (2023) studied *D. magna* behavior because they were fish prey. As a consumer, zooplankton could be herbivore or filterer, as cladoceran or small copepods, or active predator, as the larger species. About filterer, Hong et al. (2012), in an ecotoxicology study, measured 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 it was done for larvae of the damselfly *Ischnura elegans* exposed to boat noise, and showing an increase of its handling time (Villalobos-Jiménez et al., 2017). Note that these behavioral measurements are useful to explain results when the studied species is a prey or a predator. In the noise context, to reminder, Tremblay et al., (2019), Kühn et al. (2023), and Aspirault et al. (2023) studied ingestion rate of copepods. About behavior 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 cladorecans (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 behavioral changes will directly affect the population dynamics of species and therefore that of the community. However, current research focused mainly on individual responses which is not sufficient, 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 Decaestecker et al. (2015) demonstrated in the case of water fleas infection by a pool of parasite. Therefore, it is possible to assume that effects on zooplankton could induce top-down effect, through cascading effects, and bottom-up effects (Sommer et al., 2001; Banerji et al., 2015; Wollrab & Diehl, 2015). Mesocosms studies have highlighted how the change in biological (community response) and spatial (from microcosm to mesocosm) scales affects the 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 communities' studies (Spisla et al., 2021). To study community, it is possible to study community dynamics, or stability, and composition. It is also possible to perform individual measurement as the physiology and the behavior. For instance, the stable isotopes are a good tool to assess long-term effect on community (Boisnoir et al., 2020), which targets dietary shifts over time. To reminder in the noise context, see the community studies of Rojas et al. (2022), 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 of 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) asking 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. 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 than by alterations in predator behaviors. 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 would allow to understand the role of zooplankton mobility (diel migration, noise escape, natural current) in a temporally and spatially structured noise pollution.

5. Discussion

I proposed various measurements to do about noise effects on zooplankton on several aspects. However, we need to have in mind that all these levels are interconnected. For instance, the effect on mobility should affect directly their survival or their fecundity, through an alteration of energy allocation. Prosnier, Rojas, et al. (2022) explained their surprising increase of fitness by the lower mobility of *D. magna* exposed to noise. The lower consumption of *A. tonsa* (Kühn et al., 2023) ask for repercussion on their fitness. The 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 fitness of zooplanktonic organisms. It is also possible to link behavior 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 behavior, on their ability to detect prey or predator, thus on their fitness. These various, and generally independents, studies presented in the review are not only on numerous interesting impacts of noise, but highlight also 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 affect ecosystems, particularly marine mammals and fish species. The current perspective highlights that the few studies on zooplankton response in marine and freshwater systems 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 term of particle movement, might affect zooplankton diversity, (2) using few model organisms to understand whether noise impacts physiology, fitness and behavior to a greater or lesser extent, i.e., to understand mechanisms, then enlarge model number of models to assess whether generalizations are possible, and (3) understanding, through experiments and models, how noise affects structure and stability of zooplankton communities. Consequently, zooplankton species seem good models to study many effects of noise from physiology to community, from short term to 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 an necessitate correction (e.g., Prosnier et al., 2023). Olivier et al. (2023) designed a *larvosonic* system to study the effects of noise on larvae; but this system should be also useful for all zooplanktonic studies.

It is important to consider that this perspective paper focus 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 have been 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.

Acknowledgment

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 anonymous reviewer for his useful comments.

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