How the noises could affect marine food webs? A lack of zooplankton's studies.

Loïc Prosnier

- Equipe Neuro-Ethologie Sensorielle, ENES/CRNL, CNRS UMR 5292, Université de Lyon/Saint-Etienne, Saint-Etienne, France
- Pôle emploi, 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

Running title: How anthropogenic noises affect zooplankton?

Number of words: 3000

Number of figures: 1

Number of table: 0

Abstract

There is a growing interest in the effects of noise pollution on marine ecosystems. To date, these works mainly focus on hearing species, especially fish and mammals. Because these species are generally at the upper trophic levels, key species from lower levels, like zooplankton species, are less studied under noise effects. Zooplankton is already used as bioindicators, to understand fluxes, ecological dynamics and global change effects; however, it remains a lack of knowledge on the effect of noise. Previous works demonstrate that they could detect vibrations. Consequently, noise is susceptible to affect the perception of their environment and to induce stress. Combining their short life cycle, their phylogenetic and ecological diversity, zooplankton could be useful organisms to understand a diversity of noise effects. They can be used to study the effects at individual scales as modifications of physiology, development, and behavior. Responses, 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). Here, we bring out, from studies in ecology, ecotoxicology, and parasitology, methods that can be adapted to our current questions. We might expect further development of acoustic studies on zooplankton, in order to better apprehend how anthropogenic noises affect marine environments.

Keyword: Zooplankton, Anthropogenic noises, Marine ecosystems, Physiology, Fitness, Behavior, Community

1. Introduction

Anthropogenic noise is now considered as a common pollutant in marine systems. Human activities, like seismic survey, shipping, and wind farms, increase ambient noise levels, from few minutes to many years and from few meters to several thousand kilometers (Duarte et al., 2021). Noises are extremely diversified in their structure – i.e., each frequency differs in intensity – and in their temporal pattern – i.e., punctual noises, repeated noises (regular or random), continuous noises (with or without structural and intensity variations). Sound perception remains a crucial ability for aquatic animals to communicate, forage or avoid threatening situations. There have been developments in how hearing species, i.e., with identified hearing structures, are affected by anthropogenic noises. Consequently, many studies highlight effects of noises on marine mammals and fish (see the numerous reviews as Weilgart, 2007; Erbe et al., 2016; Cox et al., 2018; de Jong et al., 2020).

During the last few years, few studies focused on invertebrate responses to noises (Wale et al., 2021). These non-hearing specialists, i.e., without identified hearing organs, are, in majority, at lower trophic levels. Consequently, it is important to understand how they are affected by noises, to expect having a good overview of the noise effects on ecosystems. It has been shown that noises affect crustaceans (Edmonds et al., 2016), mollusks (André et al., 2011) and cnidarian species (Solé et al., 2016), however these studies remain rare. In the current perspective, I overview how zooplankton responses to noise could be described, based on current knowledge and many other possibilities.

2. Noises effects on zooplankton species: a quasi-exhaustive review

2.1. Noise affects marine zooplankton

Investigation on noise effects began in the 90th with the effect of vibration on copepods (crustaceans). In fact, Gassie et al. (1993) showed that copepods, using mechanoreceptors of their first antennae, are able to detect environmental vibrations. Then, Buskey et al. (2002)

demonstrated the behavioral responses of copepods with an increase of their speed few milliseconds after vibration stimuli. These works have offered the first important information: small crustaceans, constitutive of zooplankton, are able to detect and react to environmental vibration, and thus, probably, to environmental noises.

Consequently, following researches wondered whether anthropogenic noises such as seismic airguns could affect zooplankton knowing the important impacts found in vertebrates (McCauley et al., 2003; Fewtrell and McCauley, 2012). In their *in-situ* experiments, McCauley et al. (2017) obtained an increase of mortality of various zooplankton species, in particular of crustaceans, as copepods, cladocerans, and krill larvae. They hypothesized that this mortality, observed the day after noise exposition, results from damages of their mechanoreceptors. This explanation could be limited for a one-day mortality; however, it suggests that an acute exposure to airgun noises could have long-term effects. Nevertheless, Fields et al. (2019) showed a more limited effect of airgun with a small increase of copepods' mortality, and no effect on their behavior. They also suggest a modification of gene expression – but they did not know the effects of these genes on organisms. A chronic noise exposition of copepods, done by Tremblay et al. (2019), also leads to physiological impacts with an alteration of ROS (Reactive Oxygen Species) activities. Therefore, these few studies showed that marine zooplankton can perceive and respond to anthropogenic noises, but their responses remain poorly investigated.

2.2. Some information from freshwater zooplankton

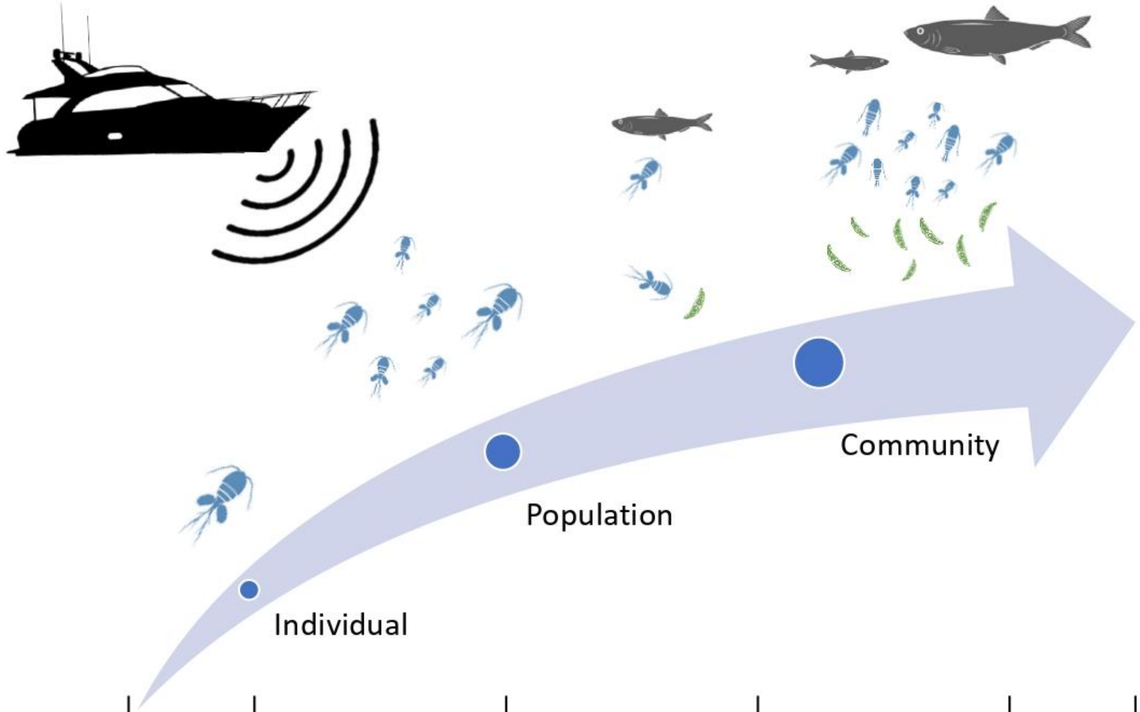
There are also some experiments on how noise affects freshwater zooplankton. Many of these groups are both present in marine and freshwater systems, consequently, these studies could offer us useful complementary information. Freshwaters are threatened by the omnipresence of shipping activities that overlap with prominent frequencies used by aquatic animals (Mickle and Higgs, 2018). Researches focused on behavioral responses and predation, as zooplankton represents an important resource for fish in the food web process. However, contrasting results were obtained, showing difficulties in generalizing the effects of anthropogenic noises. For instance, Sabet et al. (2019) did not show a difference in *Daphnia magna* behavior due to a noise exposition. However, for insect larvae exposed to noise, two effects are documented. *Chaoborus* increase their body rotations, an anti-predator behavior, when they are exposed to boat noises (Rojas et al., 2021). The damselfly *Ischnura elegans* reduce their predation, through an increase of handling time (Villalobos-Jiménez et al., 2017). Therefore, motorboat noises, less intense but with a longer duration than airgun noises, seem also able to affect small arthropods. Consequently, the combination of all these works indicates that various noises seem able to affect both behavior and survival of zooplanktonic organisms.

1.1. Works in progress

These studies are the basis for the numerous ongoing works. For instance, Kühn et al. (in prep.) study copepods' diet, and find that boat noise 24h-exposure on *Acartia tonsa* affects their feeding rate. Another interesting aspect of noise pollution is long-term effects and chronic noise expositions. To my knowledge, some works are asking how noise has long-term effects on zooplankton, as it was done for fish, and recently for mussels, showing ability to habituate to noises (Rojas et al., 2021; Hubert et al., 2022). On one side, researchers investigate the effects of airguns on copepods *A. tonsa* (Utne-Palm et al., 2022), as on mortality and development within six days after exposure (Vereide et al., in prep.). Long-term effects of airguns should be consequences of the mechanism hypothesized by McCauley et al. (2017): airgun damage mechanoreceptors that affect their ability to detect food, resulting in post-exposition effects. On the other hand, Prosnier et al. (2022b, 2022c) experiment effects of chronic exposure to noise (boat noises and broadband noise) along all *D. magna* life. Only chronic broadband noise seems to affect both survival and fecundity of these small crustaceans, that could be explained by a reduction of water fleas' speed. The difference between the two noises exposure asks how the noise type is important to understand effects of noise pollution. Vereide et al. (in prep.) also investigate the effects of noises on copepods' mobility. All these new results ask for a final and important ecological question: the effect on complex communities. The only study (Rojas et al., 2022, in prep.) shows that boat noise effects in the zooplankton community, during a few weeks' exposition, are more noticeable in the absence of fish, than in their presence, despite the known effect of noise on fish predation.

1.2. And now?

All these recent studies highlight that many interesting questions start to be explored (Francis and Barber, 2013). I distinguished five axes in which it seems important to continue (Fig. 1) . The four firsts are on isolated individuals (or almost). Firstly, it is necessary to understand which sounds are able to affect organisms. Until now, A wide variety of noises were used, some more realistic (airgun, boat), others more artificial (broadband). A better understanding of noise perception by organisms would allow us to select useful noises to study, and thus standardize used noises to improve study comparisons. The second axis is to understand physiological aspects. How this stress affects directly individuals, i.e., genes expression, metabolism, energetical cost, developmental alteration. These points are mandatory to determine in which ways zooplankton could habituate to noises, how acute exposition could lead to long-term effect, and if chronic exposition could be more or less deleterious. The third axis is the direct effect on zooplankton populations, the effects on survival and fecundity. It mainly results from the previous axis (energetical cost of stress could reduce survival), and could also be affected by the next axis. The fourth axis is the impact on behavior, obviously linked with previous axes (energy requirement could affect behavior, and behavior could affect fecundity). In the same axis, I directly rely on the ability to prey and the vulnerability to predation. Finally, the last axis is the effects at community level, that is the repercussion of alteration of individual's survival, fecundity and behavior. It is the ultimate axis because I think that a large part of researchers



	Neurology	Physiology		Fitness		Behavior		Community
	Noise perception	Genetic expression	ROS, Composition	Development	Survival, Fecundity	Mobility	Predation, Feeding	Composition, dynamic
Marine	Gassie et al. (1993) Buskey et al. (2002)	Fields et al. (2019)	Tremblay et al. (2019)	Vereide et al. (in prep.)	McCauley et al. (2017) Fields et al. (2019) Vereide (in prep.)	Fields et al. (2019) Vereide (in prep.)	Kühn et al. (in prep.)	
Freshwater					Prosnier et al. (2022b, 2022c)	Sabet et al. (2019) Rojas et al., (2021) Prosnier et al. (2022c)		Rojas et al. (2022, in prep.)

Figure 1. Summary of the main objectives and the known effects of noises on zooplankton species. The table indicates the studies, described in the article, on noise effects (published and in preparation) on each interesting aspects in marine (upper line with a copepod) and freshwater (lower line with daphnid) systems.

developed, or will develop, studies on the other axes to understand how anthropogenic noises could affect marine communities. To answer these questions researchers could be inspired by many previous works on various zooplankton questions in other close domains, as, for instance, in fundamental ecology, in ecotoxicology, or in parasitology.

2. Various measures on zooplankton organisms

2.1. Noise perception

Before asking how organisms are affected by noises, it seems important to understand how it could detect the noise. Because zooplankton species have not developed a hearing system, they use only external mechanoreceptors. Consequently, the main characteristic of the sound that is important is not the pressure level (i.e., the classical measure in dB), 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 noises (André et al., 2016; Popper and Hawkins, 2018). 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). These methods could allow us to know noise thresholds (both in terms of intensity, frequency, and particle motion). Similar to ecotoxicological methods, Tyack and Thomas (2019) proposed a dose-response method, allowing to link intensity of noises and their impacts. In complementarity, measure of particle motions of various marine noises (airgun, shipping) is mandatory to predict which real noise could affect zooplankton communities, and to perform realistic experiments (in field or in laboratory).

2.2. Physiology

We consider anthropogenic noises as a pollutant that should negatively impact organisms as a stressor. Consequently, many physiological markers of stress could be measured on zooplankton species (from individual experiments to natural community), as it was done for fish with cortisol measures (Nichols et al., 2015; de Jong et al., 2020). For instance, since many years, numerous methods have been developed in ecotoxicology (Handy and Depledge, 1999) and part of them are available for zooplankton species: the copepods seem now marine models in ecotoxicology (Raisuddin et al., 2007; Dahms et al., 2016), as water fleas are as freshwater model (Bownik, 2020; Ebert, 2022). For short- and long-term experiments, we could measure the various parameters as the ROS, the organisms' composition, and the gene expression, providing information regarding the basis of the chain reaction (Dahms et al., 2016). For instance, Lee et al. (2019) used various ROS (Glutathione, GST, Glutathione Reductase, GR, Glutathione Peroxidase, GPx, Superoxyde Dismutase, SOD) to determine how ocean acidification affected *T. japonicus*, and Tremblay et al. (2019) observed similar effects for a chronic noise exposition of the copepods *Acartia tonsa*. Won et al. (2014) measured concentration of a copepods' fatty acid due to UV exposition, whereas Prosnier et al. (2022a) measured the quantity of carbohydrates, lipids and protein of *D. magna* infected by a virus. I have already noted the study of Fields et al. (2019), on the copepod *Calanus finmarchicus* exposed to airgun noise, that shows a higher expression of two genes of unknown effects. Measuring physiological markers should be a good tool for having information on the ability of zooplankton to habituate to noises, i.e., if they return to a basal level after some time of exposition. These physiological alterations could directly result from the noise stress, or be a by-product of behavior modifications.

2.3. Fitness: survival and reproduction

Due to the physiological stress, or due to behavioral modifications, anthropogenic noises could directly affect zooplankton species. These most visible effects, with evident repercussions on zooplankton populations and communities, are effects on fitness, i.e., on survival and fecundity. A great interest of zooplankton species is the possibility to obtain much information in small to large, and controlled to realistic experimentations, on isolated individuals and populations. We could observe effects on eggs, juveniles/larvae, and adult survival, fecundity, and development of each stage (Dahms et al., 2016). There is currently an increase of these measures, see for instance: McCauley et al. (2017) and Vereide et al. (in prep.) for mortality measurement on marine zooplankton, and Prosnier (2022a, 2022b) for both mortality and fecundity on a freshwater zooplankton. Effects on development are also being developed such as the use of size or stage duration (Vereide et al., in prep.).

2.4. Behavior and predation

Behavior is surely one of the main studied aspects of anthropogenic noise impacts, because noise should affect communication and environmental perception of the vertebrates. Zooplankton's behaviors were mainly studied during fish predation experiments, to control if noises affected their vulnerability (Sabet et al., 2015; Rojas et al., 2021; Fernandez Declerck et al., 2022) through behavioral alterations. Moreover, many other behaviors, more or less linked to predation, could be measured in zooplankton studies. For instance, Bownik (2017) proposed to measure swimming speed (see also, in noise experiments, Sabet et al., 2019; Prosnier et al., 2022c; Rojas, in prep.), swimming time, hopping frequency (used for water fleas, but 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. In case of population studies, swarming should also be an interesting measure (Buskey et al., 1996). It should be also interesting to study how their sound production (Kühn et al., 2022) is affected, considering the known effects on marine mammals and fish's one (Putland et al., 2018).

Therefore, noises can affect environmental perception, physiology (energy requirement), and behavior, thus are susceptible to affect a key interaction in communities: the predator-prey interaction. On this aspect, it is mandatory to consider zooplanktonic organisms as prey and as predators. For instance, Fernandez Declerck et al. (2022) studied the effect of motorboat noises on fish functional response (i.e., the predator-prey relationship), but also on the fish's speed, i.e., the predator behavior, and on the chironomid larvae's activity, i.e., the prey behavior). This method of functional response could be used for larger predators, as for damselfly larvae preying on *D. magna* (Villalobos-Jiménez et al., 2017). For the smaller predators, i.e., a large part of the zooplankton, it is possible to measure clearance rate and ingestion rate, as done by Kühn et al. (in prep.), and any particular behaviors as feeding appendage beating (Hong et al., 2012).

3. From individual to community

3.1. Experimental approaches

The investigations, already started, show that zooplankton is affected by noises. However, focusing on individual responses is not enough, it requires also to assess complex communities to obtain global responses (Kunc et al., 2016). For instance, if a noise affects development rate, survival and fecundity, it can therefore alter competitiveness, as Decaestecker et al. (2015) highlighted in case water fleas' infection. Effects on zooplankton can induce trophic top-down effect, through cascading effects, and bottom-up effects (Sommer et al., 2001; Banerji et al., 2015; Wollrab and Diehl, 2015). In fact, mesocosms studies highlighted how the change of biological (community response) and spatial (mesocosms) scales affects dynamics, thus they showed that responses are more complex than expected when increasing the complexity of communities (Gérard Lacroix, pers. comm. with freshwater experiments). The only noise-freshwater mesocosm study (Rojas et al., 2022, in prep.) showed how zooplankton community composition was affected by motorboat noises, despite the absence of a vertebrate predator. In marine systems, the assessment of others stressors, such as acidification, spotlights the study of plankton communities (Spisla et al., 2021). These complex community studies allowed indirect effects on organisms that are, maybe, less impacted by noises, such as the phytoplankton (but see Solé et al., 2021). Other measurements, such as stable isotopes (Boisnoir et al., 2020) could be useful to see how noises affect trophic relationships in complex communities.

3.2. Theoretical approaches

Until now, only experimental approaches were done to understand how noise affects organisms and communities. An exception is the work of Roca (2018), that modelled predator-prey relationships depending on the intensity of the ambient noise. Models are useful tools to study the effects of pollutants (Lamonica et al., 2022) from simple systems, such as a predator-prey interactions (Prosnier et al., 2015) to more complex food webs (Clements and Rohr, 2009). Theoretical studies allow us to better understand mechanisms through which noises affect community structure and stability (Wollrab and Diehl, 2015). For instance, Hulot et al. (2000) used models to understand the importance of bottom-up and top-down effects in freshwater mesocosms. In an infected tri-trophic system, Banerji et al. (2015) used a model to understand that trophic alterations are more due to the host mortality than the alterations of predator behaviors. Moreover, 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 to develop spatially structured models.

4. Discussion

Since the last decades, there has been a growing interest on how anthropogenic noises affect ecosystems, and particularly marine mammals and fish species. This perspective highlights the few studies on zooplankton response in both in marine and freshwater systems, scanning all aspects from individuals to communities. However, there is still huge gaps of knowledge that could be filled with developed methodologies found in ecology, ecotoxicology and parasitology studies. Three important areas should be investigated: (1) determine which noises (structure, temporality) could affect the diversity of zooplankton, (2) use few model organisms to understand if noises affect more or less physiology, fitness and behavior, and (3) understand, through experiments and models, how noises affect structure and stability of zooplankton communities.

It is also important to consider that, in this article, I only focus on zooplankton species (mainly arthropods), however many other groups are, in part of their life cycle, constitutive of zooplankton. These organisms can also be affected by noises when they are zooplanktonic at larval stages (Simpson et al., 2011; Aguilar de Soto et al., 2013; Nedelec et al., 2015), or when they are nekton (fish, Rojas et al., 2021), benthos (crabs, Wale et al., 2013) or fixed (mussels, Hubert et al., 2022). Consequently, due to the diversity of zooplankton communities and their ecological roles, presented methods need to be developed for all of these organisms. This enlarged point of view is mandatory to understand how anthropogenic noises affect marine 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 reviews, and Théophile Turco too; Marta Solé, for the opportunity to write this article, Vincent Médoc, Joël Attia, Marilyn Beauchaud, and Wenjing Wang, the ENES team and AN2022 meeting for many interesting discussions.

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