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Chronic noise unexpectedly increases fitness of a freshwater zooplankton

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Abstract

Although there is an increasing interest in the effects of anthropogenic noise on animals, aquatic studies mainly focus on organisms with hearing systems (marine mammals, fish, great arthropods) while many others of substantial ecological importance are not considered. Here we show that the water flea *Daphnia magna*, a widespread zooplankton species serving as food source for higher trophic levels, could be affected by noise pollution in a way that we did not expect. We found that isolated individuals exposed to a continuous broadband sound have a higher survival and fecundity, thus a higher fitness. We also found that they are slower than individuals not exposed to additional noise. It could be that the energy saved from reduced mobility is reallocated to fitness. In natural systems, this reduced velocity should result in a more negative outcome for *Daphnia*'s fitness due to competition and predation. Our result highlights that, despite the absence of a known hearing system, a small crustacean can be affected by noise. Consequently, anthropogenic noise can not only affect communities through top-down cascading effects, when it changes the behaviour of top-predators like fish, but also via bottom-up effects with alterations in zooplankton.

Keyword: *Daphnia magna*, Acoustic pollution, Broadband noise, Fitness, Mobility.

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1. Introduction

The increasing anthropic pressure on our aquatic ecosystem leads not only to chemical pollution but also to a newly recognized pollution: man-made noise (Hildebrand, 2009; Frisk, 2012). In the last decade, various scientific researches have highlighted the negative effects of terrestrial and aquatic noise pollution (Shannon et al., 2016; Popper & Hawkins, 2019), with a special focus on the marine ecosystem (Williams et al., 2015). Studies on noise effects are dominated by works on marine mammals' communication and behaviour (Richardson et al., 1985; Erbe et al., 2016; Mortensen et al., 2021), and byon fish communication (Radford et al., 2014), physiology (Wysocki et al., 2006), behaviour (Nedelec et al., 2017; Rojas et al., 2021), and fitness (Read et al., 2014; de Jong et al., 2020) - mainly on marine species rather than freshwater species (Mickle & Higgs, 2018). It is now admitted that noise pollution could greatly disturb marine and freshwater vertebrates. However, vertebrate groups seem overstudied compared with others, if we consider their relative biomass (Jerem & Mathews, 2021), and knowing effects on various taxa and functional groups is mandatory to be able to understand how noise pollution affects aquatic ecosystems. For instance, rarer is the research on the effects of anthropogenic noise on other aquatic taxa such as crustaceans (Celi et al., 2013), molluscs (Hubert et al., 2022) and cnidarians (Solé et al., 2016).

Many invertebrate taxa are constitutive of an ecologically important group, potentially used as bioindicators: the zooplankton (Jeppesen et al., 2011; Muñoz-Colmenares et al., 2021). Zooplankton gathers organisms from various taxa including cnidarians (jellyfish), molluscs (larvae), fish (larvae), insects (larvae) and crustaceans (larvae and adults). These organisms have, generally, no hearing system, however they have external mechanoreceptors and thus should be able to detect sound vibrations (Popper et al., 2001). For instance, copepods have mechanoreceptors on their antennae that detect sound vibrations (Gassie et al., 1993; Weatherby

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& Lenz, 2000), and show behavioural reaction to vibrations (Buskey et al., 2002) and to sound (Waggett & Buskey, 2008). Environmental vibrations are used as cues to detect predators (Buskey et al., 2011). Consequently, because zooplankton are able to perceive vibrations, noise vibrations could affect physiology, behaviour and fitness (fecundity and survival) of zooplankton. McCauley et al. (2017) showed that air guns (very high and acute sound, i.e., from 150 to 180 dB SEL) kill zooplankton (various marine species like copepods, cladocerans, or krill larvae). Short-term studies showed no effect of boat noise (acute exposition of low sound, i.e., 126 dB SPL) on *Daphnia magna* behaviour (Sabet et al., 2015, 2019) whereas, in insects species, boat noise increases the body rotations of *Chaoborus* sp. larvae (Rojas et al., 2021) and increases damselfly larvae predation (Villalobos-Jiménez et al., 2017).

Effects of chronic (i.e., long-term) noise pollution on zooplankton remain unknown (Hawkins et al., 2015) while for short-lived zooplankton organisms, a chronic exposition means an exposition along all their life. We could consider noise as a stressor, on the one hand because all listed effects are negative, one the other hand because noise should continuously stimulate mechanoreceptors leading to much information analysis and an unability to obtain other information to the environment as predator attacks. Thus, as a stressor, the noise could affect development and behaviour, as well as fitness (fecundity and survival). There are, in general, very few studies on noise effects on fitness, and the rare observed effects on behaviour and physiology after short-term exposure does not preclude adverse effects on fitness under chronic noise pollution. In this study, we exposed a common freshwater zooplankton frequently used for ecotoxicological studies (offering many information on how various stress affect *D. magna*), the water flea *Daphnia magna* (Lampert, 2011; Reynolds, 2011; Bownik, 2017, 2020; Tkaczyk et al., 2021) to a continuous broadband noise along all their life (around a month). Therefore, to evaluate the effects on *D. magna*, we measured their survival, their fecundity, their size, and their speed. If noise affects *D. magna* as a stressor. We expected under noise exposure a

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reduction of fitness (lower survival and/or fecundity). Effects on behaviour could be a direct consequence of the stress or environmental perception (because noise stimulates strongly the mechanoreceptors (Gassie et al., 1993)), or a more indirect effect thought of developmental alteration (de Soto et al., 2013; Nedelec et al., 2014), as lower size leading to a lower speed (Baillieul & Blust, 1999).

2. Material and Methods

2.1. Collection and maintenance of organisms

Daphnia magna were purchased from Aqualiment (Grand Est, France) two months before the first experiment. They were stored in two 20-L aquariums (50 *D. magna*/L), filled with aged tap water at 18°C, and under a 12:12 light:dark cycle. *D. magna* were fed each two days with 0.05g powder of algae, a mix of 80% of *Arthrospira platensis* and 20% of *Aphanizomenon flos-aquae* (Algo'nergy® Spiruline + Klamath, from organic agriculture), per aquarium.

2.2. Fecundity and mortality

D. magna 24-h newborns were isolated in microcosms during all their life and exposed to the acoustic treatments during which reproductive success and survival were assessed. Gravid *D. magna* were collected (from the storage aquarium) and isolated in 50mL jars containing Volvic® water, known as a good medium for *D. magna* (B. Prosnier from Eau de Paris, a french water industry, pers. com.). Newborns (<24h) were transferred individually into 150mL glass-microcosms, closed on top with a mesh net to promote water and sound exchange while preventing escape. Exposure took place in four 90L rectangular tanks (75 x 60 x 20 cm) filled with aged tap water at 20-22°C under a 12:12 light:dark cycle and equipped with an underwater loudspeaker (UW30 Electro Voice®) in the top-middle at water surface. Each tank received 18 glass-microcosms placed at equal distance (10 cm) from the speaker. We broadcasted silence in two mesocosms (control) and noise in the two others (treatment, see 2.4 for further detail).

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To account for parental and genetic effects, for each *D. magna* mother, half of the newborns were allocated to the control and the other half to the treatment. Neonates were fed every two days with 2 ml of algae (1g/L), and glass-microcosms' water was changed once a week. Each day, we controlled if individuals were alive, if they produced newborns – if that, newborns were counted and taken off. In case of death during the first days (i.e., before the first hatching of the experiment), dead *D. magma* were replaced by newborns to increase the number of replicates. A total of 116 *D. magna* adults were used to obtain a total of 204 neonates, with 119 allocated to the control and 85 to the treatment.

2.3. Speed and size

We determined the speed and size of *D. magna* around day 15. We simultaneously put four individuals from their microcosm in a 4-well dish (dxh 6x1.5 cm) disposed in a 20L-aquarium filled with aged tap water, under natural light. An underwater loudspeaker (UW30 Electro Voice®) was located on the left and the dish was placed on the right side. After an acclimatisation period of 30-sec, an audio track of four minutes with successively 1 min of silence, 1 min of noise, 1 min of silence and 1 min of noise was broadcasted. Thus, we tested together effects of chronic exposition (in their microcosm) and acute exposition of 1 min (exposition in the 4-well dish).

D. magna were filmed using a GoPro Hero 4 Session camera and videos were analysed using the Kinovea software (0.9.1 beta). The software gave instantaneous velocity every 33 ms and we used the videos to assess body size from the top of the head to the base of the caudal spine.

2.4. The acoustic broadcasts: Silence and Noise

Two stereo WAV files were created for the experiments, one composed of silence and the second composed of a continuous broadband noise (100-20,000 Hz) generated in the Adobe Audition software (13.0.0.519, Adobe Systems Inc., Mountain View, CA, USA). Sounds were

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played by an underwater UW30 loudspeaker (Electro Voice®) connected to an amplifier (DynaVox® CS-PA 1MK), itself connected to a ZOOM H4next Handy recorder.

To assess the sound spectrum and intensity in each glass-microcosm, sounds were recording with a hydrophone (Aquarian Audio H2A-HLR Hydrophone, frequency response from 10 to 100 kHz) coupled to a Zoom® H4n previously calibrated with a hydrophone (8104, Brüel & Kjær, Naerum, Denmark; sensitivity –205 dB re. 1 V µPa−1; frequency response from 0.1 Hz to 180 kHz) connected to a sound level meter (Bruël & Kjaer 2238 Mediator, Naerum, Denmark). Broadband noise spectrum was corrected (Fig. 1a), to be as close as possible to a white noise between 100 to 20,000 Hz, using Adobe Audition 2020 software (13.0.0.519, Adobe Systems Inc., Mountain View, CA, USA). The average sound level (in equivalent

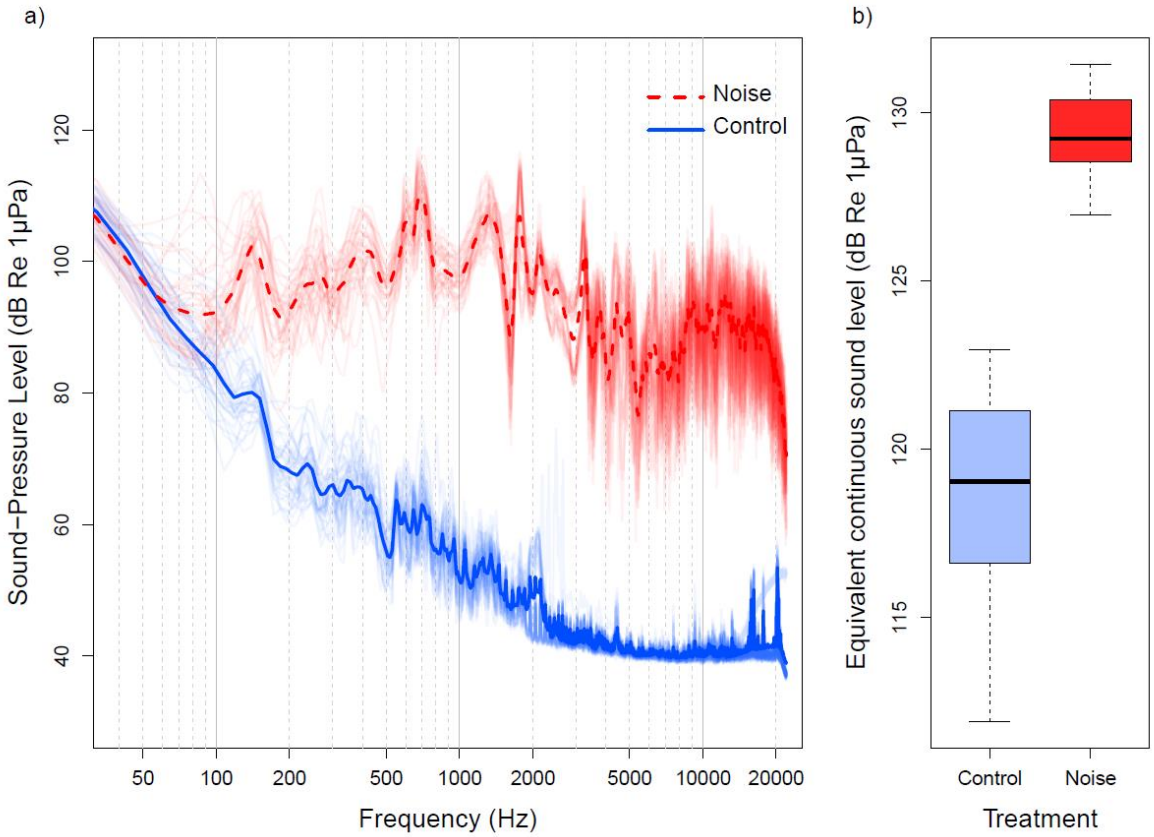

Figure 1. Acoustic treatments. a) Sound measures in the microcosms. Thick lines are means for control (full blue line) and noise treatment (dashed red line). Transparent lines are original sound spectrum for each microcosm. b) Sound levels in all microcosms. Central bars represent the median, boxes the interquartile range, and dots the outliers (> 1.5 times the interquartile range).

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continuous sound level, Leq) was around 118 dB Re 1µPa in the control condition and around 128 dB Re 1µPa in the treatment condition (Fig. 1b).

2.5. Statistical analyses

Statistical analyses were performed using the R software (version 4.0.3) with a significant threshold at 5%. We performed a survival analysis (Log-Rank test) to compare survival (death age) and age at maturity (first clutch age) between the two noise conditions. Because data were non-normal, according to a Shapiro test, we used a Wilcoxon signed-rank test on clutch frequency (i.e., mean time between two clutches) and mean clutch size. The effect of the treatment on the total numbers of clutches and offsprings along life were modelled using a GLM with log link function for quasi-Poisson distribution. The size of individuals was compared with a t-test (after testing normality with a Shapiro test and homoscedasticity with a Bartlett test). For *D. magna* speed, we performed two analyses. First, we tested the effect of noise exposition (and also controlled for size and age effects) on the average speed during the four minutes with a type II Analysis of Variance (ANOVA, after controlling for normality and homoscedasticity). Then, we tested the effects of both chronic and acute noise exposition by comparing the mean speed during each one-minute period (from the 5th to the 55th s) with Tukey contrast on a Linear Mixed Model with individual as random effect.

3. Results

3.1. Fecundity and mortality

Daphnia magna survival was significantly higher with broadband noise compared to the control (p.value = 0.002, Fig. 2a). About fecundity, clutch size was significantly higher under noise than without noise (p-value = 0.01, Fig. 2c) but there was no difference in clutch frequency (p-value = 0.99, Fig. 2b) nor in age at maturity (p-value = 0.3). Overall, noise

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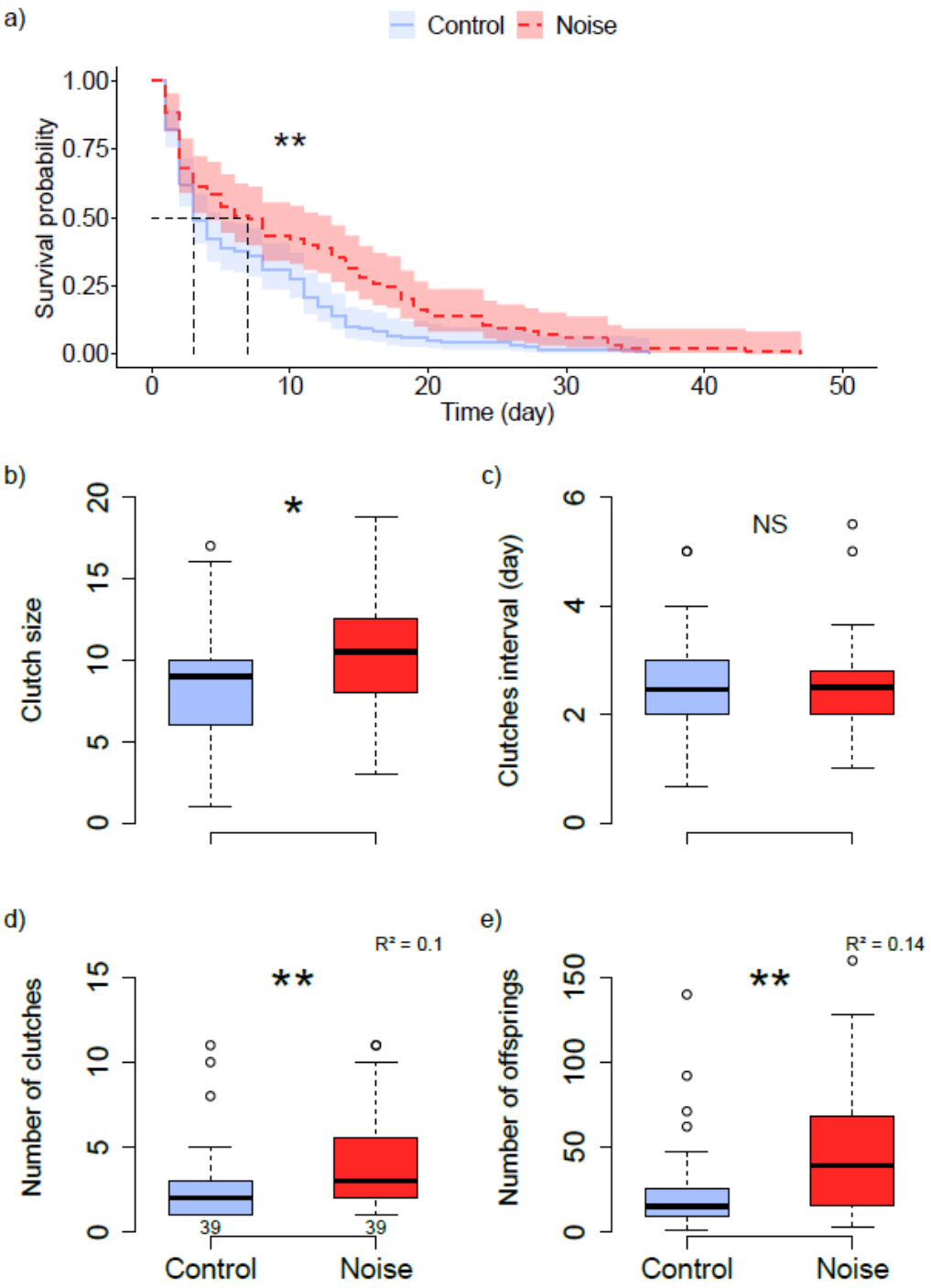

Figure 2. Effects of noise treatments on *Daphnia magna* survival and fecundity. a) Survival of *D. magna*; b) clutch size; c) clutch frequency; d) total number of clutches during lifetime; and e) total number of offspring during lifetime. Numbers in d) are the numbers of *D. magna* for the two treatments. a) Representation according to the Kaplan-Meier method; b-e) central bars represent the median, boxes the interquartile range, and dots the outliers (> 1.5 times the interquartile range). Statistical analysis: dot P < 0.1, * P < 0.05; ** P < 0.01; NS P>0.1.

exposition significantly increased the total number of clutches (p-value = 0.01, Fig. 2d) and the total offspring production (p-value = 0.001, Fig. 2e).

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3.2. Size and speed

We did not observe any difference in body size between the two noise conditions (p-value = 0.675). Concerning speed, *D. magna* chronically exposed to broadband noise were 16% slower than control ones (p-value = 0.008, Fig. 3) – a result not explained by differences in size or age (p-values > 0.36). About the acute exposition, i.e., when considering the four sequences of silence and broadband noise, the only significant speed reduction is between control individuals and those reared with noise during the second silence period (p-value = 0.031). Otherwise, there was no average speed difference between the two groups of *D. magna* in each acute exposition (p-values > 0.15), nor within the two groups of *D. magna* between each acute exposition (p-values > 0.88).

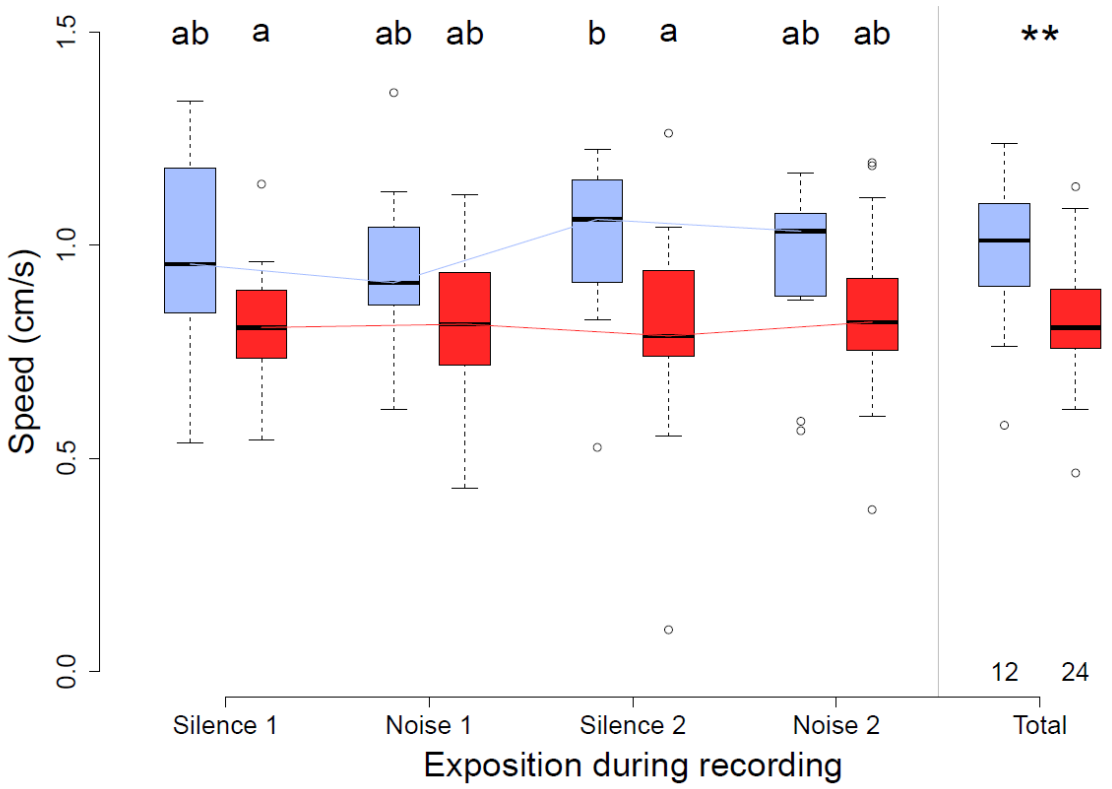

Figure 3. Effects of noise treatments on *Daphnia magna* mobility depending of living conditions, i.e., from control (in light blue) and noise treatment (in dark red). The *D. magna* mean speed (in cm/s) during the four sequences of 1 min of silence (Silence 1 and Silence 2) and noise (Noise 1 and Noise 2) broadcast, and during the total of 4 min (Total). Numbers are the number of *D. magna* from each treatment. Central bars represent the median, boxes the interquartile range, and dots the outliers (> 1.5 times the interquartile range). Lines rely median speed of the same *D. magna* along the 4 min. The same letters indicate groups that are not significantly different at 0.05 between the four sequencies and the two group of *D. magna*. ** P<0.01 for the total mean

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4. Discussion

In this work, we experimentally studied effects of a continuous broadband noise on *Daphnia magna*, a widespread zooplankton serving as a basal resource in freshwater food webs. Because sound could be considered as a stressor, we expected reduced fitness either because of decreased lifespan, fecundity or both. Surprisingly, we found that isolated individuals from the treatment showed higher survival and larger clutch size, leading to higher offspring production. This unexpected effect could result from an alteration in energy allocation as we also found reduced mobility under noise.

Both fitness parameters, survival and fecundity, are greater during the noise exposition. It is an unexpected result because we considered noise as a stressor (due to the over-stimulation of the mechanoreceptor leading to a perceived stressful environment), and thus should negatively affect individuals as airguns done (McCauley et al., 2017). Moreover, we also find a reduced speed of individuals exposed to noise, contrary to Sabet et al. (2019) which observed any effect. Both the sound type and intensity (as they suggested - we exposed *D. magna* to a more intensive sound on a larger frequency range) and the chronic exposition could explain this difference. We did not identify the cause of the speed difference, because the size, highly linked to the mobility (Dodson & Ramcharan, 1991), is not affected by the chronic exposition. Perhaps, they are slower because individuals in noise are not able to perceive differences in environmental vibrations (due to the over-saturation of their mechanoreceptors), and thus are like blind (as we are in a dark environment). This lower speed could explain the higher fitness of exposed *D. magna*: slower individuals save energy that could be reallocated for higher survival and fecundity. A trade-off between mobility and fitness was already reported for *D. magna* (Prosnier et al., 2022) and for the codling moth *Cydia pomonella* (Gu et al., 2006). However, we need to keep in mind that they are isolated with food *ad libitum*; probably, in more realistic

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environment, the lower speed could have opposite results, because mobility is important for *Daphnia spp.*: it allows them to find food, to escape to predators, and more generally to do their diel migration (Larsson & Kleiven, 1996; Dodson et al., 1997; O'Keefe et al., 1998; Roozen & Lürling, 2001; Chang & Hanazato, 2003). This prediction is consistent with a lower abundance of daphniids in a zooplankton community exposed to chronic boat noise (Rojas et al., 2022), despite the absence of observed effects by Prosnier et al. (2022) with chronic boat noise, but asks how other zooplankton species are affected.

More than the direction of the effects, the main result is to show that chronic noise exposition could affect an important zooplankton. Consequently, it highlights that to study the effects of various acoustic pollution on ecosystems it is mandatory to consider effects on all trophic levels, from plants (Solé et al., 2021) to predators (Rojas et al., 2021), passing by zooplankton. A second interesting point, already discussed for noise effects, is the type of sound, and their various effects depending of phylogenetic and/or functional groups of exposed species. Nichols et al. (2015) showed that fish are more stressed (higher cortisol concentration) when noise is intermittent and random (e.g., boat noise) compared to continuous and regular sound (e.g., broadband sound). However, opposite to our experiment with broadband noise, a similar experiment with boat noise, known to affect both fish and insect larvae (Rojas et al., 2021), showed no effect on *D. magna* survival nor fecundity (Prosnier et al., 2022). Thus, it suggests that an unpredictable noise (intermittent and irregular) should have more effect on fish (due to their habituation ability, e.g., Wysocki et al., 2006; Nichols et al., 2015, whereas a permanent intense sound (continuous and regular) should have more effect on small arthropods. Thus, the complexity of the ecosystem response to anthropogenic noise (various frequency and various temporal patterns like boats and turbines) could be explained, and thus studied, by considering the diverse response of each species, or at least each type of organism.

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