Chronic broadband noise increases the fitness of a freshwater zooplankton

Loïc Prosnier[*1,2], Emilie Rojas[1,3], Olivier Valéro[1] and Vincent Médoc[1]

1. ENES Bioacoustics Research Laboratory, CRNL, University of Saint Etienne, CNRS, Inserm, Saint-Etienne, France
2. France Travail, Saint-Etienne, France.
3. Departement of Biology, Norwegian University of Science and Technology (NTNU), Trondheim, Norway.

* 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:

- Loïc Prosnier: 0000-0001-5576-3601
- Emilie Rojas: 0000-0001-8236-0517
- Vincent Médoc: 0000-0002-4888-1914

Abstract

Although there is an increasing interest in the effects of anthropogenic noise on underwater wildlife, most studies focus on marine mammals and fishes while many others taxa of substantial ecological importance are still overlooked. This is the case for zooplankton species which ensure the coupling between primary producers and fishes in pelagic food webs. Here, we measured lifespan, reproduction and mobility of laboratory-raised water fleas *Daphnia magna*, a widespread freshwater zooplankton species, in response to continuous broadband noise. Surprisingly, we found a significant increase in survival and fecundity, leading to a higher fitness when considering total offspring production and a slight increase in population growth rate, according to the Euler-Lotka equation. Exposed water fleas were found slower than control individuals and we hypothesised that the energy saved from reduced mobility was reallocated to survival and fecundity. Our results can have implications in aquaculture where the acoustic environment receives little attention. Chronic broadband noise can be associated with certain human activities but the consequences on natural *Daphnia* populations might differ as reduced velocity could have negative outcomes when considering competition and predation. Our result highlights for the first time that, despite the absence of a known hearing system, a zooplanktonic crustacean is affected by chronic noise.

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

1. Introduction

Underwater sounds can be of biological (i.e., vocalisations), geological (i.e., rain, wind) and anthropogenic (i.e., human activities) sources and serve as important cues for reproduction, orientation, settlement, territoriality and foraging in both vertebrates and invertebrates (Popper et al., 2020). Anthropogenic noise is now recognised as a ubiquitous pollutant (Hildebrand, 2009; Frisk, 2012) as well as light or chemical pollutants. The noise emissions from seismic surveys, sonar, or pile-driving activities are short and intense ("peak") while those from recreational and commercial shipping or wind farms are less intense but last longer ("continuous" and “intermittent”) (Francis & Barber, 2013). The frequency range of anthropogenic noise (<2 kHz) overlaps with that used by most animals (Duarte et al., 2021) and many studies document the negative effects on terrestrial and aquatic wildlife (Shannon et al., 2016; Popper & Hawkins, 2019), with greater attention to the marine environment compared to freshwaters (Williams et al., 2015; Solé et al., 2023 ; but see Mickle & Higgs, 2018). Examples of noise-induced alterations in behaviour and physiology abound in the literature (Richardson et al., 1985; Wysocki et al., 2006; Read et al., 2014; Radford et al., 2014; Nedelec et al., 2017; Rojas et al., 2021) but consequences beyond the individual level, for instance on population and community dynamics, remain to be explored (Reid et al., 2019).

Another critical step to take to better understand the ecological impact of noise is to get knowledge on the response of invertebrates (Jerem & Mathews, 2021; Solé et al., 2023). There have been calls for more research on invertebrates (Morley et al., 2014) and despite a growing number of studies on crustaceans (Celi et al., 2013), molluscs (Hubert et al., 2022), cnidarians (Solé et al., 2016), and insects (Villalobos-Jiménez et al., 2017), other groups have received little attention so far. This is the case for zooplankton (Prosnier, 2022; Vereide & Kühn, 2023), which includes from small protozoans to large metazoans with gelatinous species (jellyfish,

salps and ctenophores), rotifers, crustaceans but also larvae of fishes, molluscs, bryozoans, and insects. Zooplankton has a pivotal role in the functioning of pelagic food webs (Ratnarajah et al., 2023) through the coupling of primary producers with consumers at higher trophic levels, and is commonly used as bioindicator in ecological quality assessment (Jeppesen et al., 2011; Muñoz-Colmenares et al., 2021). Although zooplankton species generally do not have dedicated hearing systems (but see the chordotonal organ in some crustaceans), they possess external mechanoreceptors that can detect changes in particle motion and acoustic pressure (Popper et al., 2001; Nedelec et al., 2016; Solé et al., 2023). For instance, copepods have such receptors on their antennae (Gassie et al., 1993; Weatherby & Lenz, 2000) and have shown behavioural changes to emitted vibrations in water (Buskey et al., 2002) and to sound (Waggett & Buskey, 2008). Particle motion is an important cue for zooplankton species because it enables them to detect predators (Chan et al., 2010; Buskey et al., 2011).

Available evidence suggests that noise pollution can have contrasting effects on zooplankton depending on the species and noise features. Short-term exposures (less than four days) to air gun (intense acute noise, 150-180 dB SEL Re 1 µPa) result in the mortality of several marine species (McCauley et al., 2017) and negative effects on copepod physiology and development (Fields et al., 2019; Vereide et al., 2023). Short exposures to less intense motorboat noise (i.e., few days exposure at 126 dB RMS Re 1 µPa) do not affect the behaviour of the water flea *Daphnia magna* (Sabet et al., 2015, 2019; Rojas, Prosnier, et al., 2023) but decrease copepod feeding rate (Kühn et al., 2023) and rotifer fecundity (Aspirault et al., 2023). For short-lived organisms, noise exposure can easily last a substantial part of the lifespan or even exceed it. When working on zooplankton, it is therefore important to consider the consequences on fitness as the absence of behavioural response does not preclude detrimental effects on survival and/or fecundity. In a previous study, we exposed the water flea *Daphnia magna*, a common freshwater zooplankton often used as model species in ecotoxicological studies (Lampert, 2011;

Reynolds, 2011; Bownik, 2017, 2020; Tkaczyk et al., 2021; Ebert, 2022), to a playback of nautical activity from birth to death and found no effect on survival nor fecundity (Prosnier, Rojas, et al., 2023). To our knowledge, there are only two other long-term studies on zooplanktonic community (including or not fish as top predator) exposed to boat noise (Rojas, Desjonquères, et al., 2023; Rojas, Gouret, et al., 2023). They show complex effects with different impact on the various species.

Considering the successive boat passages as a succession of acute stressors, whilst being not exactly the same, nautical activity could be classified as a chronic intermittent stress (Ladewig, 2000). If the impact of noise is dose-dependent (Tyack & Thomas, 2019), for instance through the simulation of mechanoreceptors, then a continuous exposure to noise such as near water catchment systems or in aquatic husbandries could be more impactful than nautical activity (intermittent noise (Prosnier, Rojas, et al., 2023; Vereide et al., 2023)) and one-day exposure (acute noise (Fields et al., 2019; Kühn et al., 2023)). To test this hypothesis, we did a laboratory experiment where we exposed *D. magna* to continuous broadband noise for their entire life (about one month, from birth to death). We measured fecundity parameters through clutch size and frequency, total offspring production, survival, size and swimming speed. Based on the assumption that continuous stimulation has long-term costs, we expected a reduction in fitness in exposed daphnia.

2. Material and Methods

2.1. Animal collection and maintenance

Daphnia magna were purchased from Aqualiment (Grand Est, France) two months before starting experiment. They were stored in two 20-L aquariums (50 *D. magna*/L), filled with aged tap water (see on Zenodo repository for the physicochemical composition (Prosnier et al., 2022)) at 18°C, and under a 12:12 light:dark cycle. Every two days, *D. magna* were fed 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

The protocol is similar to that of Prosnier, Rojas, et al. (2023). Gravid *D. magna* were collected (from the storage aquarium) and isolated in 50-mL 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 individually transferred into 150-mL (5.6 x 8.6 cm) glass-microcosms, sealed at the top with a 0.3-mm mesh net to promote water and sound exchange while preventing escape. The experiment took place in four black rectangular plastic tanks filled with 90 L (75 x 60 x 20 cm) of 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 middle just below the water surface. Each tank received 18 glass-microcosms placed on the bottom, equidistant from each other, and all at 20 cm from the speaker. We broadcasted silence in two tanks (control) and broadband noise in the two others (noise treatment). Control *D. magna* therefore experienced laboratory background noise (see section 2.4 for further detail). To account for the parental and genetic effects, half of the newborns from each single mother were allocated to the control and the other half to the treatment. They were fed every two days with 2 ml of algae (1g/L), and water in the glass-microcosms was changed once a week. Every day, the survival of each individual was checked and the offspring (when there were) were counted and removed. In case of death during the eight first days (i.e., before the first hatching of the experiment), dead *D. magma* were replaced by 24h-newborns to keep the number of replicates. We used a total of 116 *D. magna* adults to obtain a total of 204 neonates, with 119 allocated to the control and 85 to the treatment (the different number of individuals in the two treatments result in a difference in the death quantity of the eight-days individual, i.e., the replacement previously described). Both in the control and in the noise treatment, 39 individuals reached maturity and

produced offspring at least once. The experiment lasted until the death of the last individual (the oldest *D. magna* survived 47 days).

From these daily survival and fecundity data, we analysed the effect of noise on populational growth using Euler-Lotka equation, $\sum f_x m_x e^{-rx} = 1$, with f_x the fecundity at age *x* (i.e., the number of offspring), m_x the survival at age *x* (i.e., the proportion of survival individuals), and *r* the intrinsic rate of increase. We considered each treatment as a population and calculated for each the reproductive output R_0 ($R_0 = \sum f_x m_x$), the generation time G_t $\left(G_t = \frac{\sum x f_x m_x}{\sum f_x m_x}\right)$, and the intrinsic rate of increase *r* $\left(r = \frac{\log R_0}{G_t}\right)$ (Leung et al., 2007; Starke et al., 2021; Prosnier, Rojas, et al., 2023).

2.3. Speed and size

We measured the speed and size of *D. magna* around day 15. We simultaneously put four individuals from their microcosm in a 4-well dish (6 cm diameter x1.5 cm heigh) placed in a 20-L aquarium (20x25x40cm) filled with aged tap water, under natural light. An underwater loudspeaker UW30 was located on the left and the dish was placed on the right side, on a brick to be in the middle of the aquarium. After an acclimatisation period of 30 s, a four-minutes audio track (WAV file) was played, comprising successively 1 min of silence, 1 min of noise, 1 min of silence and 1 min of noise.

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

2.4. Sound conditions

Two stereo WAV files were created for the experiment: one made of silence (to take into account electromagnetic effects) and the second of continuous broadband noise (100-

20,000 Hz) generated in the Adobe Audition software (13.0.0.519, Adobe Systems Inc., Mountain View, CA, USA). The audio tracks were played by an UW30 underwater loudspeaker (Electro Voice®) connected to an amplifier (DynaVox® CS-PA 1MK), itself connected to a ZOOM H4next Handy recorder.

To assess acoustic spectra and noise levels in each glass-microcosm, we recorded the playbacks with a hydrophone (Aquarian Audio H2A-HLR Hydrophone, frequency response from 10 to 100 kHz) coupled to a Zoom® H4n, which was 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). Because the characteristics of the experimental units induce acoustic distortion, we adjusted the spectrum of the broadband noise (Fig. 1a) to make

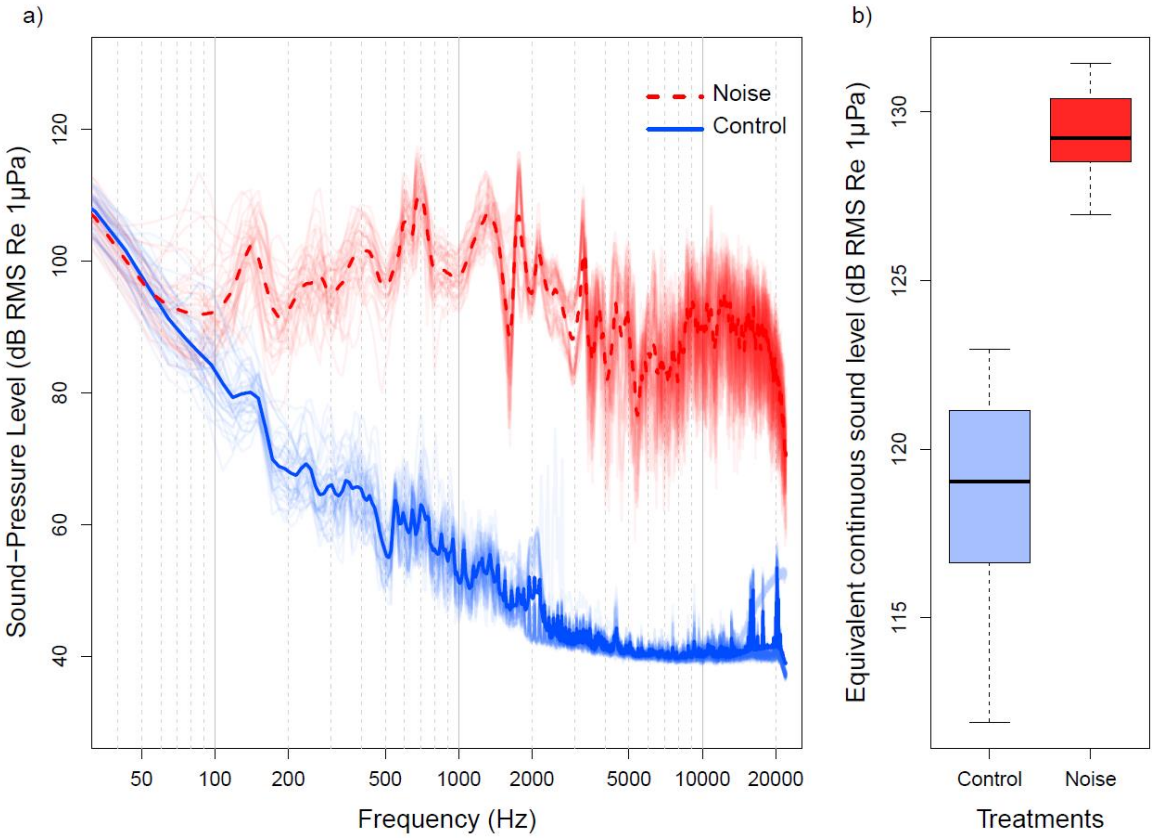

Figure 1. Microcosm acoustic treatments. a) Averaged (thick lines) sound pressure spectra for the control (full blue line) and noise (dashed red line) treatments. Transparent lines are the original sound spectra for each microcosm. b) Box plot of the sound levels in all microcosms with central bars showing the medians, boxes the interquartile ranges and dots the outliers (> 1.5 times the interquartile range).

it as close as possible to a white noise between 100 to 20,000 Hz, using the equalizer of Adobe Audition 2020 software (13.0.0.519, Adobe Systems Inc., Mountain View, CA, USA). The average sound pressure level (in equivalent continuous sound level, Leq) was around 118 dB RMS Re 1µPa in the control condition and around 128 dB RMS Re 1µPa in the treatment condition (Fig. 1b). We cannot measure particle motion, as it is the main noise characteristic for non-hearing species (Nedelec et al., 2016), however the difference of sound levels between treatments based on sound pressure level should be qualitatively relevant (Olivier et al., 2023).

2.5. Statistical analyses

Statistical analyses were performed using the R software (version 4.2.2) with a significant threshold at 5%. According to our data, we analysed separately the effects of noise on mortality (death age and adult survival) and fecundity (age at maturity, clutch frequency, mean clutch size, and daily clutch size). We considered the total production of offspring, considering both survival and fecundity, as a proxy for fitness. We performed a survival analysis (Log-Rank test) to compare survival (death age and adult duration) and age at maturity (first clutch age) between the two noise conditions. For the fecundity parameters, we only considered individuals that reached maturity. We used a linear mixed-effect model, with clutch frequency (i.e., mean time between two clutches) and mean clutch size as response variable, and tanks and mother (i.e., clone effect) as random effects. We analysed the effect of both, noise and age, on the daily clutch size with a type II analysis of variance, followed by a Wilcoxon pairwise test between the two noise treatments for each age. The effect of the treatment on the total number of clutches and offspring along life were modelled with a generalized linear mixed-effects models, with tanks and mother as random effects and a log function as the link function for the Poisson distribution. We also obtained the growth as fitness proxy at population scale using the Euler-Lotka equation (but with no statistical analysis due to absence of populational replicates). The

difference in body size between the two noise treatments was tested 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 exposure (including 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 (i.e., with *D. magna* coming from the noisy microcosms) and acute (i.e., with *D. magna* coming from the noiseless microcosms) exposure to noise by comparing the mean speed during each one-minute period of treatment (from the 5th to the 55th s) using Tukey contrast on a linear mixed model, with individual ID as random effect.

3. Results

3.1. Fecundity and mortality

Survival of *Daphnia magna* was significantly higher with broadband noise compared to the control (p-value = 0.002, Fig. 2a, Table 1), as adult duration was longer (p-value = 0.015) with four additional days (median value) with noise. Regarding fecundity, mean clutch size was significantly higher under noise than in the control (p-value = 0.005, Fig. 2b) but there was no significant difference in clutch frequency (p-value = 0.82, Fig. 2c) nor in age at maturity (p-value = 0.3), with nine days for the two groups. Noise had no effect on daily clutch size (all p-values > 0.17, Fig. A1), which was only influenced by age (p-value < 0.001). Overall, noise exposure significantly increased the total number of clutches (p-value = 0.01) and the total offspring production (p-value = 0.009, Fig. 2d,e).

Using the Euler-Lotka equation to study population growth confirmed that the reproductive output (R_0) was higher for the noise treatment (39 offspring) compared to the control (12 offspring). The generation time (G_T) seemed three days longer for the noise treatment (17 days)

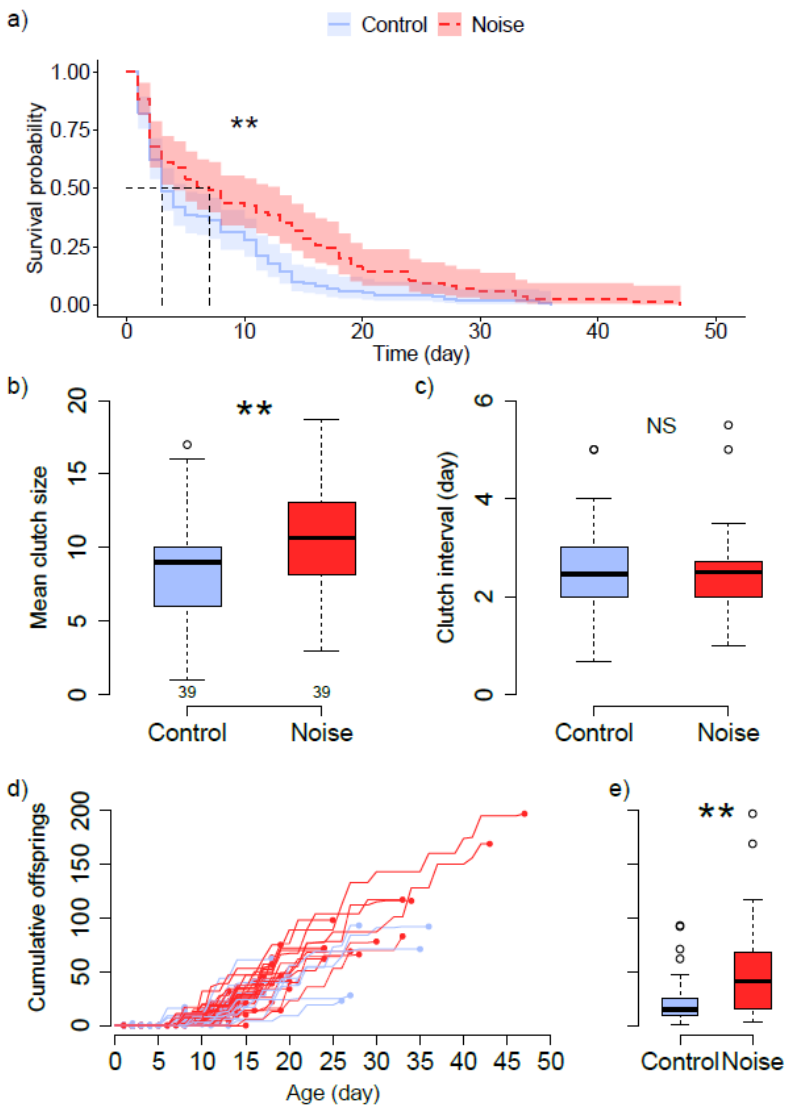

Figure 2. Survival and fecundity of laboratory-raised *Daphnia magna* exposed to broadband noise. a) Survival of *D. magna* according to the Kaplan-Meier method; b) mean clutch size; c) clutch frequency; d) dynamic of offspring production; and e) total number of offspring during lifetime. Numbers in b) are the quantities of *D. magna* for the two treatments (light blue: control, dark red: broadband noise) for b, c and e. b, c, e) box plots with central bars for the medians, boxes for the interquartile ranges and dots for the outliers (> 1.5 times the interquartile range). Statistical analysis: ** P < 0.01; NS P>0.1. See Table A1 for the statistical values.

compared to control (13.9 days). The combination of these two parameters resulted in a higher intrinsic rate for the noise treatment (0.22 day^{-1}) than for the control (0.18 day^{-1}).

3.2. Size and speed

We did not observe any difference in body size between the two noise conditions (p-value = 0.675, Table A2). Regarding speed, *D. magna* chronically exposed to broadband noise in the

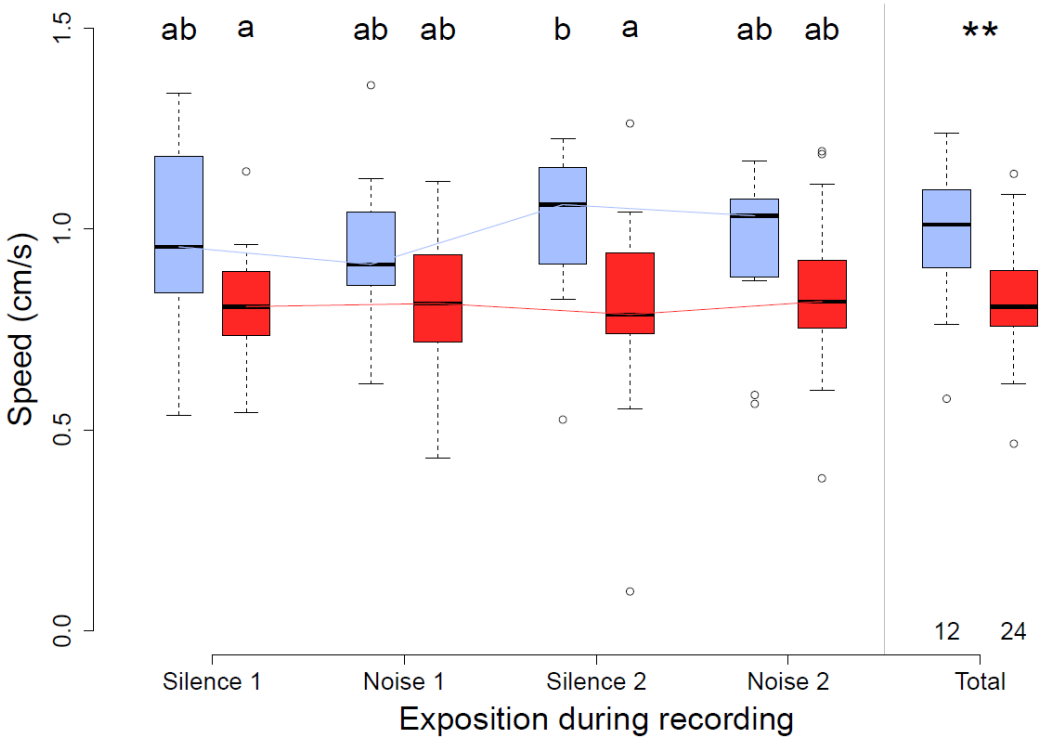

Figure 3. Swimming speed of *Daphnia magna* exposed to successive silent and noisy (broadband noise) periods and coming from control (in light blue) or noisy (in dark red) microcosms. Median and interquartile ranges (with dots for the outliers: > 1.5 times the interquartile range) of *D. magna*'s speed (in cm/s) during each of the four 1-min sequences of silence (Silence 1 and Silence 2) and noise (Noise 1 and Noise 2), and, in the right, during the total of 4 min (Total). Numbers are the quantities of *D. magna* from each treatment. Paired data are shown with lines. The same letters indicate groups that are not significantly different at the level of 0.05 between the four sequencies and the two groups of *D. magna*. ** P<0.01. See Table A3 for the statistical values.

mesocosms were 16% slower than control ones, both in the whole experiment (p-value = 0.008, Fig. 3 and Table A3), and during the second period of silence (p-value = 0.031) – a result not explained by differences in size or age (p-values > 0.36). For the acute exposure, i.e., the 1-min of noise, there was no difference in mean speed between the two groups of *D. magna* in each acute exposure (p-values > 0.15), nor within the two groups of *D. magna* between each acute exposure (p-values > 0.88).

4. Discussion

We did a playback experiment to study the effects of continuous broadband noise on the fitness and mobility of laboratory-raised *Daphnia magna*, a widespread freshwater zooplankton

coupling primary producers with higher trophic-level consumers of the pelagic food web. It seems to be the first study to show that long-term noise exposure could affect fitness and behavior of a zooplanktonic species. However, contrary to our prediction that constant stimulation would have long-term costs ultimately decreasing fitness, we found that exposed individuals had a higher survival and a larger clutch size, resulting in higher offspring production. Noise also made *D. magna* less mobile and it might be that the energy saved from reduced mobility was reallocated to survival and reproduction.

Previous laboratory investigations on *D. magna*'s response to anthropogenic noise did not provide evidence for any alteration. Sabet et al. (2015) used 6-min playbacks of continuous or intermittent 300-1500 Hz band-pass filtered white noise with sound pressure levels (SPL) elevated from 95 to 122 dB Re 1 μPa between the control and the sound treatments. Mobility was not affected despite a slight, but not significant, decrease in swimming speed under continuous noise, which could be consistent with our result. *D. magna* also seems insensitive to motorboat noise in Rojas et al. (2023) where they found unchanged swimming speed in response to 24 motorboat sounds distributed over a 45-min playback track with SPL values from 4.81 to 27 dB RMS Re 1 μPa above a 95-dB background noise. Using the same protocol as in the present study, Prosnier, Rojas, et al. (2023) assessed *D. magna*'s fitness when exposed from birth to death to a playback mimicking realistic boat traffic with various motorboats passing between 9 a.m. and 6 p.m., for a 2-h daily cumulative noise, with SPL values between 108 and 136 dB RMS Re 1 μPa. They found no effect on survival, clutch size and offspring production. When considering frequency bandwidth, noise levels and the duration of the stimulation, we can assume that the "amount" of noise received was greater in the present study compared to the abovementioned investigations. An interesting perspective would be to conduct additional experiments to test the hypothesis of a dose-response relationship relative to

noise pollution (Tyack & Thomas, 2019) and to identify potential thresholds above which individual responses are triggered, or at least detectable.

In addition to the increased fitness, daphnia also showed reduced mobility in the noisy environment. Mobility is known to be linked with body size in the closely related *D. pulex* (Dodson & Ramcharan, 1991) but body size did not differ between the two noise conditions in the present study. It might be that continuous stimulation of the mechanoreceptors made *D. magna* less able to perceive their surroundings, resulting in lower mobility. Although we did not assess food intake, *D. magna* were fed *ad libitum* so reduced mobility probably did not result in reduced energy input, showed for copepods exposed to noise (Kühn et al., 2023), as it could be in natural populations (Read et al., 2014). Consequently, if we consider that energy input was preserved, then the energy saved from mobility might have been reallocated to tissue maintenance and reproduction, explaining the higher fitness. A trade-off between mobility and fitness was already reported for *D. magna* (Prosnier, Loeuille, et al., 2023) and for the codling moth *Cydia pomonella* (Gu et al., 2006).

Evolutionary theory predicts investment in short-term reproduction when expectation of future offspring production decreases and under perception of increased mortality risk (Williams, 1966). Such life-history strategy, referred to as the *terminal investment hypothesis* (Clutton-Brock, 1984), might explain the noise-induced increase in fitness that appears counterintuitive at first sight. Fecundity compensation through early reproduction has already been reported in *D. magna* following exposure to the horizontally-transmitted microsporidian *Glugoides intestinalis* (Chadwick & Little, 2005) and to the sterilizing bacterial pathogen *Pasteuria ramosa* (Vale & Little, 2012). However, increased short-term reproduction is predicted to go with increased mortality under the terminal investment hypothesis and our study does not provide evidence for any mortality following exposure to noise.

Whether our results can be extrapolated to wild *D. magna* populations needs further investigation. Animals can show deviations in behaviour between the laboratory and the field (Tiselius, 1995; Prosnier, Loeuille, et al., 2023), and reduced mobility might have detrimental outcomes in the field as mobility is important to find food, to escape predators and more generally to do diel vertical migrations (Dodson et al., 1997; Larsson & Kleiven, 1997; O'Keefe et al., 1998; Roozen & Lürling, 2001; Chang & Hanazato, 2003). Knowing the indirect effects of this mobility reduction would be useful to understand noise effects on zooplanktonic community (Rojas, Desjonquères, et al., 2023; Rojas, Gouret, et al., 2023). Continuous noise can occur in the vicinity of certain infrastructures such as water pumping systems of compressors on the bank and an interesting perspective to our work would be to study how water fleas use these noisy areas. Water fleas represent key model species for ecotoxicological studies, as well as in many ecological and evolutionary studies (Ebert, 2005, 2022; Bownik, 2020) and our results suggest that rearing facilities' background noise matters in that it could interact with tested stressors, influence population dynamics and the biological responses investigated.

Acknowledgment

The authors would like to thank all those who contributed to the success of this experiment: Nicolas Boyer and Aurélie Pradeau for rearing the *Daphnia* and providing material, Léo Papet and Joël Attia for their acoustic expertise, Marilyn Beauchaud and Paolo Fonseca for the acoustic calibration, and Théophile Turco and all the EYD (ENES Young Discussion) for the useful discussions.

Data, script, and code availability

Data, script, and code are available on Zenodo. DOI: 10.5281/zenodo.10614973 (Prosnier et al., 2024)

References

Aspirault A, Winkler G, Jolivet A, Audet C, Chauvaud L, Juanes F, Olivier F, Tremblay R (2023) Impact of vessel noise on feeding behavior and growth of zooplanktonic species. *Frontiers in Marine Science*, **10**, 1–10. https://doi.org/10.3389/fmars.2023.1111466

Bownik A (2017) Daphnia swimming behaviour as a biomarker in toxicity assessment: A review. *Science of The Total Environment*, **601**–**602**, 194–205. https://doi.org/10.1016/j.scitotenv.2017.05.199

Bownik A (2020) Physiological endpoints in daphnid acute toxicity tests. *Science of The Total Environment*, **700**, 134400. https://doi.org/10.1016/j.scitotenv.2019.134400

Buskey EJ, Lenz PH, Hartline DK (2002) Escape behavior of planktonic copepods in response to hydrodynamic disturbances: high speed video analysis. *Marine Ecology Progress Series*, **235**, 135–146. https://doi.org/10.3354/meps235135

Buskey EJ, Lenz PH, Hartline DK (2011) Sensory perception, neurobiology, and behavioral adaptations for predator avoidance in planktonic copepods. *Adaptive Behavior*, **20**, 57–66. https://doi.org/10.1177/1059712311426801

Celi M, Filiciotto F, Parrinello D, Buscaino G, Damiano A, Cuttitta A, D'Angelo S, Mazzola S, Vazzana M (2013) Physiological and agonistic behavioural response of Procambarus clarkii to an acoustic stimulus. *Journal of Experimental Biology*, **216**, 709–718. https://doi.org/10.1242/jeb.078865

Chadwick W, Little TJ (2005) A parasite-mediated life-history shift in Daphnia magna. *Proceedings of the Royal Society B: Biological Sciences*, **272**, 505–509. https://doi.org/10.1098/rspb.2004.2959

Chan AAY-H, Giraldo-Perez P, Smith S, Blumstein DT (2010) Anthropogenic noise affects risk assessment and attention: the distracted prey hypothesis. *Biology Letters*, **6**, 458–461. https://doi.org/10.1098/rsbl.2009.1081

Chang K-H, Hanazato T (2003) Vulnerability of cladoceran species to predation by the copepod Mesocyclops leuckarti: laboratory observations on the behavioural interactions between predator and prey. *Freshwater Biology*, **48**, 476–484. https://doi.org/10.1046/j.1365-2427.2003.01021.x

Clutton-Brock TH (1984) Reproductive effort and terminal investment in iteroparous animals. *The American Naturalist*, **123**, 212–229. https://doi.org/10.1086/284198

Dodson S, Ramcharan C (1991) Size-specific swimming behavior of Daphnia pulex. *Journal of Plankton Research*, **13**, 1367–1379. https://doi.org/10.1093/plankt/13.6.1367

Dodson SI, Ryan S, Tollrian R, Lampert W (1997) Individual swimming behavior of Daphnia: Effects of food, light and container size in four clones. *Journal of Plankton Research*, **19**, 1537–1552. https://doi.org/10.1093/plankt/19.10.1537

Duarte CM, Chapuis L, Collin SP, Costa DP, Devassy RP, Eguiluz VM, Erbe C, Gordon TAC, Halpern BS, Harding HR, Havlik MN, Meekan M, Merchant ND, Miksis-Olds JL, Parsons M, Predragovic M, Radford AN, Radford CA, Simpson SD, Slabbekoorn H, Staaterman E, Van Opzeeland IC, Winderen J, Zhang X, Juanes F (2021) The soundscape of the Anthropocene ocean. *Science*, **371**, eaba4658. https://doi.org/10.1126/science.aba4658

Ebert D (2005) *Ecology, epidemiology and evolution of parasitism in* Daphnia. Bethesda (MD).

Ebert D (2022) Daphnia as a versatile model system in ecology and evolution. *EvoDevo*, **13**, 16. https://doi.org/10.1186/s13227-022-00199-0

Fields DM, Handegard NO, Dalen J, Eichner C, Malde K, Karlsen Ø, Skiftesvik AB, Durif CMF, Browman HI (2019) Airgun blasts used in marine seismic surveys have limited effects on mortality, and no sublethal effects on behaviour or gene expression, in the copepod Calanus finmarchicus (P Ratilal, Ed,). *ICES Journal of Marine Science*, **76**, 2033–2044. https://doi.org/10.1093/icesjms/fsz126

Francis CD, Barber JR (2013) A framework for understanding noise impacts on wildlife: an urgent conservation priority. *Frontiers in Ecology and the Environment*, **11**, 305–313. https://doi.org/10.1890/120183

Frisk G V. (2012) Noiseonomics: The relationship between ambient noise levels in the sea and global economic trends. *Scientific Reports*, **2**, 437. https://doi.org/10.1038/srep00437

Gassie D V., Lenz PH, Jeannette Y, Hartline DK (1993) Mechanoreception in zooplankton first antennae: electrophysiological techniques. *Bulletin of Marine Science*, **53**, 96–105.

Gu H, Hughes J, Dorn S (2006) Trade-off between mobility and fitness in Cydia pomonella L. (Lepidoptera: Tortricidae). *Ecological Entomology*, **31**, 68–74. https://doi.org/10.1111/j.0307-6946.2006.00761.x

Hildebrand J (2009) Anthropogenic and natural sources of ambient noise in the ocean. *Marine Ecology Progress Series*, **395**, 5–20. https://doi.org/10.3354/meps08353

Hubert J, Booms E, Witbaard R, Slabbekoorn H (2022) Responsiveness and habituation to repeated sound exposures and pulse trains in blue mussels. *Journal of Experimental Marine Biology and Ecology*, **547**, 151668. https://doi.org/10.1016/j.jembe.2021.151668

Jeppesen E, Nõges P, Davidson TA, Haberman J, Nõges T, Blank K, Lauridsen TL, Søndergaard M, Sayer C, Laugaste R, Johansson LS, Bjerring R, Amsinck SL (2011) Zooplankton as indicators in lakes: a scientific-based plea for including zooplankton in the ecological quality assessment of lakes according to the European Water Framework Directive (WFD). *Hydrobiologia*, **676**, 279–297. https://doi.org/10.1007/s10750-011-0831-0

Jerem P, Mathews F (2021) Trends and knowledge gaps in field research investigating effects of anthropogenic noise. *Conservation Biology*, **35**, 115–129. https://doi.org/10.1111/cobi.13510

Kühn S, King F, Heubel KU (2023) Decreased feeding rates of the copepod Acartia tonsa when exposed to playback harbor traffic noise. *Frontiers in Marine Science*, **10**, 1134792. https://doi.org/10.3389/fmars.2023.1134792

Lampert W (2011) *Daphnia: Development of a model organism in ecology and evolution* (O.Kinne, Ed,). International Ecology Institute, Oldendorf/Luhe.

Larsson P, Kleiven OT (1997) Food search and swimming speed in Daphnia. In: *Zooplankton: sensory ecology and physiology* (eds Lenz PH, Hartline DK, Purcell JE, Macmillan DL), pp. 375–387. Gordon-Breach, Amsterdam. https://doi.org/10.1201/9780203733615-28

Leung KMY, Grist EPM, Morley NJ, Morritt D, Crane M (2007) Chronic toxicity of tributyltin to development and reproduction of the European freshwater snail Lymnaea stagnalis (L.). *Chemosphere*, **66**, 1358–1366. https://doi.org/10.1016/j.chemosphere.2006.06.051

McCauley RD, Day RD, Swadling KM, Fitzgibbon QP, Watson RA, Semmens JM (2017) Widely used marine seismic survey air gun operations negatively impact zooplankton. *Nature Ecology & Evolution*, **1**, 0195. https://doi.org/10.1038/s41559-017-0195

Mickle MF, Higgs DM (2018) Integrating techniques: a review of the effects of anthropogenic noise on freshwater fish. *Canadian Journal of Fisheries and Aquatic Sciences*, **75**, 1534–1541. https://doi.org/10.1139/cjfas-2017-0245

Morley EL, Jones G, Radford AN (2014) The importance of invertebrates when considering the impacts of anthropogenic noise. *Proceedings of the Royal Society B: Biological Sciences*, **281**, 20132683. https://doi.org/10.1098/rspb.2013.2683

Muñoz-Colmenares ME, Soria JM, Vicente E (2021) Can zooplankton species be used as indicators of trophic status and ecological potential of reservoirs? *Aquatic Ecology*, **55**, 1143–1156. https://doi.org/10.1007/s10452-021-09897-8

Nedelec SL, Campbell J, Radford AN, Simpson SD, Merchant ND (2016) Particle motion: the missing link in underwater acoustic ecology (D Fisher, Ed,). *Methods in Ecology and Evolution*, **7**, 836–842. https://doi.org/10.1111/2041-210X.12544

Nedelec SL, Radford AN, Pearl L, Nedelec B, McCormick MI, Meekan MG, Simpson SD (2017) Motorboat noise impacts parental behaviour and offspring survival in a reef fish. *Proceedings of the Royal Society B: Biological Sciences*, **284**, 20170143. https://doi.org/10.1098/rspb.2017.0143

O'Keefe TC, Brewer MC, Dodson SI (1998) Swimming behavior of Daphnia : its role in determining predation risk. *Journal of Plankton Research*, **20**, 973–984. https://doi.org/10.1093/plankt/20.5.973

Olivier F, Gigot M, Mathias D, Jezequel Y, Meziane T, L'Her C, Chauvaud L, Bonnel J (2023) Assessing the impacts of anthropogenic sounds on early stages of benthic invertebrates: The "Larvosonic system." *Limnology and Oceanography: Methods*, **21**, 53–68. https://doi.org/10.1002/lom3.10527

Popper AN, Hawkins AD (2019) An overview of fish bioacoustics and the impacts of anthropogenic sounds on fishes. *Journal of Fish Biology*, **94**, 692–713. https://doi.org/10.1111/jfb.13948

Popper AN, Hawkins AD, Thomsen F (2020) Taking the Animals' Perspective Regarding Anthropogenic Underwater Sound. *Trends in Ecology & Evolution*, **35**, 787–794. https://doi.org/10.1016/j.tree.2020.05.002

Popper AN, Salmon M, Horch KW (2001) Acoustic detection and communication by decapod crustaceans. *Journal of Comparative Physiology A: Sensory, Neural, and Behavioral Physiology*, **187**, 83–89. https://doi.org/10.1007/s003590100184

Prosnier L (2022) How could noise affect aquatic ecosystem? A lack of zooplankton studies. *EcoEvoRxiv*, X2NK58. https://doi.org/10.32942/X2NK58

Prosnier L, Loeuille N, Hulot FD, Renault D, Piscart C, Bicocchi B, Deparis M, Lam M, Médoc V (2023) Parasites make hosts more profitable but less available to predators. *bioRxiv peer-reviewed and recommended by PCI Ecology*, 2022.02.08.479552. https://doi.org/10.1101/2022.02.08.479552

Prosnier L, Rojas E, Médoc V (2022) Datasets and R source code of manuscript "No evidence for an effect of chronic boat noise on the fitness of reared water fleas." *Dataset on Zenodo*. https://doi.org/10.5281/zenodo.7339910

Prosnier L, Rojas E, Médoc V (2023) No evidence for an effect of chronic boat noise on the fitness of reared water fleas. *bioRxiv peer-reviewed and recommended by PCI Ecotoxicology and Environmental Chemistry*. https://doi.org/10.1101/2022.11.20.517267

Prosnier L, Rojas E, Valéro O, Médoc V (2024) Datasets and R source code of manuscript “Chronic broadband noise increases the fitness of a freshwater zooplankton.” *Dataset on Zenodo*. https://doi.org/10.5281/zenodo.10614973

Radford AN, Kerridge E, Simpson SD (2014) Acoustic communication in a noisy world: can fish compete with anthropogenic noise? *Behavioral Ecology*, **25**, 1022–1030. https://doi.org/10.1093/beheco/aru029

Ratnarajah L, Abu-Alhaija R, Atkinson A, Batten S, Bax NJ, Bernard KS, Canonico G, Cornils A, Everett JD, Grigoratou M, Ishak NHA, Johns D, Lombard F, Muxagata E, Ostle C, Pitois S, Richardson AJ, Schmidt K, Stemmann L, Swadling KM, Yang G, Yebra L (2023) Monitoring and modelling marine zooplankton in a changing climate. *Nature Communications*, **14**, 564. https://doi.org/10.1038/s41467-023-36241-5

Read J, Jones G, Radford AN (2014) Fitness costs as well as benefits are important when considering responses to anthropogenic noise. *Behavioral Ecology*, **25**, 4–7. https://doi.org/10.1093/beheco/art102

Reid AJ, Carlson AK, Creed IF, Eliason EJ, Gell PA, Johnson PTJ, Kidd KA, MacCormack TJ, Olden JD, Ormerod SJ, Smol JP, Taylor WW, Tockner K, Vermaire JC, Dudgeon D, Cooke SJ (2019) Emerging threats and persistent conservation challenges for freshwater biodiversity. *Biological Reviews*, **94**, 849–873. https://doi.org/10.1111/brv.12480

Reynolds CS (2011) Daphnia: Development of Model Organism in Ecology and Evolution - 2011 Winfried Lampert (2011) Excellence in Ecology Series. *Freshwater Reviews*, **4**, 85–87. https://doi.org/10.1608/FRJ-4.1.425

Richardson WJ, Fraker MA, Würsig B, Wells RS (1985) Behaviour of bowhead whales Balaena mysticetus summering in the Beaufort Sea: Reactions to industrial activities. *Biological Conservation*, **32**, 195–230. https://doi.org/10.1016/0006-3207(85)90111-9

Rojas E, Desjonquères C, Agostini S, Fiorini S, Decencière B, Danger M, Felten V, Médoc V (2023) Response of freshwater zooplankton communities to chronic anthropogenic noise. In: *The Effects of Noise on Aquatic Life: Principles and Practical Considerations* (eds Popper AN, Sisneros J, Hawkins AD, Thomsen F), p. . Springer International Publishing, Cham. https://doi.org/10.1007/978-3-031-10417-6_139-1

Rojas E, Gouret M, Agostini S, Fiorini S, Fonseca P, Lacroix G, Médoc V (2023) From behaviour to complex communities: Resilience to anthropogenic noise in a fish-induced trophic cascade. *Environmental Pollution*, **335**, 122371. https://doi.org/10.1016/j.envpol.2023.122371

Rojas E, Prosnier L, Pradeau A, Boyer N, Médoc V (2023) Anthropogenic noise does not strengthen multiple-predator effects in a freshwater invasive fish. *Journal of Fish Biology*, **102**, 1470–1480. https://doi.org/10.1111/jfb.15397

Rojas E, Thévenin S, Montes G, Boyer N, Médoc V (2021) From distraction to habituation: Ecological and behavioural responses of invasive fish to anthropogenic noise. *Freshwater Biology*, **66**, 1606–1618. https://doi.org/10.1111/fwb.13778

Roozen F, Lürling M (2001) Behavioural response of Daphnia to olfactory cues from food, competitors and predators. *Journal of Plankton Research*, **23**, 797–808. https://doi.org/10.1093/plankt/23.8.797

Sabet SS, Karnagh SA, Azbari FZ (2019) Experimental test of sound and light exposure on water flea swimming behaviour. *Proceedings of Meetings on Acoustics*, **37**, 010015. https://doi.org/10.1121/2.0001270

Sabet SS, Neo YY, Slabbekoorn H (2015) The effect of temporal variation in sound exposure on swimming and foraging behaviour of captive zebrafish. *Animal Behaviour*, **107**, 49–60. https://doi.org/10.1016/j.anbehav.2015.05.022

Shannon G, McKenna MF, Angeloni LM, Crooks KR, Fristrup KM, Brown E, Warner KA, Nelson MD, White C, Briggs J, McFarland S, Wittemyer G (2016) A synthesis of two decades of research documenting the effects of noise on wildlife. *Biological Reviews*, **91**, 982–1005. https://doi.org/10.1111/brv.12207

Solé M, Kaifu K, Mooney TA, Nedelec SL, Olivier F, Radford AN, Vazzana M, Wale MA, Semmens JM, Simpson SD, Buscaino G, Hawkins A, Aguilar de Soto N, Akamatsu T, Chauvaud L, Day RD, Fitzgibbon Q, McCauley RD, André M (2023) Marine invertebrates and noise. *Frontiers in Marine Science*, **10**, 1129057. https://doi.org/10.3389/fmars.2023.1129057

Solé M, Lenoir M, Fontuño JM, Durfort M, van der Schaar M, André M (2016) Evidence of Cnidarians sensitivity to sound after exposure to low frequency noise underwater sources. *Scientific Reports*, **6**, 37979. https://doi.org/10.1038/srep37979

Starke CWE, Jones CLC, Burr WS, Frost PC (2021) Interactive effects of water temperature and stoichiometric food quality on Daphnia pulicaria. *Freshwater Biology*, **66**, 256–265. https://doi.org/10.1111/fwb.13633

Tiselius P (1995) Can we use laboratory-reared copepods for experiments? A comparison of feeding behaviour and reproduction between a field and a laboratory population of Acartia tonsa. *ICES Journal of Marine Science*, **52**, 369–376. https://doi.org/10.1016/1054-3139(95)80052-2

Tkaczyk A, Bownik A, Dudka J, Kowal K, Ślaska B (2021) Daphnia magna model in the toxicity assessment of pharmaceuticals: A review. *Science of The Total Environment*, **763**, 143038. https://doi.org/10.1016/j.scitotenv.2020.143038

Tyack PL, Thomas L (2019) Using dose–response functions to improve calculations of the impact of anthropogenic noise. *Aquatic Conservation: Marine and Freshwater Ecosystems*, **29**, 242–253. https://doi.org/10.1002/aqc.3149

Vale PF, Little TJ (2012) Fecundity compensation and tolerance to a sterilizing pathogen in Daphnia. *Journal of Evolutionary Biology*, **25**, 1888–1896. https://doi.org/10.1111/j.1420-9101.2012.02579.x

Vereide EH, Kühn S (2023) Effects of anthropogenic noise on marine zooplankton. In: *The Effects of Noise on Aquatic Life: Principles and Practical Considerations* (eds Popper AN, Sisneros J, Hawkins AD, Thomsen F), p. . Springer International Publishing, Cham. https://doi.org/10.1007/978-3-031-10417-6_63-1

Vereide EH, Mihaljevic M, Browman HI, Fields DM, Agersted MD, Titelman J, de Jong K (2023) Effects of airgun discharges used in seismic surveys on development and mortality in nauplii of the copepod Acartia tonsa. *Environmental Pollution*, 121469. https://doi.org/10.1016/j.envpol.2023.121469

Villalobos-Jiménez G, Dunn AM, Hassall C (2017) Environmental noise reduces predation rate in an aquatic invertebrate. *Journal of Insect Conservation*, **21**, 839–847. https://doi.org/10.1007/s10841-017-0023-y

Waggett RJ, Buskey EJ (2008) Escape reaction performance of myelinated and non-myelinated calanoid copepods. *Journal of Experimental Marine Biology and Ecology*, **361**, 111–118. https://doi.org/10.1016/j.jembe.2008.05.006

Weatherby T., Lenz P. (2000) Mechanoreceptors in calanoid copepods: designed for high sensitivity. *Arthropod Structure & Development*, **29**, 275–288. https://doi.org/10.1016/S1467-8039(01)00011-1

Williams GC (1966) Natural selection, the costs of reproduction, and a refinement of Lack's principle. *The American Naturalist*, **100**, 687–690. https://doi.org/10.1086/282461

Williams R, Wright AJ, Ashe E, Blight LK, Bruintjes R, Canessa R, Clark CW, Cullis-Suzuki S, Dakin DT, Erbe C, Hammond PS, Merchant ND, O'Hara PD, Purser J, Radford AN, Simpson SD, Thomas L, Wale MA (2015) Impacts of anthropogenic noise on marine life: Publication patterns, new discoveries, and future directions in research and management. *Ocean & Coastal Management*, **115**, 17–24. https://doi.org/10.1016/j.ocecoaman.2015.05.021

Wysocki LE, Dittami JP, Ladich F (2006) Ship noise and cortisol secretion in European freshwater fishes. *Biological Conservation*, **128**, 501–508. https://doi.org/10.1016/j.biocon.2005.10.020

Appendix: Tables of statistics and supplementary figure

Table A1. Statistical results of chronic boat noises effects on fecundity and mortality of *Daphnia magna* (Fig. 2)

	Mortality		Reproduction			Fitness	
	Survival	Adult duration	Age at maturity	Clutch interval	Mean clutch size	Number of clutches	Number of offspring
df	1	1	1	1	1	1	1
χ^2/W	9.9	5.9	1.1	0.0497	8.0469	5.9514	6.9065
p-value	**0.002**	**0.015**	0.3	0.82	**0.005**	**0.01**	**0.009**
R2	0.05	0.07	0.01	NA	NA	0.21	0.71

Table A2. Statistical results of chronic boat noises effects on size of *Daphnia magna*

	Size
df	34
t	-0.4226
p-value	0.675

Table A3. Statistical results of chronic boat noises effects on mobility of *Daphnia magna* (Fig. 3)

		Speed
Global effect	df	3-32
	F	3.215
	p-value (trait)	**0.008**
	p-value (size)	0.361
	p-value (age)	0.529
	R^2	0.232
N vs S	p-value (S1)	0.152
	p-value (N1)	0.351
	p-value (S2)	**0.031**
	p-value (N2)	0.689

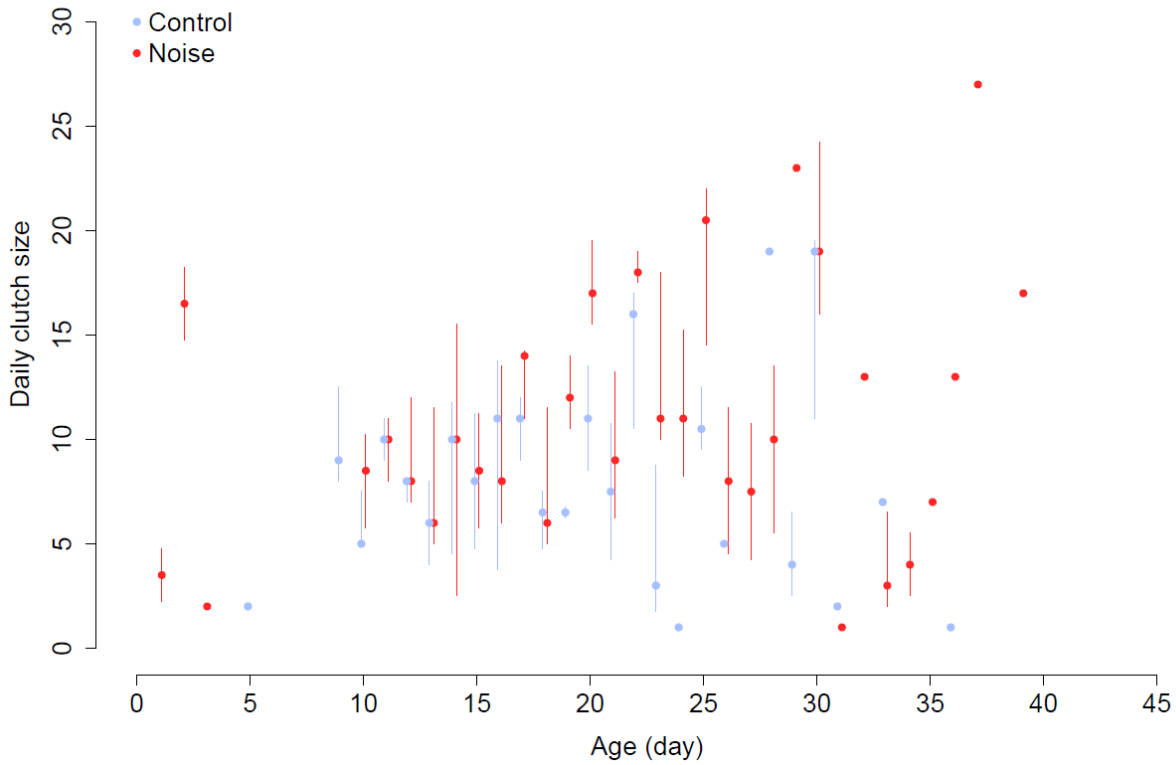

Figure A1. Effects of noise treatments on *Daphnia magna* daily clutch size. Dots represent the median of the daily clutch size and lines are interquartile ranges. See Fig. 3a,d as complement for the number of individuals at each age. Note that there could be only one clutch for an age (i.e., no interquartile lines) or clutches only for one treatment (i.e., only one point for an age).