



Behavioral and Ecological Responses of an Invasive Freshwater Mussel to Noise Pollution

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TITLE

Behavioral and ecological responses of an invasive freshwater mussel to noise pollution

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ABSTRACT

Biological invasions and anthropogenic noise represent two major threats to fresh water ecosystems but the response of invasive species to noise and how it can modulate their behavior and ecological impact have received scant attention. In this study, we conducted a two-phase laboratory experiment to investigate the effect of motorboat noise on the quagga mussel *Dreissena bugensis*, one of the world's most invasive species causing detrimental ecological and economic impacts. We first measured aggregation patterns during a 14 to 18-day rearing phase where the mussels experienced laboratory background noise supplemented or not with motorboat sounds that mimic nautical activity during summer. Afterwards, we monitored the valve activity and estimated the filtration rate of mussels from both rearing conditions in the presence or absence of motorboat noise for 12 hours. Our results showed that aggregation rate and mean aggregate size were higher with motorboat noise. Conversely, valve activity did not differ between the two noise conditions but was significantly increased by the previous repeated exposure to noise during the rearing phase. The relationship between valve activity and filtration rate was positive for the mussels not exposed to boat noise, positive but weaker for the mussels that experienced boat noise during one of the two experiment and not significant for those under boat noise during the whole investigation. Further research is needed to understand the physiological origins of the response to noise and the consequences on life-history traits and mussel-based ecosystem processes such as phytoplanktonic primary production, benthification and biofouling.

KEY WORDS: Noise pollution, Biological invasions, Quagga mussel, Filtration activity, Aggregation

1. INTRODUCTION

Sound emissions from human activities, also referred to as anthropogenic noise or noise pollution, have recently been considered an emerging threat to fresh waters (Reid et al., 2019). Public and authorities' concern for freshwater noise pollution is late compared to marine noise pollution that is part of international agendas and guidelines including the [United Nations Convention on the Law of the Sea](#) and the [European Marine Strategy Framework Directive 2008/56/EC](#). With the growing of human needs, the desire to reconnect with nature and the diversification of nautical leisure activities, anthropic pressures on inland waters and their associated sound emissions are not expected to ease (Duarte et al., 2021; Miret-Pastor et al., 2020; Vázquez, 2020).

Almost all living organisms are concerned with noise pollution as it can mask important acoustic cues involved in communication, reproduction, prey or predator detection (Kunc et al., 2016; Slabbekoorn et al., 2010; Vieira et al., 2021). Animals can be distracted, allocating part of their finite attention to noise at the expense of other important activities (Chan et al., 2010; Sal Moyano et al., 2023; Slabbekoorn et al., 2010). Noise can also be perceived as a threat and elicit physiological or behavioral stress responses that can ultimately compromise reproductive success (Kunc et al., 2016). Even primary producers are not spared when the individual responses to noise of consumers propagate downward the food chains through nested ecological interactions (Di Franco et al., 2020; Kühn et al., 2023). However, ecological consequences at the levels of communities and ecosystems remain poorly documented, particularly in fresh water environments.

Next to noise pollution, historical threats to fresh waters are still ongoing, and among them biological invasions. Climate change, habitat degradation, global trade as well as some

socio-economic aspects can contribute to the steadily increasing number of invasive alien species (Essl et al., 2020). Consequences are dramatic and include trillion-dollar economic burdens worldwide, degradations of social well-being and biodiversity decline with the extirpation of native species through competition, predation or even disease transmission (Diagne et al., 2021; Ogden et al., 2019). Impacts are exacerbated when invasive species are also ecosystem engineers such as riparian trees, macrophytes, crayfishes or mussels (Emery-Butcher et al., 2020). Many invasive species use anthropogenic corridors to spread out of their historical range (Reid et al., 2019) while introduction points are often highly transformed and disturbed by human activities, like urban areas and natural socio-ecosystems. Because anthropized environments are expected to be noisy, we can reasonably assume that biological invasions and noise pollution are two interacting threats. It is therefore surprising to note that little research has been done on how invasive species respond to noise pollution (Fernandez-Declerck et al., 2023; Rojas et al., 2021). Do they better cope with noise than native species? Is tolerance to noise an attribute of successful invasive species? Does noise modulate the behavior and impacts of invasive species?

In the present study, we assessed for the first time the behavioral and ecological responses to chronic motorboat noise of one of the most aggressive freshwater invasive species worldwide (Karatayev et al., 2021; Mei et al., 2016), the Quagga mussel *Dreissena bugensis*. Native to Ukraine (Nalepa and Schloesser, 2013), this bivalve has spread to western Europe in the 1940s and to North America in the 1980s, to gradually replace its relative the Zebra mussel *Dreissena polymorpha* (Nalepa et al., 2010; Ram et al., 2012). In France, it was reported for the first time in the Moselle in 2011 (bij de Vaate and Beisel, 2011), from where it moved south to reach the French perialpine lakes region in 2015 (Haltiner et al., 2022). The Quagga mussel has a high reproductive potential, free-swimming planktonic larvae

facilitating the colonization of new environments and a highly efficient suspension-feeding benthic adult stage (Karatayev et al., 2015). Invasive dreissenids can reach very high densities in their new environments and become a major determinant of their functioning, mainly though their impact on the phytoplankton biomass and the transfer of matter and energy from the pelagic realm to the benthos, a process referred to as benthification (Higgins and Zanden, 2010; Karatayev et al., 2015). The reefs they build also facilitate the establishment of other non-native invertebrates or shift in dominance structure of the community (Verstijnen et al., 2019; Ward and Ricciardi, 2007) while fouling has negative impacts on many infrastructures involved in energy production, water supply and boat traffic (Nalepa and Schloesser, 2013). Between the impacted years 1980-2020, the *Dreissenidae* family generated significant costs estimated for a total of 51.1 billion dollars worldwide (Haubrock et al., 2022).

We did playback experiments in tanks to assess aggregation rate, valve opening activity and filtration rate under acute and chronic exposure to motorboat noise. Enhanced aggregation has been shown to be a good behavioral proxy for stress, like the presence of predatory fish (Kobak and Kakareko, 2009; Kobak et al., 2010; Naddafi and Rudstam, 2013). We therefore expected noise to induce the formation of more and larger aggregates. Concerning valve opening, contrasted responses have been reported. For instance, Charifi et al. (2017) found a rapid decrease in valve opening in the Pacific oyster *Magallana gigas* in response to pure tones, a behavior that could protect soft bodies from a threat. At the opposite, the blue mussel *Mytilus edulis* showed larger valve spacing for a similar opening period when exposed to ship noise (Wale et al., 2019). This behavior has been attributed to a relaxation of the abductor muscles to save energy and cope for a costly noise-induced physiological response. Because valve opening regulates both the feeding and respiratory activities (Riisgard and Randløv, 1981), we expected filtration rate to change accordingly with valve

opening. Finally, we expected a weaker response to noise after repeated exposure (*i.e.*, chronic versus acute noise) as previously reported for *M. edulis* (Hubert et al., 2022). This would suggest habituation while the absence of any response, even with acute noise exposure, would suggest tolerance.

2. MATERIALS AND METHOD

2.1. General design

Laboratory experiments were carried out from March to June 2022. In a first phase, mussels were kept in rearing aquaria to compare aggregation rates under laboratory background noise and loudspeaker playing silence (Ambient noise treatment) either alone or supplemented with motorboat noise (Boat noise treatment) for 16 to 20 days. In a second phase of 12 hours, mussels were placed in dedicated experimental units to accurately quantify valve activity and filtration rate in both noise conditions. It resulted in four treatments depending on the noise condition during the two successive phases: (i) Ambient / Ambient (AA) for the full control, (ii) Ambient / Boat (AB) to assess the response to first exposure, (iii) Boat / Ambient (BA) to detect persistent effects, and (iv) Boat / Boat (BB) to assess the response to chronic exposure.

2.2. Animal collection and maintenance

Sampling of mussels took place in Lake Bourget, the French largest natural lake (Jacquet et al., 2005). Once a week, we dived to collect by hand at 3m depth around 400 quagga mussels of all sizes in an area inaccessible to boats (in front of the public beach, 45°39'22.374"N,

5°51'40.481"E, Le Bourget-du-Lac, France). Back to the laboratory, they were kept in the transport cooler with water aeration in a rearing room thermoregulated at 18°C, corresponding to the average temperature experienced by mussels in Lake Bourget at the end of spring. Two hours before the beginning of the rearing phase, adult specimens with a shell length ranging from 1.95 to 2.3 cm (mean \pm SD: 2.17 ± 0.05 cm) were selected, cleaned using a toothbrush to remove organic matter and epibionts, and kept in a mix of lake water and tap water treated with water conditioner (Aquasafe, TETRA®, treated water hereafter) for a 1-h acclimatization period.

2.3. Rearing phase and aggregation

The rearing phase took place in two glass aquariums (120 x 50 x 60 cm, one *per* noise treatment) filled with 240 L of treated tap water and equipped with two synchronized underwater loudspeakers (ElectroVoice UW30, 0.1 to 10 kHz) face down and 3 cm below the water surface (“rearing aquariums” in Fig. 1A). To limit acoustic reflection, we covered the inner sides of the aquariums with a 5-cm thick foam (0.1-mm mesh) and added a 2-cm bottom layer of Loire sand (granulometry between 1,5 et 3mm, Aquasand Nature, Zolux deco). Below each loudspeaker, we placed at equidistance three rough floor tiles with a 3*3mm-mesh polyethylene cylinder glued on it to delimit a 18-cm diameter area (experimental arena hereafter). Preliminary experiments showed that mussel fixation was optimal on the rough floor tiles while mussels did not climb neither attach on the plastic mesh. Light was artificial and standardized around 200 lux within and between the tanks with a 12L:12D regime. We did not measure the in-situ lightening but 200 lux corresponding to a dim light condition and within the plausible field value range (Kobak and Nowacki, 2007). The light:dark regime

ranged from 12L:12D to 18L:6D from March to June and we acclimatized all the mussels to 12L:12D during the rearing phase for practical reasons (see 2.4). We renewed 30% of the water twice a week while aeration was ensured by turning on the air pump for 15 min three times a day.

We placed 50 mussels equidistant of ~2 cm from each other in each of the four experimental arenas (one *per* loudspeaker for both aquariums) dedicated to the first sampling session (numbers 1 in Fig. 1A). The remaining experimental arenas were filled with mussels from the next sampling sessions: one and two weeks later (numbers 2 and 3, respectively, in Fig. 1A). Each group of mussels was fed twice a week with a 10-mL algal suspension of *Chlamydomonas reinhardtii* (between 10000 and 30000 cells/mL). This species is a handy and relevant food source to later assess filtration rates (Dionisio Pires and Van Donk, 2002; Sprung and Rose, 1988), see 2.4). The few mussels that died during the rearing phase were counted and removed without replacement.

To assess aggregation, we took a photo of the mussels 96 hours after their introduction into the experimental arena, most of the movements occurring within the first three days (D'Hont et al., 2020 and personal observation), to then count the number (AN) and size (AS) of mussel aggregates. The mussels were considered as belonging to the same aggregate when separated by a maximum of three millimeters and single mussels (singletons, S) were considered as aggregates of size one. For each experimental arena, we calculated mean aggregate size (\overline{AS}) and aggregation rates (AR) as follow:

$$\overline{AS} = \frac{\sum AS}{AN}$$

$$AR = \frac{n_m - S}{n_m} * 100$$

where n_m corresponds to the total number of live mussels.

2.4. Filtration experiment

The experiment was performed under the same light and temperature conditions (200 lux, LD 12:12 and 18°C) in four 110-L aquaria (110 x 40 x 30 cm) filled with 80 L of treated tap water. Two aquaria were used for the starvation period and the two others for the measure of filtration rates (starvation and filtration aquaria hereafter, respectively). Each aquarium was equipped with one underwater loudspeaker (ElectroVoice UW30, 0.1 to 10 kHz) fixed in the middle, face down, and 3 cm below the water surface (Fig. 1B).

We randomly selected twelve mussels (six *per* experimental arena) from each of the two rearing aquaria (one *per* noise condition), which were gently detached from the floor tile and glued on a small PVC rack (Fig. 1C). We added a white dot at the tip of the free valve to maximize contrast and promote the assessment of valve opening activity. Before the filtration experiment and to standardize hunger, the mussels (on their racks) were transferred for 24 hours into the starvation aquaria whose water was filtered (0.42 µm) to remove potential food particles, and where the mussels experienced the same noise condition as during the rearing phase. At the end of the starvation period, we placed the mussels in a 4-L glass aquarium (20 x 12 x 20 cm, “filtration aquaria” in Fig. 1C) filled with filtered, treated tap water whose continuous flow was ensured by a peristaltic pump (flow rate: 3.5 L/h). Each 4-L aquarium was placed inside one of the two large aquaria with the loudspeaker broadcasting either silence or boat noise (see 2.5) to get the four treatments when considering the noise condition previously experienced during the rearing phase (AA, AB, BA and BB, see 2.1).

We monitored valve opening over two consecutive 6-hr periods: the first with light from 2 to 8 PM to mimic daytime and with or without boat noise depending on the treatment,

and the second from 8 PM to 2 AM in darkness and background noise to mimic night. After a 30-min acclimatization period, the experiment started with the introduction of *C. reinhardtii* at a concentration of 22000 Cel/mL. We used an automated image acquisition system made of a video sensor (μ Eye UI-1540-MM with a 25 mm lens) and infra-red lights. Images were acquired every 20 s and combined into AVI format movies using an image analysis software (Aviexplore, Romero-Ramirez et al., 2016). Valve gape was then assessed frame-by-frame directly from the 2,158-frame movies using the same software. Gape tracking was automatically determined, based on the coordinates of the barycenter of the white dot on the free valve. In case of loss of the tracking (hidden by the siphon for instance), the x - y position of the barycenter was determined manually. The reference position of the white dot (valve gape = 0) was determined by triggering the closing of each mussel. For each image, the coordinates of reference position was subtracted at tracking coordinates to obtain the valve gape (Maire et al., 2007). To accurately estimate filtration rate, we sampled 10 ml of water at the beginning of the experiment and then every hour during the day phase, fixed the algae with lugol and stored the samples at 3°C for later counting (see below). Because water sampling may trigger mussel closing, we excluded the ten minutes (corresponding to 30 frames) before and after each sampling event, resulting in a total of 1,835 frames analyzed (756 during the day phase and 1,079 during the night phase).

The mussels that never opened were considered as in bad condition and removed from the data set (six mussels among the 336 monitored, with a maximum of two mussels for a given PVC rack, and no difference between the treatments, Chi-squared test: $\chi^2 = 6.1091$, $df = 3$, $P = 0.106$). To improve comparison between individuals, gape values were divided by the maximum gape recorded during the twelve hours (normalized gape in proportion, NG). For each mussel, we calculated the average normalized gape (\overline{NG}) and the relative time spent

open (TO), considering only NG values from 10 % to account for uncertainty in the measure (NG_{10}), with the formulae:

$$\overline{NG} = \frac{\sum NG}{n}$$

$$TO = \frac{\sum NG_{10}}{n}$$

where n corresponds to the total number of frames analyzed *per* mussel: 756 and 1,079 for the day and night phases respectively.

Filtration was assessed using the clearance method (Coughlan, 1969) which has proved reliable with many filter feeding bivalves including the quagga mussel (Pedersen et al., 2020). Algae cell density was determined by Malassez cells counts under an optical microscope and clearance rate (CR) was calculated using the following formula (Riisgård, 2004):

$$CR = \frac{V * a}{n_m}$$

where V is the volume of water (in mL), n_m the number of active (i.e. filtering) mussels, and a the coefficient of the linear regression between algal concentration and time estimated with least squares methods. Algal sedimentation being negligible, we attributed the decrease in algal concentration to mussel activity.

Since the size of *C. reinhardtii* (6 microns) is above the threshold of 100% retention efficiency mentioned by Sprung and Rose, 1988, quagga mussels clearance rates were equivalent to filtration rates.

To test whether the link between valvometry during day and filtration was affected by the noise condition, we reduced valvometry during day to one dimension through the calculation of valve activity (VA) as follow:

$$VA = \overline{NG} * TO$$

Where \overline{NG} is the average normalized gape and TO the relative time spent open during day.

2.5. Playback tracks

Audio tracks were played as WAV files using either a desktop computer or a ZOOM H4next Handy player connected to an amplifier (Dynavox CS PA 1MK) and to an underwater speaker (Electrovoice Lubell UW30). Recordings for calibration were done with an Aquarian Audio H2A-HLR hydrophone (frequency response from 10 Hz to 100 kHz) connected to a capture card (Steinberg®) and a computer.

Mussels from the ambient noise treatment were exposed to a playback track of silence to account for the potential effect of the electromagnetic field generated by the speakers when turned on. They experienced the natural background noise of the experimental room, measured at 104 dB re 1 μ Pa. Lake background noise was around 98-100 dB re 1 μ Pa, which falls into the range of values usually reported for lakes (Wysocki et al., 2007). For this reason, we did not use as control a playback of background noise that would have been masked by room background noise.

Regarding the boat noise treatments, we used different boat sounds recorded in July 2021 at 21-m depth in Lake Bourget (45°39'35.5"N, 5°53'9.599"E, France) using a hydrophone (Colmar GP1516, frequency response from 5 Hz to 70 kHz) connected to an underwater acoustic recorder (RTsys SYLENCE-LP). We manually calculated the boat traffic (*i.e.*, temporal distribution of the sounds) and quantified the levels (in dB) at which 90

randomly-selected boat sounds emerged from lake natural background noise using the Signal-to-Noise Ratio (SNR):

$$\text{SNR} = 20\log_{10}(\text{RMS}_{\text{boat sound}}/\text{RMS}_{\text{background noise}})$$

where RMS corresponds to the root-mean-square sound pressure.

During the rearing phase, we generated a one-week playback track in which 738 motorboat sounds were added to silence with fade in and out. The track was looped until the end of the rearing phase. The 738 sounds were randomly selected from 30 original boat recordings made in Lake Bourget (each original sound was therefore played several times) and distributed so as to mimic the daily and hourly nautical activity of the lake in July 2021. Total boat number *per* day ranged from 87 to 121 with the first boat at 5:32 am and the last at 00:10 am, the position of the boat sounds within each hour being random (Table S1a).

For the filtration experiment, we played silence track during the 30-min acclimatization period and then a 6-hr playback track with 43 boat sounds randomly selected from the 30 original recordings, added to silence, and distributed so as to generate a 180-min period of high activity surrounded by two 90-min periods of low activity (sound position was random within each period, Table S1b).

Three acoustic biases can provoke sound distortion during tank-based acoustics studies: low frequency attenuation, resonant frequencies, and sound reverberation (Akamatsu et al., 2002). To limit sound distortion, we used a dedicated software (Adobe Audition 2020) to modify the frequency content of the input signals and make the playbacks as close as possible to the original signals (Fig.2). We also adjusted sound levels to reach SNR values ranging from 7.79 to 32.28 dB, corresponding to what we found *in-situ* (Table S2, Fig.2).

2.6. Statistics

We performed all the statistical analyses using the R software version 4.1 (R Core Team, 2023) with a 5% confidence level. Because the data on mussel aggregation did not meet the normality and homoscedasticity assumptions of parametric statistics, we used Wilcoxon tests with Bonferroni correction to compare the difference in \overline{AS} and AR between the two noise conditions. For the filtration activity, we used generalized linear mixed models with beta regression using the "glmm TMB" R package to explain in two separate analyses the variations in \overline{NG} and TO as a function of three qualitative predictors with two modalities each: the noise condition of the rearing phase (Ambient/Boat), the noise condition of the filtration experiment (Ambient/Boat) and the period (Day/Night). We accounted for the nested design and possible time effect through a random term with individual mussels nested within their PVC rack, itself nested within the day of experiment. We used linear models to explain CR as a function of VA as a quantitative predictor, the noise condition of the rearing phase (Ambient/Boat), the noise condition of the filtration experiment (Ambient/Boat), and their interaction. We expected the relationship between CR and VA to be linear based on previous studies with closely related species (Maire et al., 2007; Albert et al., 2022).

3. RESULTS

Aggregation rate (AR) was significantly higher with boat noise (mean \pm SD: $84.12 \pm 3.73\%$) compared to ambient noise (mean \pm SD: $76.13 \pm 7.76\%$) (Wilcoxon's tests with Bonferroni's correction, $P = 0.002$, effect size $r = 0.53$, Fig. 3). Mean aggregate size (\overline{AS}) was also significantly higher with boat noise (mean \pm SD: 2.86 ± 0.51 mussels/aggregate) compared to

ambient noise (mean \pm SD: 2.40 ± 0.51 mussels/aggregate) (Wilcoxon's tests with Bonferroni's correction, $P = 0.025$ and effect size $r = 0.39$).

Regarding filtration activity during day, the average normalized gape (\overline{NG} , Fig. 4A) and the relative time spent open (TO , Fig. 4B) were significantly influenced by the period with higher values at night compare to day (ANOVA, $Df=1$ and $P < 0.001$ for \overline{NG} , $Df=1$ and $P = 0.017$ for TO). They were also significantly impacted by the noise condition experienced during the rearing phase with higher values under boat noise ($Df=1$ and $P < 0.001$ for \overline{NG} , $Df=1$ and $P = 0.002$ for TO). However, neither the noise condition during the filtration experiment nor the interaction between the noise conditions of the two successive experiments had a significant effect on \overline{NG} and TO (all $P > 0.05$).

Filtration rate (FR) was significantly influenced by VA (ANOVA, $Df=1$ and $P = 0.004$), the noise condition of the filtration experiment ($Df=1$ and $P = 0.006$), the interaction between VA and the noise condition of the filtration experiment ($Df=1$ and $P = 0.026$), and by the interaction between VA and the noise condition during the rearing phase (ANOVA, $Df=1$ and $P = 0.034$). In other words, the relationship between CR (Clearance Rate) and VA was positive when the mussels experienced ambient noise only, weaker with boat noise during one of the two phases (rearing condition or filtration measurement), and null when the mussels experienced boat noise during the two phases (Fig. 5).

4. DISCUSSION

In the aim of sustainable management of vulnerable ecosystems like fresh waters, it is critical to gain knowledge on the interplay between exotic invasive species and anthropogenic noise, two threats facing biodiversity and moreover tightly interacting. In the present work, we

conducted a laboratory experiment to investigate the response of the invasive quagga mussel *Dreissena bugensis* to motorboat noise. We found a positive effect on aggregation behavior and a disruption of the positive correlation between valve activity and filtration rate, possible alteration of animal's physiology and feeding activity, with potential upscaling cascading effects on population dynamic and ecological processes.

The quagga mussel has a natural tendency to approach and settle close to conspecifics or their empty shells and to form large clusters on the substrate (Stańczykowska, 1978). During the rearing phase, where the mussels experienced or not motorboat noise, we observed an amplification of this behavior with more aggregates and more mussels *per* aggregate in the noisy aquaria compared to control. Increased aggregation has been documented in the presence of chemical release from fish or crushed conspecifics and interpreted as a direct stress response (Kobak and Kakareko, 2011; Naddafi and Rudstam, 2013). In the natural environment, this anti-predator defense strategy is expected to promote survival by making individual mussels less exposed to predators and harder to handle, and also through the dilution and confusion effects (Kobak and Kakareko, 2009). On the other hand, increased aggregation has costs including stronger intraspecific competition for food, oxygen resources, waste accumulation (Burks et al., 2002) and pathogen transmission (Berkhout et al., 2023). Consequently, under low environmental stress, individuals living in very large aggregates would be in a lower physiological state with reduced growth compared to individuals from smaller groups (Naddafi and Rudstam, 2013). Given the natural tendency of invasive mussels to form large aggregates and considering all the environmental factors that promote aggregation like limited space and predation threat, the relative contribution of anthropogenic noise to the aggregation patterns of wild mussel populations is probably small. However, our laboratory result has the merit of showing that quagga mussels are able to perceive motorboat

sounds and react as they do under natural threats such as predation (Kobak and Kakareko, 2011; Naddafi and Rudstam, 2013).

Increased aggregation is often associated with increased adhesion strength through the production of byssal filaments by the byssogenic gland (Kobak and Kakareko, 2011; Naddafi and Rudstam, 2013). Anchoring to hard substrates protects against dislodgement by predators (Czarnoleski et al., 2011) and can induce huge costs when it concerns man-made structures, an issue referred to as biofouling (Haubrock et al., 2022; Kusku et al., 2022). An interesting perspective to our work would be to test whether chronic motorboat noise also affect adhesion strength, which might have consequences on mussels' fitness and on the ecological and economic issues related to mussel fouling.

Valve activity was higher at night compared to day as reported by (Borcherding, 2006; Christoforou et al., 2023) and this increase was not influenced by the acoustic treatment. Thanks to their ability to appreciate light condition through photoreceptor cells (Ramirez et al., 2011) mussels generally display a circadian rhythm in their filtration activity linked to the light/dark cycle (Borcherding, 2006). From an evolutionary point of view, higher valve activity at night would minimize predation risk when foraging (Gnyubkin, 2010).

The presence of motorboat sounds during the filtration experiment did not change valve activity even for the mussels coming from the noiseless rearing aquaria. When analyzing the video recordings, we did not observe any immediate response to noise like in the blue mussel *Mytilus edulis* that was found to partially close its valve in response to impulsive pure tones (Hubert et al., 2022) but also to broadband boat noise with a softer start compared to pure tones (Hubert et al., 2023), the magnitude of the response decreasing over repeated exposures to return to baseline levels. Our results on aggregation, which was positively influenced by motorboat noise, suggests that the absence of immediate effect on

valve activity is not because the quagga mussels did not perceive the acoustic cues. On the contrary, repeated exposure to motorboat noise over the rearing phase (*i.e.*, chronic noise) had a positive effect on valve activity with an increase in valve opening and to a lesser extent in the time spent open, and this even in the absence of boat noise during the filtration experiment. It might be that the effect of boat noise increases with the amount of noise received and persists over time even when noise stops. A greater valve opening has also been reported in *M. edulis* in response to a shorter ship noise exposure compared to our study (Wale et al., 2019). Additional experiments with comparable protocols are needed to conclude that the quagga mussel tolerates a greater amount of noise than the blue mussel before altering its activity.

Valve opening is generally considered to be a proxy for filter-feeding and respiration (Dorgelo and Smeenk, 1988), with a positive linear correlation between valve opening and filtration rate usually reported in mussels (Maire et al., 2007; Riisgård, 2004). Interestingly, we found such positive relationship between valve activity and filtration rate in the control quagga mussels (*i.e.*, which never experienced motorboat noise during our investigation) but not in the quagga mussels always exposed to motorboat noise (*i.e.*, over both the rearing phase and the filtration experiment), despite higher valve activity compared to control mussels. For quagga mussels that experienced motorboat noise during either the rearing phase or the filtration experiment, the relationship between valve activity and filtration rate was still positive but weaker compared to the control mussels. This could be consistent with our previous assumption on the cumulative effect of noise.

Closing the valves though the contraction of the adductor muscle requires energy (Livingstone, 1982) and increased valve activity that does not result in increased filtration might reflect a reduction in muscle contraction linked to altered metabolism. Previous

investigations on the response to anthropogenic noise of marine mussels have indeed reported physiological symptoms of metabolic slowdowns. The Mediterranean mussel *Mytilus galloprovincialis* showed an increase in the biomarkers of the stress response including glucose, total proteins, total hemocyte number, heat shock protein 70 expression and acetylcholinesterase activity in response to 1-s sweeps in the sound frequencies produced by shipping traffic (from 0.1 to 5 kHz) and repeated continuously over 30 min (Vazzana et al., 2016). The blue mussel *M. edulis* showed reduced oxygen consumption and filtration rate as well as DNA damages likely resulting from oxidative stress in response to ship noise playbacks lasting from one to six hours (Wale et al., 2019). As suggested by Wale et al., 2019, mussels might optimize the energy cost between the metabolic demand and the contraction of the adductor muscle thereby explaining the larger valve gape. Additional molecular investigations could also reveal the existence of physiological compensation whereby the individuals use their energy reserve to cope with altered metabolism. Such compensatory response is manifested by an increase in the glycolytic activity with a rise in the glucose levels (Vazzana et al., 2016) and could explain why the quagga mussels did not show alteration in valve activity following short noise exposure (*i.e.* when they experienced boat noise only during the filtration experiment).

Before concluding on the possible ecological implications of our results, some limitations have to be addressed. We were not able to assess nocturnal clearance rate so we cannot exclude a compensatory response whereby the mussels that experience chronic boat noise during day-time increase their clearance rate at night. Due to technical constraints, we provided sound levels in units of pressure when mussels are sensitive to particle motion. According to the lab investigation by Olivier et al., 2023 when the source level increases or decreases by N dB, both the potential energy of sound pressure and the kinetic energy of

particle motion will increase or decrease by N dB. It follows that relying solely on pressure does not allow to study dose-effect relationships or to detect thresholds, but remains suitable to find qualitative trends. Laboratory-based acoustic experiments have raised criticisms for two main reasons (Popper and Hawkins, 2019). First, laboratory conditions in general can induce deviations in natural behaviors as they do not account for all the biotic and abiotic factor that interact to influence the physiological state of organisms. Context-dependencies in the response to noise might induce shifts in risk-taking or compensatory behaviors (Halfwerk and Slabbekoorn, 2015). For instance, boat noise playback was found to reduce valve gape in marine mussels (*Mytilus* spp.) but this effect was not visible under the physical presence of a shore crab (*Carcinus maenas*) (Hubert et al., 2023). This is because valve closure was stronger in response to the crab alone. From a general perspective, much effort is needed to understand the response to noise in a multi-stress context. Second, tanks and aquaria, especially when small, can induce sound distortion (Akamatsu et al., 2002). However, compared to complex biological sounds, motorboat sounds are long and broadband and do not convey information. So even if our playbacks were a little different from the original signals due to sound distortion, we can assume that they have somewhere well mimicked what mussels experience in the field.

5. CONCLUSION

Given the few species studied, the differences in the protocols in terms of exposure time, acoustic cue and experimental conditions, and the species specificity of the response to noise, it is not possible to conclude that the quagga mussel is more or less resilient to anthropogenic noise than other bivalves. Additional investigations using standard protocols under a rigorous

experimental framework are needed to compare the response to noise between invasive and native invertebrates. Our results suggest that a moderate and realistic chronic exposure to motorboat noise increases aggregation and disrupts the positive relationship between valve activity and filtration in the invasive quagga mussel. An important perspective is to test whether these sublethal, trait-mediated, effects result in density-mediated effects in case of changes in individuals' fitness that would alter population dynamics. A next step is also to understand and quantify the broader consequences at the ecosystem level by assessing the relative contribution of noise compared to other environmental determinants to benthification and biofouling, two processes dependent on mussel activity and known to cause huge ecological and economic impacts.

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ETHIC STATEMENTS

The capture and transport of quagga mussels was approved by the Direction Départementale des Territoires de la Savoie (DDT 73, Approval no. 2022-0463). All procedures were carried out in accordance with the relevant European (Directive 2010/63/EU) and French national directives, authorizations and regulations concerning animal care and experimental use (Approval no. C42 218 0901, Direction Départementale de la Protection des Populations de la Loire, Préfecture du Rhône).

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CONFLICT OF INTEREST

The authors declare that they have no conflicts of interest.

DATA AVAILABILITY

The data that support the findings of this study are open available in Zenodo at <https://doi.org/10.5281/zenodo.8316278>.

FIGURES LEGENDS

Figure 1: Presentation of the set-up in the rearing aquaria (A): the numbers represent the experimental arenas filled simultaneously, the starvation aquaria (B) and the filtration aquaria (C).

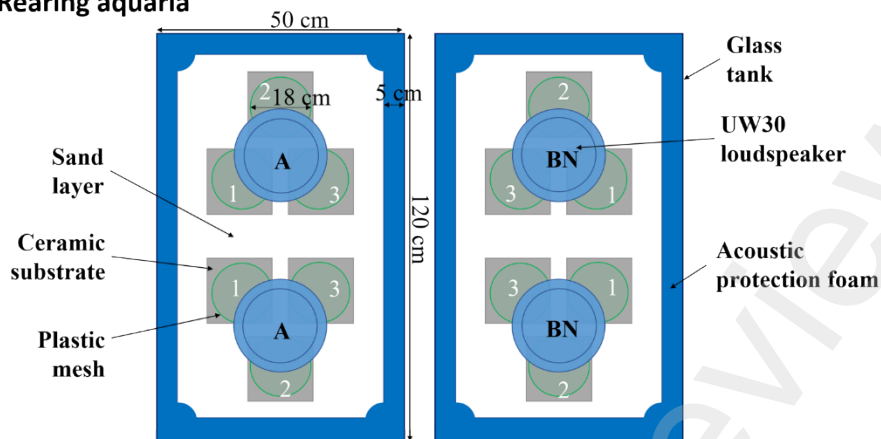
Figure 1: Relative power spectral density (left panels) and box plots of the sound pressure level (right panels) of the ambient noise treatment (control, blue) and the boat noise treatment (red) in the rearing aquaria (A), the starvation aquaria (B) and the filtration aquaria (C), see Fig. 1 for a description of each aquaria type. Solid lines are the average values of all boat sounds while shaded areas delimit the min and max values. The framed area indicates the frequency range of bivalves' sensitivity (Duarte et al., 2021).

Figure 3: Relationship between mean aggregate size (*i.e.*, the average number of mussels per aggregate, \overline{AS}) and aggregation rate (AR) in the invasive quagga mussel *Dreissena bugensis* reared in the absence (blue, $N = 17$) or presence (red, $N = 17$) of boat noise, with box plots on the corresponding axes

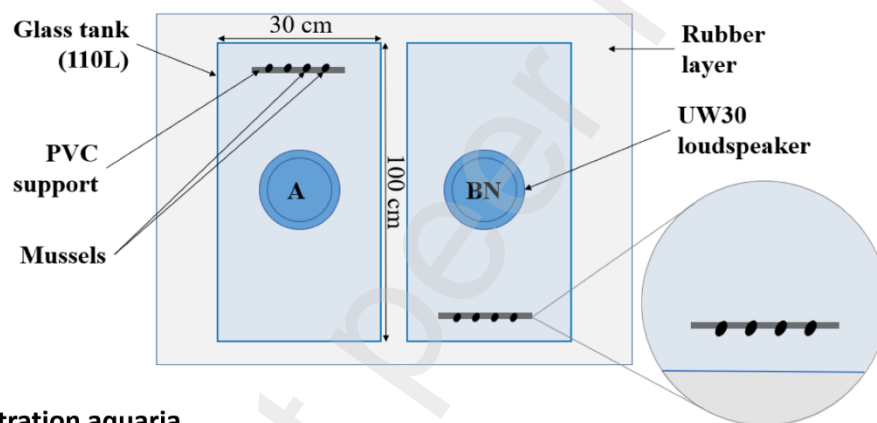
Figure 4: Box plots of the average normalized gape (\overline{NG} , A) and the relative time spent open (TO , B) of invasive quagga mussels *Dreissena bugensis* that experienced ambient noise during both the rearing phase and the filtration experiment (AA), ambient noise during the rearing phase and boat noise during the filtration experiment (AB), boat noise first and then ambient noise (BA), or boat noise during both successive experiments (BB). Lines show individual mussels whose activity was measured during the day (white) and then at night (grey, see text for further detail).

Figure 5: Linear regression between algal filtration rate (FR) and valve activity (VA) of invasive quagga mussels *Dreissena bugensis* that experienced ambient noise during both the rearing phase and the filtration experiment (AA, blue solid line and blue filled dots, $N = 7$), ambient noise during the rearing phase and boat noise during the filtration experiment (AB, blue dashed line and blue open dots, $N = 7$), boat noise first and then ambient noise (BA, red dashed line and red open triangles, $N = 7$), or boat noise during both successive experiments (BB, red solid line and red filled triangles, $N = 7$).

A) Rearing aquaria



B) Starvation aquaria



C) Filtration aquaria

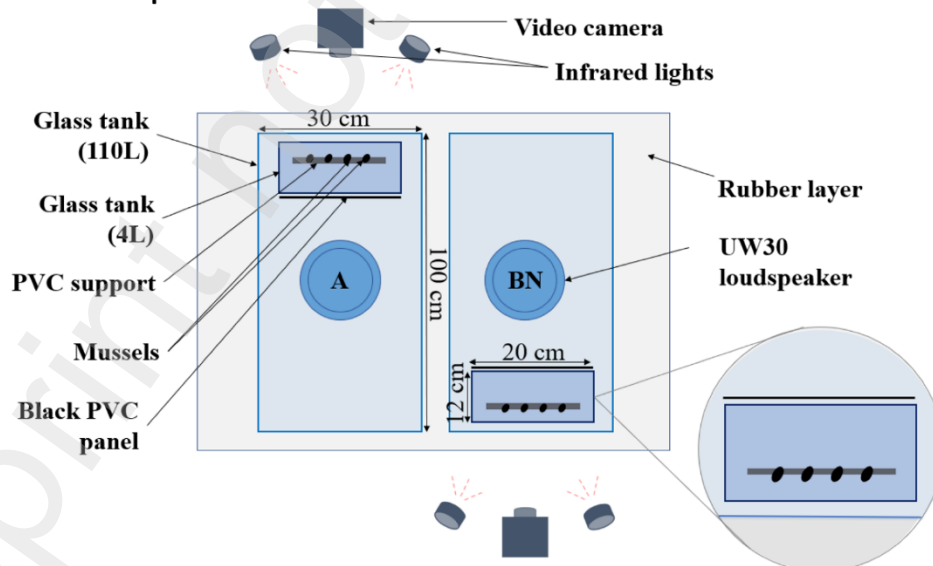


Figure 1

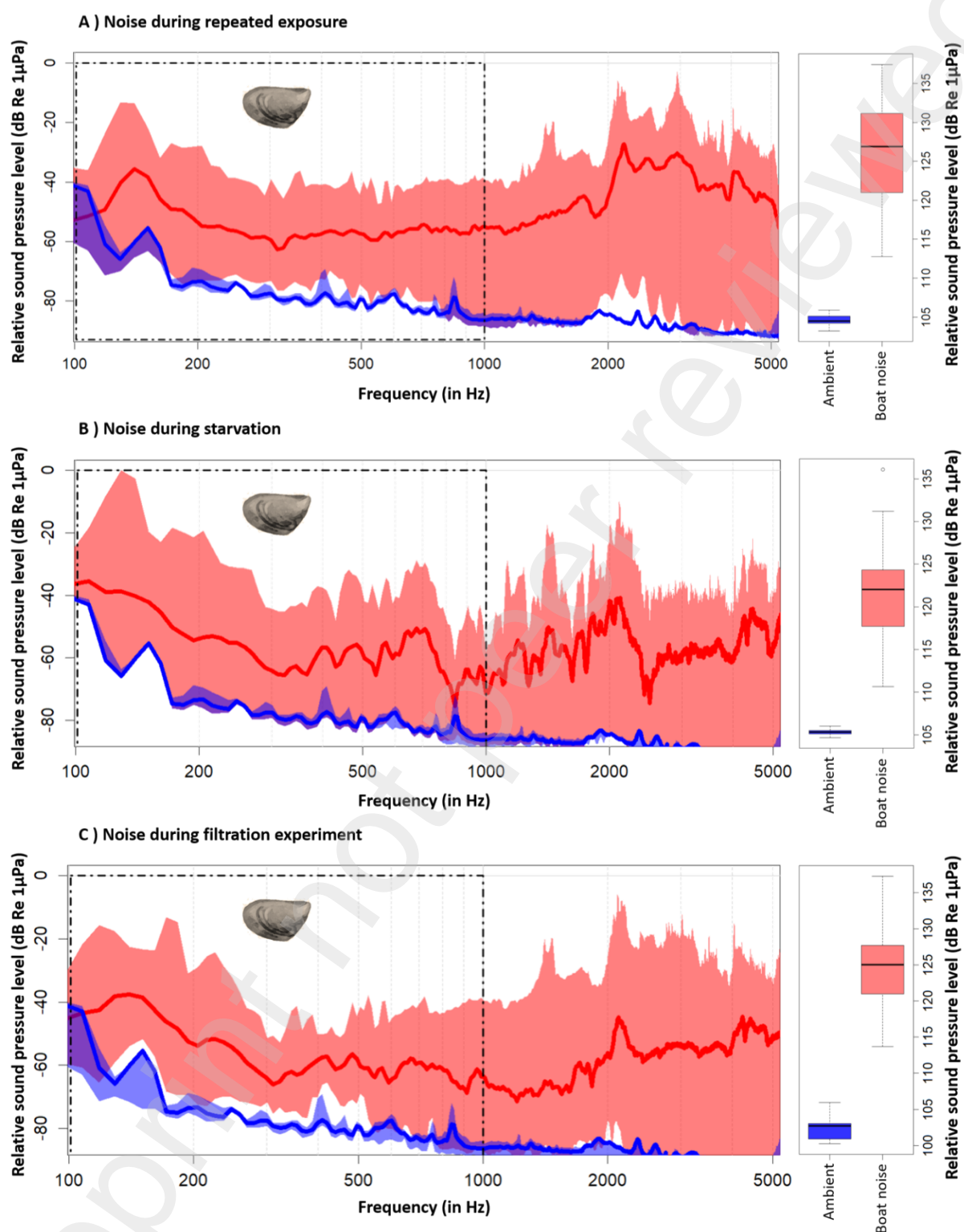


Figure 2

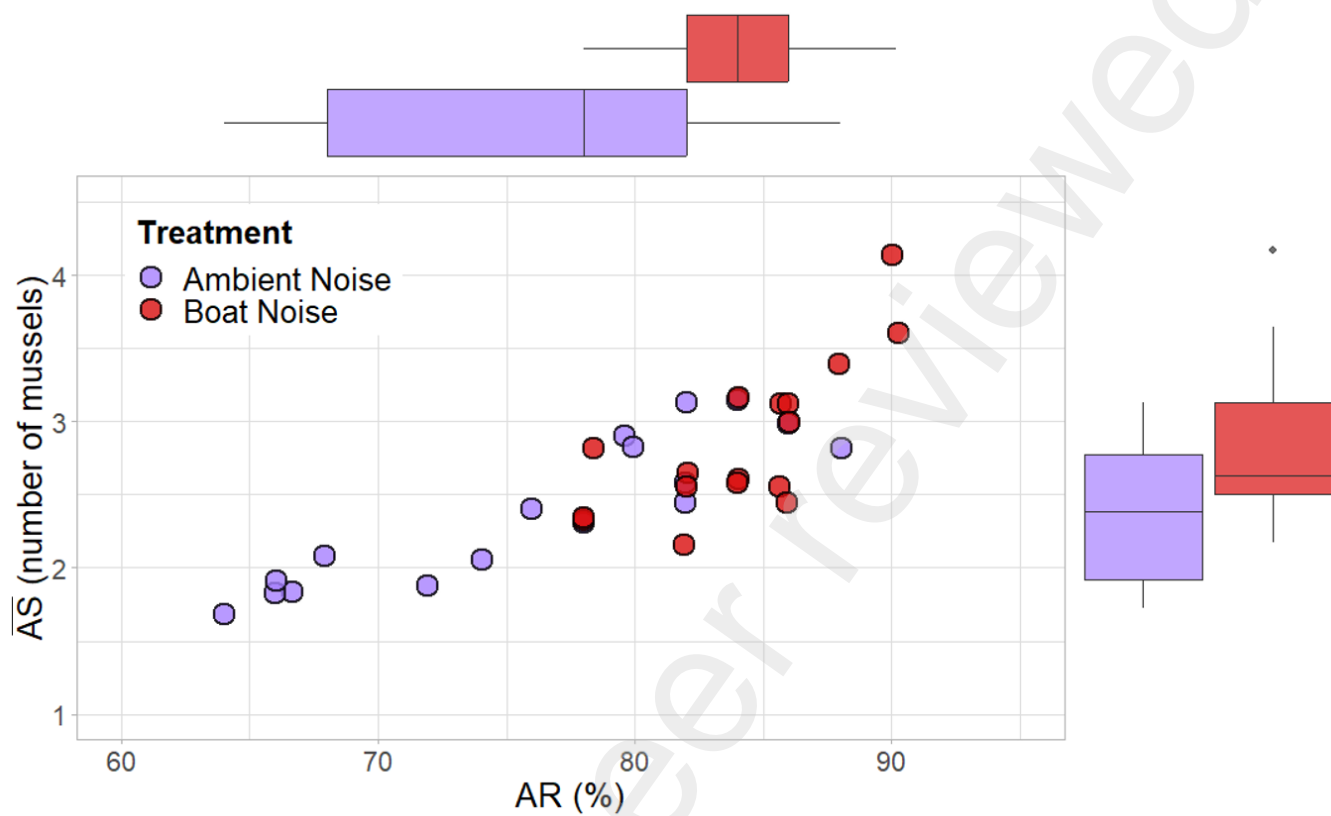


Figure 3

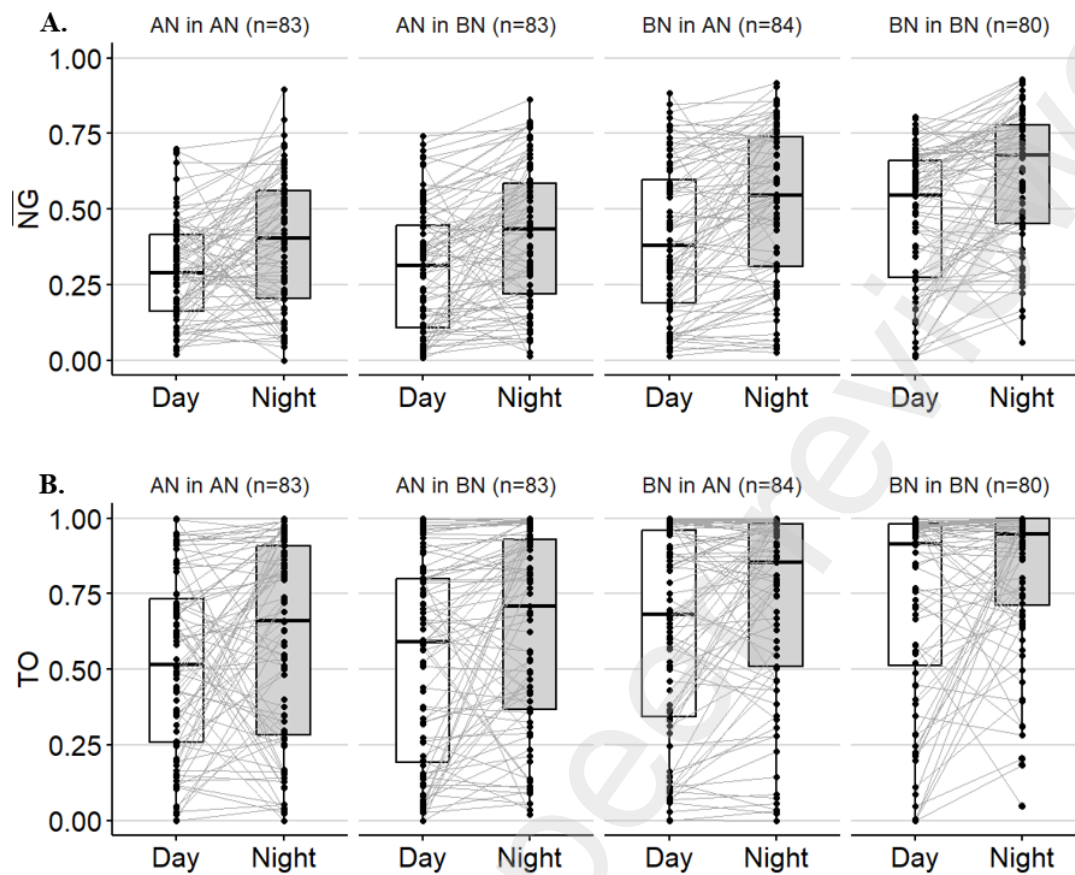


Figure 4

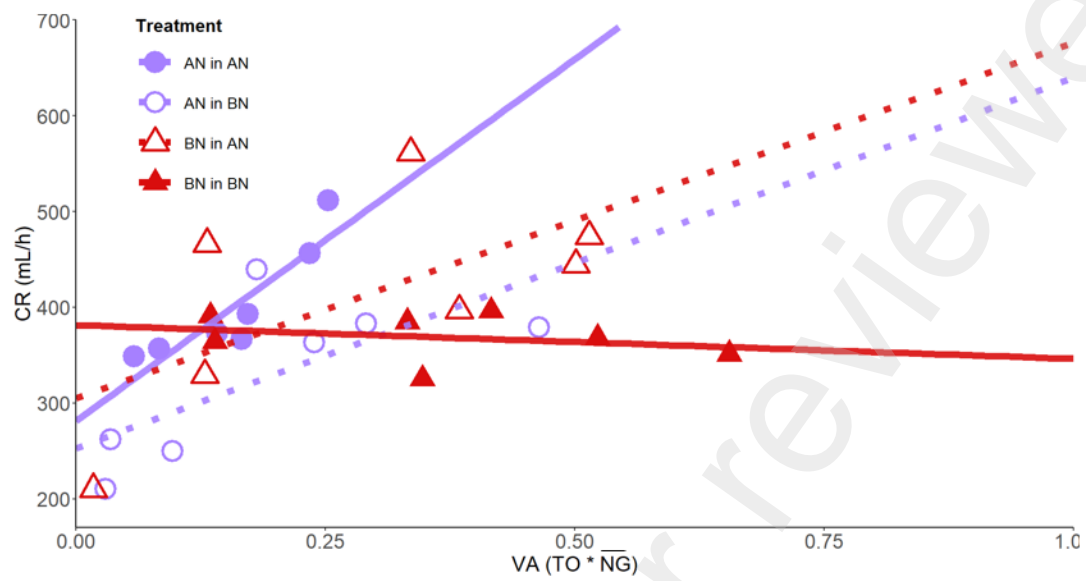


Figure 5

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