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

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► **To cite this version:**

Théophile Turco, Paola Casole, Denis Saint Marcoux, Alicia Romero-Ramirez, Marilyn Beauchaud, et al.. Behavioral and Ecological Responses of an Invasive Freshwater Mussel to Noise Pollution. 2024. hal-04705705

HAL Id: hal-04705705

<https://hal.science/hal-04705705v1>

Preprint submitted on 23 Sep 2024

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1 **TITLE**

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

3

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Preprint not peer reviewed

31 **ABSTRACT**

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

51

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

54

55 **1. INTRODUCTION**

56

57 Sound emissions from human activities, also referred to as anthropogenic noise or noise
58 pollution, have recently been considered an emerging threat to fresh waters (Reid et al.,
59 2019). Public and authorities' concern for freshwater noise pollution is late compared to
60 marine noise pollution that is part of international agendas and guidelines including the
61 [United Nations Convention on the Law of the Sea](#) and the [European Marine Strategy](#)
62 [Framework Directive 2008/56/EC](#). With the growing of human needs, the desire to reconnect
63 with nature and the diversification of nautical leisure activities, anthropic pressures on inland
64 waters and their associated sound emissions are not expected to ease (Duarte et al., 2021;
65 Miret-Pastor et al., 2020; Vázquez, 2020).

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

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

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

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

103 facilitating the colonization of new environments and a highly efficient suspension-feeding
104 benthic adult stage (Karatayev et al., 2015). Invasive dreissenids can reach very high densities
105 in their new environments and become a major determinant of their functioning, mainly
106 though their impact on the phytoplankton biomass and the transfer of matter and energy from
107 the pelagic realm to the benthos, a process referred to as benthification (Higgins and Zanden,
108 2010; Karatayev et al., 2015). The reefs they build also facilitate the establishment of other
109 non-native invertebrates or shift in dominance structure of the community (Verstijnen et al.,
110 2019; Ward and Ricciardi, 2007) while fouling has negative impacts on many infrastructures
111 involved in energy production, water supply and boat traffic (Nalepa and Schloesser, 2013).
112 Between the impacted years 1980-2020, the *Dreissenidae* family generated significant costs
113 estimated for a total of 51.1 billion dollars worldwide (Haubrock et al., 2022).

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

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

131

132 **2. MATERIALS AND METHOD**

133

134 *2.1. General design*

135

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

145

146 *2.2. Animal collection and maintenance*

147

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

151 5°51'40.481"E, Le Bourget-du-Lac, France). Back to the laboratory, they were kept in the
152 transport cooler with water aeration in a rearing room thermoregulated at 18°C, corresponding
153 to the average temperature experienced by mussels in Lake Bourget at the end of spring. Two
154 hours before the beginning of the rearing phase, adult specimens with a shell length ranging
155 from 1.95 to 2.3 cm (mean \pm SD: 2.17 \pm 0.05 cm) were selected, cleaned using a toothbrush to
156 remove organic matter and epibionts, and kept in a mix of lake water and tap water treated
157 with water conditioner (Aquasafe, TETRA®, treated water hereafter) for a 1-h acclimatization
158 period.

159

160 2.3. Rearing phase and aggregation

161

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

175 ranged from 12L:12D to 18L:6D from March to June and we acclimatized all the mussels to
176 12L:12D during the rearing phase for practical reasons (see 2.4). We renewed 30% of the
177 water twice a week while aeration was ensured by turning on the air pump for 15 min three
178 times a day.

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

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

$$195 \quad \overline{AS} = \frac{\sum AS}{AN}$$

$$196 \quad AR = \frac{n_m - S}{n_m} * 100$$

197 where n_m corresponds to the total number of live mussels.

198

199 *2.4. Filtration experiment*

200

201 The experiment was performed under the same light and temperature conditions (200 lux, LD
202 12:12 and 18°C) in four 110-L aquaria (110 x 40 x 30 cm) filled with 80 L of treated tap
203 water. Two aquaria were used for the starvation period and the two others for the measure of
204 filtration rates (starvation and filtration aquaria hereafter, respectively). Each aquarium was
205 equipped with one underwater loudspeaker (ElectroVoice UW30, 0.1 to 10 kHz) fixed in the
206 middle, face down, and 3 cm below the water surface (Fig. 1B).

207 We randomly selected twelve mussels (six *per* experimental arena) from each of the
208 two rearing aquaria (one *per* noise condition), which were gently detached from the floor tile
209 and glued on a small PVC rack (Fig. 1C). We added a white dot at the tip of the free valve to
210 maximize contrast and promote the assessment of valve opening activity. Before the filtration
211 experiment and to standardize hunger, the mussels (on their racks) were transferred for 24
212 hours into the starvation aquaria whose water was filtered (0.42 µm) to remove potential food
213 particles, and where the mussels experienced the same noise condition as during the rearing
214 phase. At the end of the starvation period, we placed the mussels in a 4-L glass aquarium (20
215 x12 x 20 cm, “filtration aquaria” in Fig. 1C) filled with filtered, treated tap water whose
216 continuous flow was ensured by a peristaltic pump (flow rate: 3.5 L/h). Each 4-L aquarium
217 was placed inside one of the two large aquaria with the loudspeaker broadcasting either
218 silence or boat noise (see 2.5) to get the four treatments when considering the noise condition
219 previously experienced during the rearing phase (AA, AB, BA and BB, see 2.1).

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

222 and the second from 8 PM to 2 AM in darkness and background noise to mimic night. After a
223 30-min acclimatization period, the experiment started with the introduction of *C. reinhardtii*
224 at a concentration of 22000 Cel/mL. We used an automated image acquisition system made of
225 a video sensor (μ Eye UI-1540-MM with a 25 mm lens) and infra-red lights. Images were
226 acquired every 20 s and combined into AVI format movies using an image analysis software
227 (Aviexplore, Romero-Ramirez et al., 2016). Valve gape was then assessed frame-by-frame
228 directly from the 2,158-frame movies using the same software. Gape tracking was
229 automatically determined, based on the coordinates of the barycenter of the white dot on the
230 free valve. In case of loss of the tracking (hidden by the siphon for instance), the x - y position
231 of the barycenter was determined manually. The reference position of the white dot (valve
232 gape = 0) was determined by triggering the closing of each mussel. For each image, the
233 coordinates of reference position was subtracted at tracking coordinates to obtain the valve
234 gape (Maire et al., 2007). To accurately estimate filtration rate, we sampled 10 ml of water at
235 the beginning of the experiment and then every hour during the day phase, fixed the algae
236 with lugol and stored the samples at 3°C for later counting (see below). Because water
237 sampling may trigger mussel closing, we excluded the ten minutes (corresponding to 30
238 frames) before and after each sampling event, resulting in a total of 1,835 frames analyzed
239 (756 during the day phase and 1,079 during the night phase).

240 The mussels that never opened were considered as in bad condition and removed from
241 the data set (six mussels among the 336 monitored, with a maximum of two mussels for a
242 given PVC rack, and no difference between the treatments, Chi-squared test: $\chi^2 = 6.1091$, $df =$
243 3 , $P = 0.106$). To improve comparison between individuals, gape values were divided by the
244 maximum gape recorded during the twelve hours (normalized gape in proportion, NG). For
245 each mussel, we calculated the average normalized gape (\overline{NG}) and the relative time spent

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

$$248 \quad \overline{NG} = \frac{\sum NG}{n}$$

$$249 \quad TO = \frac{\sum NG_{10}}{n}$$

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

252 Filtration was assessed using the clearance method (Coughlan, 1969) which has
253 proved reliable with many filter feeding bivalves including the quagga mussel (Pedersen et
254 al., 2020). Algae cell density was determined by Malassez cells counts under an optical
255 microscope and clearance rate (CR) was calculated using the following formula (Riisgård,
256 2004):

$$257 \quad CR = \frac{V * a}{n_m}$$

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

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

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

268
$$VA = \overline{NG} * TO$$

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

271

272 2.5. Playback tracks

273

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

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

286 Regarding the boat noise treatments, we used different boat sounds recorded in July
287 2021 at 21-m depth in Lake Bourget (45°39'35.5"N, 5°53'9.599"E, France) using a
288 hydrophone (Colmar GP1516, frequency response from 5 Hz to 70 kHz) connected to an
289 underwater acoustic recorder (RTsys SYLENCE-LP). We manually calculated the boat traffic
290 (*i.e.*, temporal distribution of the sounds) and quantified the levels (in dB) at which 90

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

$$293 \quad \text{SNR} = 20\log_{10}(\text{RMS}_{\text{boat sound}}/\text{RMS}_{\text{background noise}})$$

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

295 During the rearing phase, we generated a one-week playback track in which 738
296 motorboat sounds were added to silence with fade in and out. The track was looped until the
297 end of the rearing phase. The 738 sounds were randomly selected from 30 original boat
298 recordings made in Lake Bourget (each original sound was therefore played several times)
299 and distributed so as to mimic the daily and hourly nautical activity of the lake in July 2021.
300 Total boat number *per* day ranged from 87 to 121 with the first boat at 5:32 am and the last at
301 00:10 am, the position of the boat sounds within each hour being random (Table S1a).

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

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

313

314 2.6. Statistics

315

316 We performed all the statistical analyses using the R software version 4.1 (R Core Team,
317 2023) with a 5% confidence level. Because the data on mussel aggregation did not meet the
318 normality and homoscedasticity assumptions of parametric statistics, we used Wilcoxon tests
319 with Bonferroni correction to compare the difference in \overline{AS} and AR between the two noise
320 conditions. For the filtration activity, we used generalized linear mixed models with beta
321 regression using the "glmm TMB" R package to explain in two separate analyses the
322 variations in \overline{NG} and TO as a function of three qualitative predictors with two modalities each:
323 the noise condition of the rearing phase (Ambient/Boat), the noise condition of the filtration
324 experiment (Ambient/Boat) and the period (Day/Night). We accounted for the nested design
325 and possible time effect through a random term with individual mussels nested within their
326 PVC rack, itself nested within the day of experiment. We used linear models to explain CR as
327 a function of VA as a quantitative predictor, the noise condition of the rearing phase
328 (Ambient/Boat), the noise condition of the filtration experiment (Ambient/Boat), and their
329 interaction. We expected the relationship between CR and VA to be linear based on previous
330 studies with closely related species (Maire et al., 2007; Albert et al., 2022).

331

332 3. RESULTS

333

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

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

340 Regarding filtration activity during day, the average normalized gape (\overline{NG} , Fig. 4A)
341 and the relative time spent open (TO , Fig. 4B) were significantly influenced by the period
342 with higher values at night compare to day (ANOVA, $Df=1$ and $P < 0.001$ for \overline{NG} , $Df=1$ and
343 $P= 0.017$ for TO). They were also significantly impacted by the noise condition experienced
344 during the rearing phase with higher values under boat noise ($Df=1$ and $P < 0.001$ for \overline{NG} ,
345 $Df=1$ and $P= 0.002$ for TO). However, neither the noise condition during the filtration
346 experiment nor the interaction between the noise conditions of the two successive
347 experiments had a significant effect on \overline{NG} and TO (all $P > 0.05$).

348 Filtration rate (FR) was significantly influenced by VA (ANOVA, $Df=1$ and $P =$
349 0.004), the noise condition of the filtration experiment ($Df=1$ and $P = 0.006$), the interaction
350 between VA and the noise condition of the filtration experiment ($Df=1$ and $P = 0.026$), and by
351 the interaction between VA and the noise condition during the rearing phase (ANOVA, $Df=1$
352 and $P = 0.034$). In other words, the relationship between CR (*Clearance Rate*) and VA was
353 positive when the mussels experienced ambient noise only, weaker with boat noise during one
354 of the two phases (rearing condition or filtration measurement), and null when the mussels
355 experienced boat noise during the two phases (Fig. 5).

356

357 **4. DISCUSSION**

358

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

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

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

386 sounds and react as they do under natural threats such as predation (Kobak and Kakareko,
387 2011; Naddafi and Rudstam, 2013).

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

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

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

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

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

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

434 investigations on the response to anthropogenic noise of marine mussels have indeed reported
435 physiological symptoms of metabolic slowdowns. The Mediterranean mussel *Mytilus*
436 *galloprovincialis* showed an increase in the biomarkers of the stress response including
437 glucose, total proteins, total hemocyte number, heat shock protein 70 expression and
438 acetylcholinesterase activity in response to 1-s sweeps in the sound frequencies produced by
439 shipping traffic (from 0.1 to 5 kHz) and repeated continuously over 30 min (Vazzana et al.,
440 2016). The blue mussel *M. edulis* showed reduced oxygen consumption and filtration rate as
441 well as DNA damages likely resulting from oxidative stress in response to ship noise
442 playbacks lasting from one to six hours (Wale et al., 2019). As suggested by Wale et al., 2019,
443 mussels might optimize the energy cost between the metabolic demand and the contraction of
444 the adductor muscle thereby explaining the larger valve gape. Additional molecular
445 investigations could also reveal the existence of physiological compensation whereby the
446 individuals use their energy reserve to cope with altered metabolism. Such compensatory
447 response is manifested by an increase in the glycolytic activity with a rise in the glucose
448 levels (Vazzana et al., 2016) and could explain why the quagga mussels did not show
449 alteration in valve activity following short noise exposure (*i.e.* when they experienced boat
450 noise only during the filtration experiment).

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

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

475

476 5. CONCLUSION

477

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

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

492

493 **ACKNOWLEDGEMENTS**

494 The authors would like to thank Sandrine Bujaldon from IBPC (Institut de Biologie Physico-
495 Chimique, Paris) for providing the algae strains. We are also grateful to Khalil Boughalmi
496 from ENES lab for his support and interesting discussions.

497

498 **ETHIC STATEMENTS**

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

505

506 **FUNDING**

507 This study was part of the POLLUSON research project funded by the Région Auvergne
508 Rhône Alpes.

509

510 **CONFLICT OF INTEREST**

511 The authors declare that they have no conflicts of interest.

512

513 **DATA AVAILABILITY**

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

516

517 **FIGURES LEGENDS**

518

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

522

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

529

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

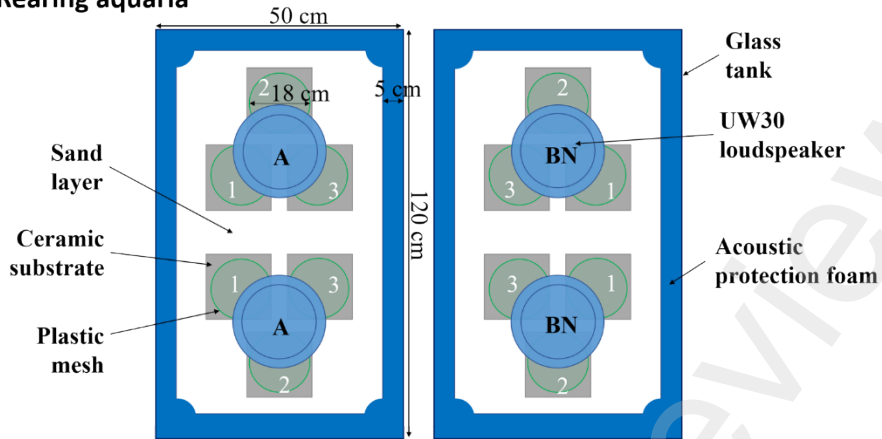
534

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

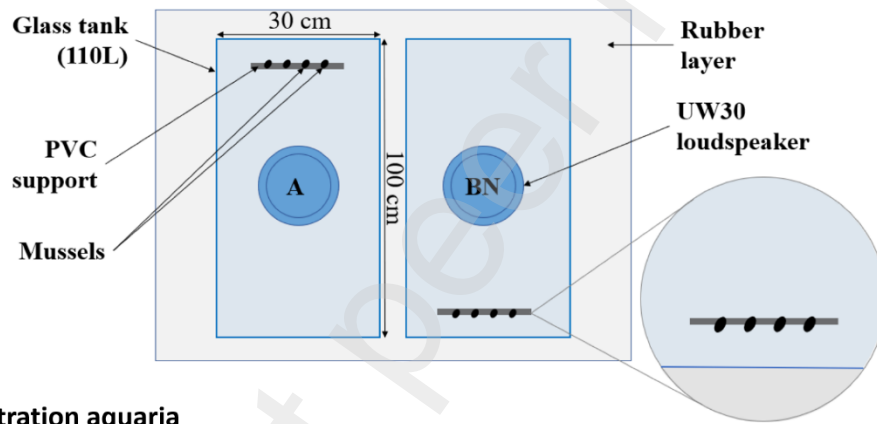
542

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

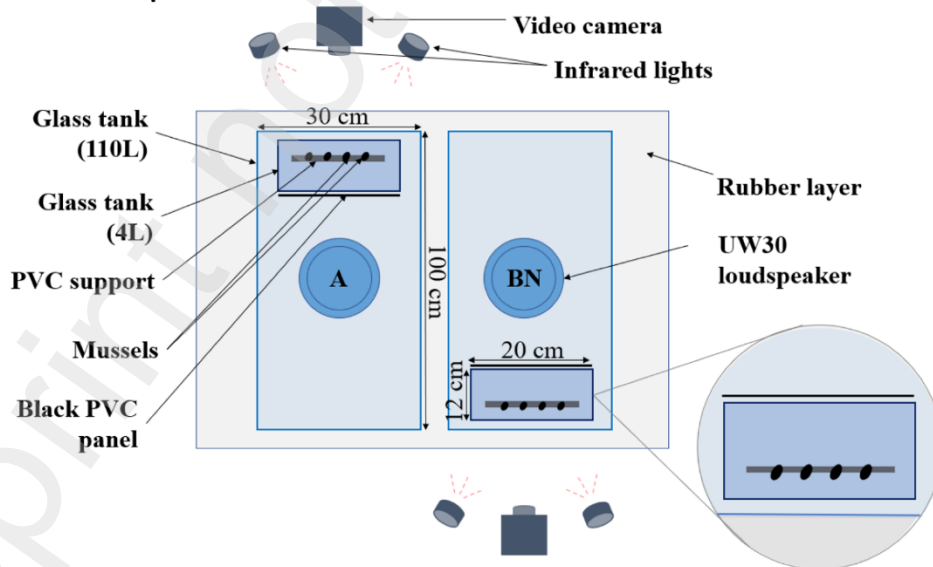
A) Rearing aquaria



B) Starvation aquaria



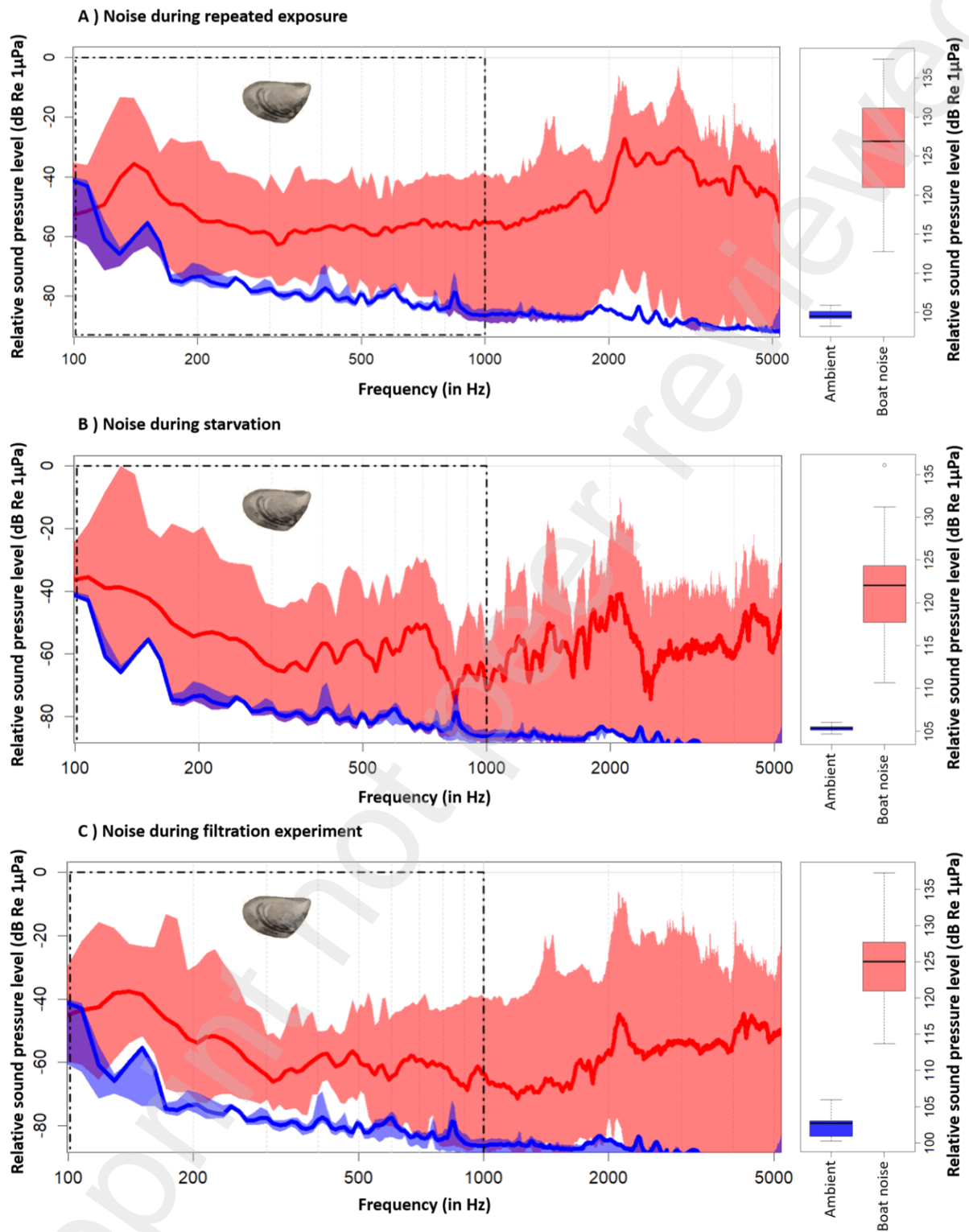
C) Filtration aquaria



550

551

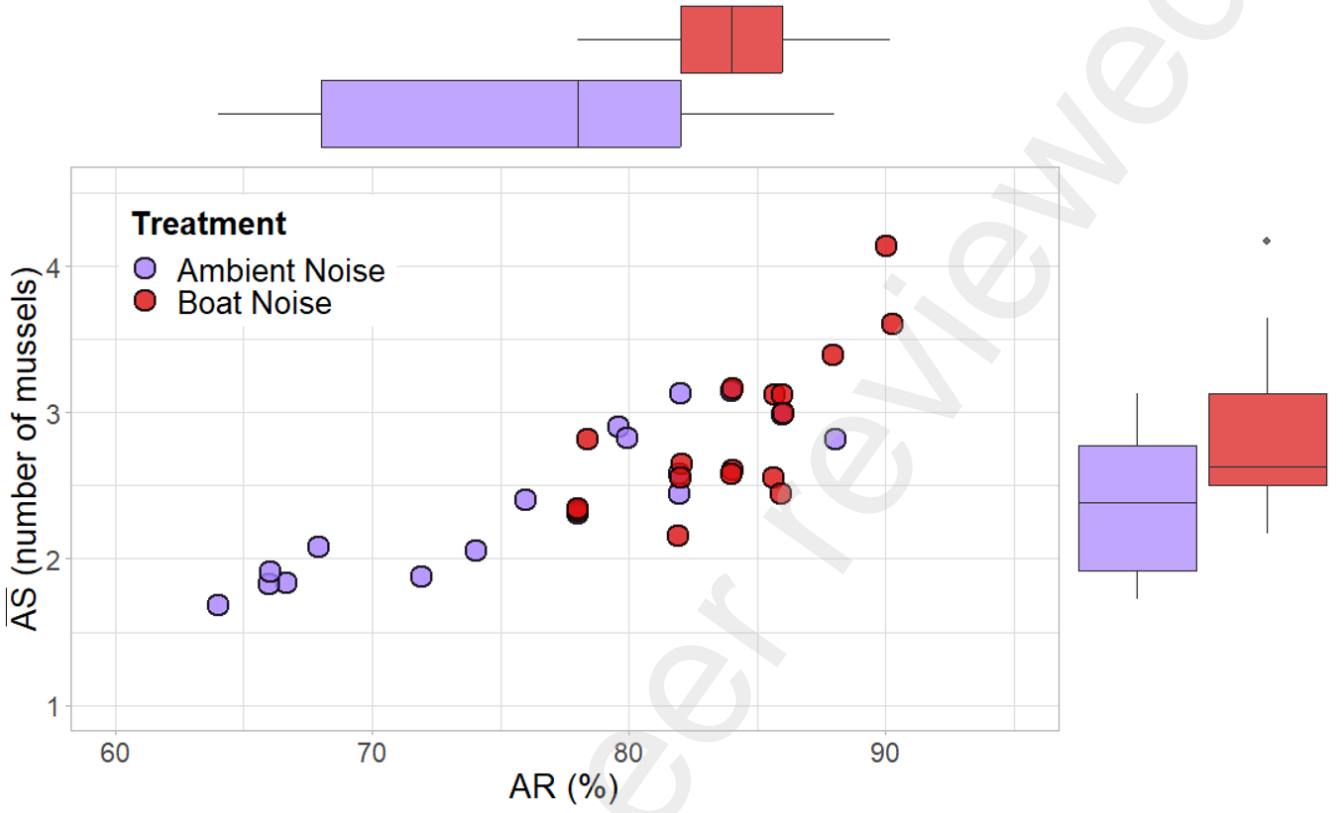
Figure 1



552

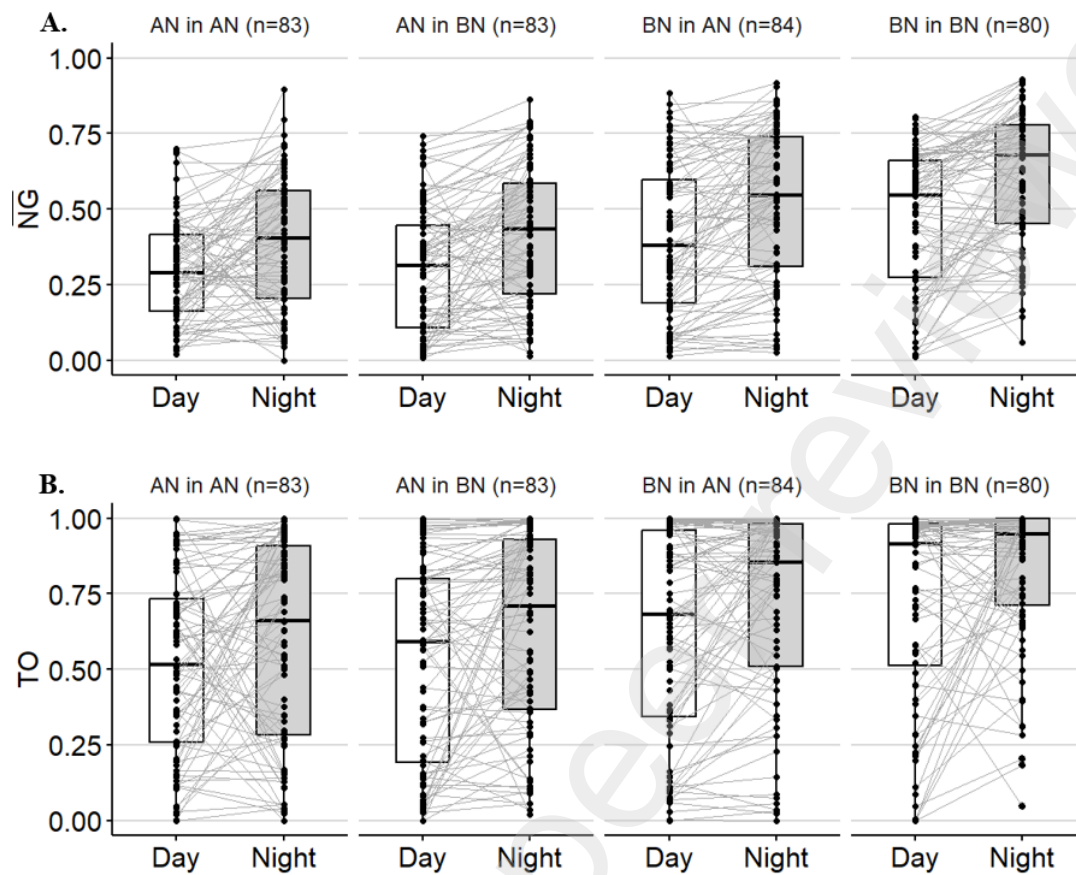
553

Figure 2



554
555
556

Figure 3

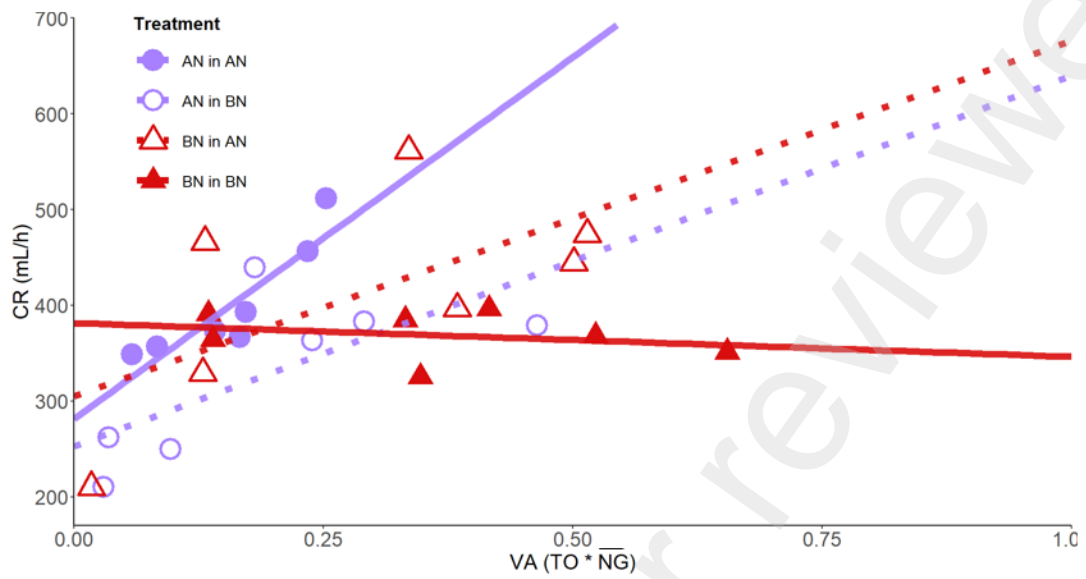


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559

Figure 4



560

561

Figure 5

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