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1 Response of freshwater zooplankton communities to chronic 2 anthropogenic noise

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28

29 30 1. Abstract 31

32 Man-made sounds are now recognized a pervasive pollutant and impacts on wildlife have
33 been researched for many years. However, less knowledge is available on certain species and
34 particularly small freshwater invertebrates, although abundant, highly diversified and
35 occupying key positions in food webs. Also, it's not clear whether the responses to noise
36 observed at the level of individuals have consequences on communities. We performed a
37 mesocosm investigation to assess the response of a freshwater planktonic community to
38 chronic motorboat noise. We expected noise to disturb trophic links within the community
39 and particularly the consumption of cladocerans by dipteran larvae. To test this hypothesis,
40 we derived the functional response recorded the behaviour of *Chaoborus* larvae feeding on
41 *Daphnia* in aquariums. Although noise did not induce obvious alteration in the community
42 composition, we found a significant increase in the abundance of cladocerans that we failed to

43 explain based on our aquarium investigation as we did not find any difference in *Chaoborus*
44 functional response and behaviour between the noisy and noiseless conditions. Our results
45 suggest that the dynamics of freshwater zooplankton is likely to be altered by chronic noise
46 and illustrate how scaling up the effects of noise from individual responses to community
47 remains difficult.

48

49 **2. Keywords**

50 Freshwater zooplankton, motorboat noise, functional response, trophic links, daphnids,
51 *Chaoborus* larvae

52

53 **3. Introduction**

54

55 Threats to freshwaters include habitat degradation, flow modification, overexploitation,
56 invasive species and disease (Dudgeon et al., 2006; Williams-Subiza & Epele, 2021), and
57 result in a decline in biodiversity at rates that exceed what is reported in most terrestrial and
58 marine habitats (McRae et al., 2017). Anthropic pressures on freshwaters are not expected to
59 ease given the growing of human needs and also because people seek to reconnect with
60 nature, a need reinforced by the recent crises like the Covid-19 pandemic. Managers of
61 freshwaters socio-ecological systems worry about the rise of recreational motorized activities
62 and their associated noise emissions (Reid et al., 2019) that can disturb the various
63 populations of users as well as wildlife.

64 Noise pollution has recently been categorized as an emergent threat to freshwaters
65 (Reid et al., 2019), with motorized boats as the most widespread source of noise. Impacts of
66 noise on fishes are well documented with physiological stress responses and alterations in
67 communication, reproduction, mobility, foraging and predator avoidance (reviewed by Mickle

68 & Higgs, 2018; Popper, 2003; Slabbekoorn et al., 2010). Although invertebrates are highly
69 diverse, widespread and possess statocysts or external sensory hairs that allow them to
70 perceive sounds through particle motion (Popper & Hawkins, 2018), interest in their response
71 to noise pollution came later compared to vertebrate species and 77% of the impact studies on
72 invertebrates are less than ten years (Wale et al., 2021). While cephalopods, large crustaceans
73 (crabs, lobsters, shrimps) and bivalves are among the most common model species studied
74 (Fernández Robledo et al., 2019; Smith et al., 2018), we know little about small zooplankton
75 despite its pivotal role in the functioning of aquatic food webs, maintaining energy flow
76 between primary producers and higher trophic levels (Turner, 2004; Vargas et al., 2010).

77 Available evidence on zooplankton shows a diversity of effects. While very loud
78 emissions from seismic surveys have been found to cause mortality in both larval and adult
79 stages of marine zooplankton (McCauley et al., 2017), vessel noise can act as a positive cue
80 for larval settlement in the blue mussel *Mytilus edulis* (Jolivet et al., 2016). Exposure to low
81 (30 Hz) and high (20 KHz) frequencies seems to promote grazing in the marine copepod
82 *Acartia tonsa* (Yiwei & Berggren, 2018) . The water flea *Daphnia magna* (Cladocera) shows
83 no alteration in mobility when exposed to either continuous or intermittent 300-1500 Hz
84 band-pass filtered white noise (Sabet et al., 2016). More recently, we found that larvae of the
85 phantom midge *Chaoborus* (Diptera) made more body rotations in response to motorboat
86 noise (Rojas et al., 2021).

87 In addition to the imbalance between vertebrates and invertebrates in the very rich
88 literature on the impacts of noise pollution, there is also a discrepancy between the biological
89 integration levels with a lack of research on ecosystems compared to behavioural and
90 physiological outcomes (Sordello et al., 2020). Although few empirical evidence from
91 terrestrial systems illustrate how noise-induced changes in behaviour can propagate through
92 nested ecological interactions (Francis & Barber, 2013; Phillips et al., 2021), scaling up the

93 effects of noise from individuals to populations and communities without any experimental
94 validation might overestimate impacts.

95 In the present study, we studied the effect of chronic motorboat noise on the dynamics
96 of a freshwater zooplankton community bringing together cladocerans, copepods, ostracods,
97 and dipterans. We expected an impact of noise on the community structure by altering its
98 abundance and/or the activity of the predators. To test this hypothesis, we evaluated the
99 response of the community in mesocosms over six weeks and, as a second part, we assessed
100 how the *per capita* predation rate of *Chaoborus* larvae (dipterans) varies with cladoceran
101 density (the functional response) under control and noisy conditions. *Chaoborus* larvae are a
102 relevant dominant predator of large filter-feeder zooplankton (cladoceran species) known to
103 be a main structuring force within the community (Castilho-Noll & Arcifa, 2007; Vanni &
104 Findlay, 1990). *Chaoborus* larvae have been found to make more body rotations in response
105 to motorboat noise (Rojas et al., 2021), which could be associated with reduced foraging.
106 Noise might therefore alter community dynamics through the modulation of the trophic
107 pressure by *Chaoborus* larvae.

108

109 **4. Materials and methods**

110

111 *4.1 Mesocosm experimental design*

112

113 The mesocosm experiment lasted six-weeks from September to October 2021 and was carried
114 out on the PLANAQUA platform of the CEREEP-Ecotron Ile -de-France research station
115 (48° 16'10.92 N. 2° 43'50.879 E, Seine et Marne, France). We applied two acoustic conditions
116 (with or without boat noise, see 2.4) in 16 outdoor plastic enclosures (diameter: 1.40 m,
117 depth: 1 m, volume: 1 m³, n = 8 replicates *per* condition) positioned in two lines and

118 distributed in a systematic way to balance the effect of spatial distribution between the two
119 conditions. All mesocosms included a 15-cm layer of Loire sand and were filled two months
120 before the experiment with water from the littoral zone of one of the two storage lakes from
121 the PLANAQUA platform, to reach a 70-cm water column. An underwater loudspeaker
122 (Electrovoice UW30, 0.1–10 kHz) was fixed 10 cm below the water surface in the middle of
123 each mesocosm. It was connected to an amplifier (Dynavox CS-PA 1MK), itself connected to
124 an audio player (Handy's H4n zoom), both placed inside a waterproof electric box next to the
125 mesocosm. One week before starting the experiment, temperature loggers attached to a ballast
126 were positioned in the sunniest part of each mesocosm. Water temperature was 24°C at the
127 beginning of the experiment and decreased with some small fluctuations over time to reach 18
128 °C at the end of experiment.

129

130 *4.2 Zooplankton dynamics*

131

132 At Day 0, +10, +26, and +42, we sampled eight liters of water with a 2-L sampling bottle at
133 four different positions and depths in each mesocosm. Water was filtered with a 50- μ m mesh
134 size nylon filter to collect zooplankton species which were immediately fixed in 15 mL of
135 90% ethanol. Species identification et classification of Day 0 and Day +42 were performed by
136 the engineering office © 2021 SAGE Environment (Annecy, France). To save costs accurate
137 classification was done for all the mesocosms at Day+42 while we pooled the data *per* noise
138 condition at Day0. At Day+10 and Day+26, we only quantified the numbers of cladocerans
139 and *Chaoborus flavicans* larvae as we expected that it was the most structuring trophic link of
140 our communities. At the end of the experiment, we used a multiparameter probe (YSI ExO-2)
141 to assess the main physicochemical parameters (temperature, pH, conductivity, turbidity,
142 chlorophyll).

143

144 *4.3 Functional response and behaviour of Chaoborus larvae*

145

146 We derived the functional response (FR) of *Chaoborus* larvae feeding on five densities (3, 6,
147 12, 24, 48) of *Daphnia* sp. coming from the storage lake with four replicates *per* density and
148 *per* noise condition. To account for potential habituation to the noise condition and better
149 explain what happened in the mesocosms, we collected larvae from the control and noisy
150 mesocosms and exposed them to the same noise condition (see 2.4) during the FR tests. The
151 experiment took place in two 90-L rectangular tank (75 x 60 x 20 cm, one *per* noise
152 condition) filled with filtered (50- μ m mesh size) water from the storage lake. A UW30
153 underwater loudspeaker was positioned in the center of each tank 20 cm above the bottom. A
154 single larva was presented to the water fleas at one of the five densities (3 to 48) for eight
155 hours in a 150-mL glass beaker (height = 7.2 cm, diameter = 7 cm) covered with a mesh
156 allowing water flow only. We placed the 20 beakers at 10 cm all around the speaker. At the
157 end of the experiment, each larva was removed and put into 90°C alcohol to be measured
158 under binocular loop and using a rule. The number of remaining prey was counted to
159 determine the number of prey eaten.

160

161 For evaluating *Chaoborus* larvae behaviour, we used a 50-L aquarium
162 (length×width×height: 60×25×35 cm) filled with filtered water from the mesocosms and
163 equipped with an UW30 underwater loudspeaker in the center and 20 cm above the bottom. A
164 150-mL glass beaker covered with a mesh allowing water flow only was positioned inside the
165 aquarium at 10 cm of the loudspeaker, where we observed with the naked eye a total of 20
166 larvae under ambient noise (recorded in one of the mesocosm) or ambient noise supplemented
167 with motorboat noise. From the 8-hour playlist of ambient and boat noise broadcast in the
mesocosms, we selected the 1-hour sequence containing the most boat noise from which 20

168 minutes were extracted for use in the behavioural test. We counted the number of body
169 rotations performed over the 20-min period.

170

171 *4.4 Playback tracks*

172

173 We used an Aquarian Audio H2A-HLR hydrophone (frequency response from 10 Hz to 100
174 kHz) connected to a ZOOM H4next Handy recorder for all the recordings and a UW30
175 underwater speaker (Electrovoice) connected to a Dynavox CS-PA 1MK amplifier itself
176 connected to a ZOOM H4next Handy player for all the playbacks.

177 Natural background noise did not differ between the mesocosms and was around 90
178 dB re 1 μ Pa. In the control mesocosms, a 1-hr audio track of silence was looped continuously.
179 To make the audio tracks of the noisy mesocosms, 25 sounds from commercial vessels and
180 recreational boats were recorded from the river Seine after the lock of Champagne sur Seine
181 (48°22'1.348 N, 2°29'37.401 E) at 1-m depth. We duplicated the 25 original sounds,
182 changing a bit the intensity between the two replicates, and distributed the resulting 50 sounds
183 over 14 consecutive 1-hr audio tracks of silence so as to mimic the mean daily activity of the
184 Champagne sur Seine lock (Table 1). We broadcasted the boat sound audio tracks from 6 am
185 to 8 pm and silence the rest of the time. The intensity of each boat sound was modified with
186 the Audacity 2.2.1 software to obtain realistic Signal-to-Noise Ratios (SNR) ranging from 25
187 to 30 dB (Fig. 1A), calculated after re-recordings in the mesocosms and using the *SNR*
188 function of *Seewave* R package (Sueur et al., 2008) with:

$$189 \quad \text{SNR} = 20\log_{10}(\text{RMS}_{\text{boat sound}} / \text{RMS}_{\text{ambient noise}})$$

190 where RMS corresponds to the Root-Mean-Square sound pressure level.

191 For the control condition of the FR experiment, we broadcasted an 8-h (playlist 1)
192 audio track of natural background noise previously recorded in one of the mesocosm and

193 whose level was adjusted to match that in the mesocosm around 90 dB re 1 μ Pa (Fig. 1A). For
194 the boat noise treatment, we processed similarly but with an 8-h recording (playlist 2) from a
195 noisy mesocosm (Fig. 1A). For the behavioural trials, we used 20 min of playlist 1 for the
196 control condition and 20 min of playlist 2 for the boat noise condition (Fig. 1B).

197

198 *4.5 Data analyses*

199

200 We used the R software version 4.0.3 (R Core Team, 2018) for all the statistics with a
201 significance level of 5%. We used a chi-square test of independence to assess the
202 homogeneity of taxa at Day+0 between both noise treatments. A generalized linear mixed
203 models with a quasi-poisson distribution (GLMMTMB) was performed to explain the
204 dynamic of cladocerans as a function of three fixed factors and their interactions: the noise
205 condition (ambient or motorboat noise), the abundance of *Chaoborus flavicans* larvae, the
206 sampling date, and considering the tank identity as random factor to account for repetitive
207 measures. A Quasi-Poisson (or quasi-likelihood) distribution was used because it is
208 recommended to consider the overdispersion (variance exceeds the mean) often found in
209 count data (Ver Hoef & Boveng, 2007). We also used a Wilcoxon test to test for significance
210 the difference in physiochemical parameters between the two noise conditions at Day+42.

211 For the FR experiment, we performed a one-way ANOVA test to detect heterogeneity
212 in the size of *Chaoborus* larvae between the two noise conditions as the data met the
213 normality and homoscedasticity assumptions. FR analysis was done with the *Frair* R package
214 (Pritchard et al., 2017). We modelled the three FR types (linear type I, Rogers' type II,
215 Hassel's type III) by maximum likelihood estimation (Bolker, 2008) with the *frair_fit* function
216 and the fits were compared using the second order Akaike information criterion (AIC). This
217 allowed to exclude the types II and III whose AIC values were always the highest (Δ AIC > 2

218 with the type I). A type I FR is characterized by a linear increase of consumption rate as a
219 function of prey density (Holling, 1959). As both FRs were of type I, we used the delta
220 method implemented by the *frair_compare* function to perform pairwise FR comparison from
221 parameter estimates with the null hypothesis that the difference in attack rates (D_a) between
222 the two FRs does not differ from zero (Pritchard et al., 2017). In addition to the delta method,
223 we also inspected how the 95% confidence intervals (BCa CIs) which corrects for bias and
224 skewness in the distribution of bootstrap estimates (a and h parameters), overlapped with the
225 *frair_boots* function (bootstrapping method, $n=2,000$) (Pritchard et al., 2017).

226 Concerning the behaviour of the *Chaoborus* larvae, we compared the total number of
227 body rotations between the two noise conditions using a generalized linear mixed models with
228 a negative binomial distribution with the noise condition (ambient or motorboat noise), the
229 sampling date as predictors and the tank where they coming as random factor to account for
230 repetitive measures.

231

232 **5. Results**

233 At Day+0, communities between ambient noise and ambient + motorboat noise did not differ
234 in taxa density (Chi-square test = 63.333, $df = 56$, p -value = 0.2336). At Day+42, we did not
235 find significant differences in the physicochemical parameters between the two noise
236 conditions (Table 2 and 3).

237 The zooplankton communities included in both treatments Cladocerans (*Daphia* sp.,
238 *Bosmina* sp., *Chidorus* sp. and *Ceriodaphnia* sp.), Copepods (especially Calanoïda and
239 Cyclopoïda), Ostracods and Dipterans (especially *Chaoborus* larvae). Cladocerans species
240 and more particularly *Daphnia* sp. were the most abundant at the beginning and the end of the
241 experiment in control mesocosms (57.31% and on average 52.11% respectively) whereas in
242 noisy mesocosms Copepods and Cladoceran were more abundant at Day+0 (48.25% and

243 39.84% respectively), but Cladocerans increased to reach 71.24% of the whole community at
244 the end of the experiment (Table 4, Fig. 2).

245 Under boat noise, the abundance of Cladocerans increased significantly (p-value =
246 0.044, Table 5, Fig. 3A) whereas the abundance of *Chaoborus*, the date and interactions
247 between predictors did not affect Cladoceran dynamic. The abundance of *Chaoborus* larvae
248 did not differ between the two noise conditions (GLMMs, Estimate = 0.026, Std.Error =
249 0.501, z-value = 0.050, p-value = 0.960, Fig. 3B).

250 Concerning the FR experiment, there was no difference in the size of the *Chaoborus*
251 larvae between the two noise conditions (one-way ANOVA: $F_{1,18} = 0.269$, p-value = 0.61).
252 Irrespectively of the noise condition, the FR was a type I (linear increase of *per capita*
253 consumption rate in function of prey density). We found no significant difference in attack
254 rate (fixing the slope) between the two noise conditions (Estimate = 0.087, Std.Error = 0.108,
255 z-value = 0.817, p-value = 0.413) and a strong overlap of the 95% BCa CIs, suggesting
256 similar FRs (Fig. 4A).

257 We found no significant difference in the number of body rotations between the two
258 noise conditions (noise: Estimates = 0.2957, Std.error = 0.4268, z-value = 0.693, p-value =
259 0.488, Fig. 4B). However, we obtained a greater inter-individual variability in both FR and
260 behaviour with boat noise than for controls.

261

262 **6. Discussion**

263

264 In the present study, we conducted a mesocosm investigation to assess the effect of chronic
265 motorboat noise on the dynamics of freshwater zooplankton. We also performed predation
266 tests in microcosms through the functional response (FR) derivation to test the prediction that
267 in case of a noise-induced alteration in community dynamics, this would be linked with a

268 change in the foraging behaviour of invertebrate predators, focusing in *Chaoborus flavicans*
269 as the main predator within the zooplanktonic community.

270 We did not find a marked effect of chronic motorboat noise on the zooplankton
271 community except for water fleas (*Daphnia* sp.), which represented the most abundant taxon
272 and were significantly more numerous in the noisy mesocosm. This apparent positive effect
273 could be indirect, considering that noise has no or a very limited direct negative effect on
274 water fleas but negatively influences their natural enemies. Although we did not investigate
275 the response of water fleas to noise, the absence of direct effect is partially supported by the
276 little literature available. Sabet et al. (2016) did not find any alteration in mobility in *Daphnia*
277 *magna* exposed to either continuous or intermittent 300-1500 Hz band-pass filtered white
278 noise, a result that we also obtained working on motorboat noise (Rojas et al., unpublished
279 data). More recently, (Yağcılar & Yardımcı (2021) found that exposure to 432 Hz and 440 Hz
280 frequency sounds resulted in lower egg numbers and heartbeats in *D. magna*. However, the
281 use of pure tones that do not refer to any kind of noise pollution in nature as well as the
282 absence of information on sound levels make these results difficult to compare with ours and
283 difficult to extrapolate to natural populations.

284 Concerning water fleas' natural enemies, we can reasonably assume from our FR
285 investigation that water fleas have experienced predation by *Chaoborus* larvae in the
286 mesocosms. However, contrary to our expectation, noise did not alter the FR of *Chaoborus*
287 larvae nor their behaviour assessed through the number of body rotations. The main
288 difference between our study and that of Rojas et al. (2021) where *Chaoborus* larvae
289 displayed more body rotations with motorboat noise is that we accounted for repeated
290 exposure (i.e., chronic noise), what Rojas et al. (2021) did not. So, it might be that *Chaoborus*
291 larvae show more body rotations when exposed to noise for the first time and then resume
292 normal behaviour with repeated exposure, a phenomenon also referred to as "habituation" that

293 we have missed as we did not test the response of “naïve” larvae. Habituation to noise has
294 been reported in many species including fishes (Johansson et al., 2016; Kusku, 2020; Rojas et
295 al., 2021) and aquatic invertebrates (Hubert et al., 2022), and could result from sensory or
296 motor fatigue, or associative learning between the repetition of a given stimulus and the
297 absence of any threat.

298 Similar FRs irrespectively of the noise condition does not support our hypothesis that
299 the water fleas of the noisy mesocosms benefited from a noise-induced reduction in
300 *Chaoborus* predation. Surprisingly, the FR of *Chaoborus* larvae was of type I (linear increase
301 of *per capita* predation rate with increasing prey density) whilst they were found to display a
302 type-II FR (decelerating rise to an asymptote) in previous studies (Cuthbert et al., 2019;
303 Krylov, 1992; Spitze, 1992; with *Daphnia pulex*, *D. longispina* and *Culex pipiens* as prey,
304 respectively). For our *Chaoborus* and *Daphnia* populations, the highest prey density that we
305 used (n=48) was not enough to reach saturation and we can’t exclude a possible effect of
306 noise at higher prey densities. Another reason why we fail to explain the increase in *Daphnia*
307 in the noisy mesocosms from the behaviour of *Chaoborus* larvae could be that predation tests
308 in small and highly-controlled experiment units are not representative of the foraging patterns
309 occurring in more complex systems (i.e. our mesocosms). For instance, many zooplanktonic
310 species including *Chaoborus* larvae and *Daphnia* show vertical migrations (Dawidowicz et
311 al., 1990; Haupt et al., 2009). Noise might disturb trophic links within zooplankton through
312 alterations in the species-specific spatial patterns. In other words, our tests in aquariums might
313 have underestimated the negative effect of noise on *Chaoborus* predation.

314 To understand how noise influenced our zooplanktonic communities, we focused on
315 the trophic link between *Chaoborus* larvae and *Daphnia* and we did not work on the other
316 ecological interactions, and in particular competition. Cladocerans are known to compete with
317 rotifers and copepods for common food resources (Gilbert, 1988; Lehtiniemi M & Gorokhova

318 E, 2008), copepods being the second planktonic group in terms of abundance in our
319 mesocosms (after cladocerans). To our knowledge, we don't know the response of freshwater
320 copepods to noise but a negative effect could make the competition even more asymmetric in
321 favor of cladocerans. The three groups are also engaged in apparent competition by sharing
322 *Chaoborus* larvae as predator (Elser et al., 1987; Swüste et al., 1973). An interesting
323 perspective would be to assess their respective contribution to *Chaoborus*' diet under chronic
324 noise.

325 To conclude, our study suggests that chronic motorboat noise is likely to disturb the
326 dynamics of freshwater zooplankton, probably through the modulation of ecological
327 interactions. It also illustrates how scaling up individual responses obtained in highly
328 controlled conditions to the level of communities remains tricky. Additional research on the
329 long-term effect of noise on freshwater zooplankton, as well as on fish-dominated planktonic
330 communities, is needed

331

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336

337

338 **7. References**

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