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## From behaviour to complex communities: Resilience to anthropogenic noise in a fish-induced trophic cascade

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1 **TITLE**

2 From behaviour to complex communities: Resilience to anthropogenic noise in a fish-induced  
3 trophic cascade

4

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35 **KEY WORDS:** chronic noise pollution, freshwater plankton, predation, mesocosms, *Rutilus*

36 *rutilus*, cascading effect

37

## 38 **SUMMARY**

39 Sound emissions from human activities represent a pervasive environmental stressor.

40 Individual responses in terms of behaviour, physiology or anatomy are well documented but

41 whether they propagate through nested ecological interactions to alter complex communities

42 needs to be better understood. This is even more relevant for freshwater ecosystems that

43 harbour a disproportionate fraction of biodiversity but receive less attention than marine and

44 terrestrial systems. We conducted a mesocosm investigation to study the effect of chronic

45 exposure to motorboat noise on the dynamics of a freshwater community including

46 phytoplankton, zooplankton, and roach as a planktivorous fish. As expected under the trophic

47 cascade hypothesis, roach predation induced structural changes in the planktonic  
48 communities. Surprisingly, although roach changed their feeding behaviour in response to  
49 noise, the dynamics of the roach-dominated planktonic communities did not differ between  
50 noisy and noiseless mesocosms. This suggests that the top-down structuring influence of  
51 roach on planktonic communities might be resilient to noise and reveals the difficulties on  
52 extrapolating impacts from individual responses to complex communities.

53

## 54 **1. INTRODUCTION**

55

56 The trophic cascade, one of the most influential concepts in ecology, specifies the effects of  
57 predators that propagate downward through food webs across multiple trophic levels [1,2].  
58 Considering a series of nested consumer-resource interactions (i.e., a food chain), top  
59 predators have a direct negative effect on mesopredators and indirect positive and negative  
60 effects alternatively on lower trophic levels. Top-down cascade effects can result from  
61 changes in predator density (density-mediated trophic cascade) or behaviour (trait-mediated  
62 trophic cascade) and much attention has focused on identifying the intrinsic and extrinsic  
63 determinants of their strength [3,4]. In particular, this helped to better understand the  
64 structural impact of several anthropogenic stressors including warming, salinization,  
65 chemical pollution or habitat degradation [5–7].

66 Noise emissions from transportation, cities, industry, military and recreational  
67 activities represent another pervasive anthropogenic stressor [8,9]. They span all ecosystems  
68 even in the most remote places [10] and have been shown to alter communication, social  
69 interactions, use of space, activity patterns, foraging and reproduction in a wide range of taxa

70 [11–13]. First evidence of the cascading effects of noise pollution came from the long-term  
71 investigations conducted in the natural gas fields of northwest New Mexico. Bird response to  
72 gas-well-compressor noise was found species-specific with some key seed dispersers  
73 (mountain bluebirds and Woodhouse’s scrub-jays) avoiding noisy areas where pollinators  
74 like hummingbirds had on the contrary higher reproductive success [14]. Long-term  
75 consequences include alterations in plant communities that persist after removal of the noise  
76 source [15]. The propensity of anthropogenic noise to indirectly affect species, and typically  
77 primary producers, through a series of nested direct interactions had also been suggested  
78 experimentally. Barton *et al.*[16] exposed a three-level terrestrial food chain to various  
79 soundscapes for 14 days in plant growth chambers and found that urban sounds and rock  
80 music made lady beetles less effective predators, reducing the strength of top-down control  
81 on aphids, whose density increased. More aphids ultimately resulted in reduced soybean  
82 biomass. Although freshwaters harbour a disproportionate fraction of earth’s biodiversity  
83 [17] and suffer a greater decline in species richness compared to terrestrial and marine  
84 habitats [18,19], they often receive less attention, and research on the impacts of noise  
85 pollution is no exception. For instance, we known that fish responses to noise include  
86 changes in behaviour and abundances [20–23] but whether these effects spread along food  
87 webs to alter planktonic communities through cascading effects remains to be investigated.  
88 Similarly, the response of freshwater plankton to noise is largely overlooked. Available  
89 evidence to date comes from water fleas, *Daphnia* spp., which are widespread pelagic  
90 crustaceans (Cladocera) and an important source of food for upper trophic levels [24,25].  
91 Surprisingly, knowing that marine invertebrates of similar size were found to adjust their  
92 swimming activity in response to natural or artificial sounds [26], water fleas exposed to

93 band-pass filtered white noise either continuous or intermittent did not show any alteration in  
94 swimming speed or depth [27,28]. However, long-term effects of chronic exposure on their  
95 survival and reproductive success have yet to be explored, and overall, we lack knowledge on  
96 the dynamics of plankton under anthropogenic noise. Here we conducted a mesocosm  
97 investigation to study the temporal dynamics of a zooplankton – phytoplankton system under  
98 the presence or absence of a planktivorous fish, with and without exposure to motorboat  
99 noise. We used the roach *Rutilus rutilus* as top predator: a widespread Eurasian cyprinid fish  
100 whose response to motorboat noise has been documented. Roach have specialized hearing  
101 structures, the Weberian ossicles, that conduct sound from the swim-bladder to the inner ear  
102 and provide high sensitivity to sound pressure [29–31]. They can detect sounds between 10  
103 Hz and 5 kHz with a maximum sensitivity of 60 dB re. 1  $\mu$ Pa between 500 and 1000 Hz [32].  
104 Roach have been found to respond to authentic motorboat sounds with fewer feeding  
105 attempts, higher latency to enter the open area and longer time spent in the vegetation, and  
106 these effects persisted after five days of exposure suggesting the absence of habituation [33].  
107 After our mesocosm investigation, and in order to get insights into fish growth and behaviour,  
108 the roach have been collected, weighted, and measured, and moved to aquaria to assess prey  
109 consumption, mobility and group cohesion in the presence or absence of boat noise. Given  
110 the lack of knowledge on how freshwater plankton respond to chronic noise exposure, we had  
111 no clear prediction on the effect of boat noise on the dynamics of the zooplankton –  
112 phytoplankton system without fish. Under the trophic cascade hypothesis, we expected roach  
113 presence to reduce the top-down control of phytoplankton by zooplankton. Considering that  
114 motorboat noise was found to negatively influence foraging in roach [33], we predicted a  
115 decrease in the strength of top-down cascading effect. Concerning roach behaviour, we

116 expected behavioural alterations consistent with the weakening of the trophic cascade in the  
117 noisy mesocosms.

118

## 119 **2. MATERIALS AND METHOD**

120

121 The investigation has been conducted at the PLANAQUA experimental platform of the  
122 CEREEP-Ecotron Île-de-France research station (48° 16'10.92 N, 2° 43'50.879 E, Seine et  
123 Marne, France) and lasted six weeks (August 31 – October 14, 2020), which corresponds to a  
124 prolonged exposure to motorboat noise following Johansson et al. (2016). We assigned three  
125 mesocosms to one of four treatments ( $N = 3$  replicates, 12 mesocosms in total): (1) no fish -  
126 no noise, (2) no fish - noise, (3) fish – no noise, and (4) fish – noise.

127

### 128 2.1 Preparation of the mesocosms and animal collection

129

130 Each mesocosm (3.4 m diameter, 1.1 m depth) was filled with 9,079 L of water from the  
131 storage lakes of the field station that naturally host zooplankton and phytoplankton  
132 communities. An underwater loudspeaker (Electrovoice UW30) was submerged five cm  
133 below the surface in the center of each mesocosm. It was connected to an amplifier (Dynavox  
134 CS-PA 1MK) and then to an audio player (Handy's H4n zoom), both placed inside a  
135 waterproof electric box next to the mesocosm. To promote the growth of phytoplankton, we  
136 added 30 mL of Algoflash® (41.4 µg of phosphorus, nitrogen, and potassium per liter) at the  
137 beginning of the investigation (August 20) and 50 additional mL at the middle of the  
138 investigation (September 19) after we detected a drop in the amount of chlorophyll in the

139 mesocosms using a multiparameter probe (YSI ExO-2). From March to April 2020, we used  
140 fish traps to gradually collect roach from the storage lakes of the PLANAQUA platform, and  
141 we stored them in a pond containing the same planktonic communities as the mesocosms.  
142 These fish were the descendants of roach used in previous investigations conducted on the  
143 platform. They grew in quiet conditions and had never experienced motorboat noise before.  
144 At Day 0, 96 roach of similar size ( $8.54 \pm 2.32$  cm for standard length, SL) were randomly  
145 collected from the storage pond using a seine net, measured, and weighted to the nearest 0.01  
146 cm and 1 g, and distributed in groups of 16 between the six mesocosms (fish – no noise and  
147 fish – noise treatments) so as to homogenize size distribution and total biomass between the  
148 mesocosms. We placed anti-bird nets on top of the mesocosms to avoid avian predation.

149

## 150 2.2 Plankton dynamics

151

152 To assess plankton dynamics, we sampled the mesocosms 13 times from Day 0 to Day 42  
153 and every two or four days. The temporal variation of phytoplankton was assessed through  
154 the quantification of green algae, cyanobacteria, and diatom densities. We sampled eight  
155 liters of water per mesocosm using a 2-L sampling bottle (Uwitec) at four different positions.  
156 Analyses were made in the laboratory using a BBE FluoroProbe<sup>TM</sup> spectrofluorometer (BBE  
157 Moldaenke GmbH, Schwentimental) on a 125-mL subsample previously kept in the dark for  
158 one hour. For detecting potential top-down effects on zooplankton, we choose to focus on  
159 mesoplankton organisms (Cladocera, copepodits and adults of Copepods, and *Chaoborus*  
160 larvae), which appeared as the most responsive organisms in previous mesocosm experiments  
161 realized in comparable conditions [34]. To assess their temporal variation in zooplankton, we



162 sampled 24 liters of water using a 2-L sampling bottle at twelve different positions and  
163 depths in each mesocosm. Water was filtered with a 50- $\mu$ m nylon filter and zooplankton  
164 fixed in 15-mL of 90% ethanol. Taxa identification and counting was made on a 3-mL  
165 subsample following [35] for cladocerans and copepods (nauplii not counted), and [36] for  
166 aquatic insects.

167

### 168 2.3 Fish growth and behaviour

169

170 The behavioural tests took place in an experimental room of the PLANAQUA platform  
171 thermo-regulated at 17°C. We equipped four 110-L aquaria (80 cm length x 35 cm width x 40  
172 cm height) with an underwater loudspeaker (Electrovoice UW30) in the middle of the left end  
173 surrounded by acoustic foam (1.5-cm thick) to attenuate vibrations, a neon light, and a  
174 camera (HD-TVI ABUS TVVR33418) above, and black plastic boards outside to avoid  
175 visual contacts with the experimenters that may provide stress. The speaker was connected to  
176 an amplifier (Dynavox CS-PA 1MK) and to an audio player (Handy's H4n zoom). The  
177 aquaria were filled with water from the control mesocosms (no fish – no noise treatment)  
178 filtered through a 50- $\mu$ m nylon mesh filter to remove zooplankton. This experimental design  
179 allowed us to run four tests simultaneously with one treatment *per* aquarium depending on  
180 the noise condition in the mesocosm and later in the aquarium (“mesocosm – aquarium”  
181 noise conditions): (1) no noise – no noise, (2) no noise – noise, (3) noise – no noise and (4).  
182 Between two consecutive runs of tests, each aquarium was assigned another treatment to  
183 avoid an effect of the aquarium, while water was changed to remove chemical cues.

184 At the end of the mesocosm investigation (Day 44), roach were removed from the  
185 mesocosms using a seine net and measured and weighted to the nearest 0.01 cm and 1 g. We  
186 matched these values with the weights and lengths measured at the beginning of the  
187 mesocosm investigation to recognize fish and calculate individual growth. Roach were then  
188 randomly assigned to groups of three individuals and moved into one of the four  
189 experimental aquaria. In total, we formed 28 groups ( $N = 7$  replicates per treatment) with two  
190 or three groups per mesocosm. Once in the aquarium, they first experienced ambient noise  
191 during an acclimatization period of one hour, and then 40 minutes of either ambient noise or  
192 ambient noise supplemented with motorboat sounds, depending on the treatment (see section  
193 2.4 for further detail on the playback tracks). At the middle of the exposure period (i.e. after  
194 20 min), we introduced 50 *Chaoborus* larvae (Diptera) and 50 *Daphnia* sp. (Crustacea:  
195 Cladocera), previously collected from the control mesocosms using a 2-L sampling bottle and  
196 50- $\mu$ m nylon mesh filter. Both invertebrates are common prey of roach, differ in terms of size  
197 and mobility, and were found in the mesocosms. Although *Chaoborus* larvae are natural  
198 predators of *Daphnia* [37], we expected no predation events considering the short duration of  
199 the experiment. At the end of the experiment, roach and invertebrates were removed from the  
200 aquarium, counted, and returned to the storage pond. The videos were analyzed using  
201 Kinovea v. 0.9.4 to get the xy coordinates of each fish each second and during each boat  
202 sound (for a total of 691s and corresponding to ambient noise for the other treatment), and  
203 then the following parameters were calculated: (1) the cumulative swimming distance (total  
204 distance covered by the three individuals) as a proxy of mobility, (2) the distance between the  
205 barycenter of each group and the center of the speaker as a proxy of aversion to noise, and (3)  
206 the area occupied by the group as a proxy of group cohesion.

207 Group's barycenter was calculated using individual coordinates as follows:

$$208 \quad X_{\text{barycenter}} = (X_{\text{fish1}} + X_{\text{fish2}} + X_{\text{fish3}}) / 3$$

$$209 \quad Y_{\text{barycenter}} = (Y_{\text{fish1}} + Y_{\text{fish2}} + Y_{\text{fish3}}) / 3$$

210 The distance between the barycenter and the loudspeaker ( $D$  in cm) was calculated as  
211 follows:

$$212 \quad D = \sqrt{((X_{\text{barycenter}} - X_{\text{loudspeaker}})^2 + (Y_{\text{barycenter}} - Y_{\text{loudspeaker}})^2)}$$

213 Group's area ( $A$  in  $\text{cm}^2$ ) was calculated as follows:

$$214 \quad A = \sqrt{((P * (P - d_{\text{fish1-fish2}}) * (P - d_{\text{fish1-fish3}}) * (P - d_{\text{fish2-fish3}})))}$$

215 Where  $d$  corresponds to the distance between two fish in cm and  $P$  to the perimeter of the  
216 group in cm with:

$$217 \quad P = \frac{1}{2} (d_{\text{fish1-fish2}} + d_{\text{fish1-fish3}} + d_{\text{fish2-fish3}})$$

218 Group barycenter and area were calculated every second during the boat sounds and then  
219 averaged.

220 The behavioural tests took place from 8 am to 6 pm and needed two consecutive days with  
221 four mesocosms (two from the fish – no noise treatment and two from the fish – noise  
222 treatment) processed on Day 43 and the two others (one *per* treatment) on Day 44. We also  
223 conducted four additional tests (two *per* noise condition) without roach to control for  
224 *Chaoborus* predation on *Daphnia* and overall invertebrate mortality in the absence of  
225 predation.

226

227 2.4 Noise treatments

228

229 We used Audacity 2.2.1 to generate the audio tracks and an Aquarian Audio H2A-HLR  
230 hydrophone (frequency response from 10 to 100 kHz) connected to a ZOOM H4next Handy  
231 recorder for all the recordings. The level of background noise did not differ between the  
232 mesocosms and ranged from 90 to 95 dB re.  $\mu\text{Pa}$ . In the mesocosms without boat noise, a 1-  
233 hr audio track of silence was looped continuously. In the mesocosms with boat noise, we  
234 used the audio tracks described in [38] where 150 sounds of small recreational boats have  
235 been distributed over the nine consecutive 1-hr audio tracks of silence going from 9 a.m. to 6  
236 p.m. so as to mimic the daily activity of a small leisure base (Fig. 1A and Supp. Mat. 1, see  
237 Rojas et al. 2021 for more details on the audio tracks and the original recordings). We  
238 broadcasted silence the rest of the time. We applied a linear fading on both ends of the boat  
239 sounds to make them emerge from background noise and adjusted their levels with Audacity  
240 to obtain naturally occurring signal-to-noise ratios (SNR) ranging from 4.81 to 27 dB. We  
241 used the SNR function of the *seewave* R package [39]:

$$242 \quad \text{SNR} = 20\log_{10}(\text{RMS}_{\text{boat sound}}/\text{RMS}_{\text{background noise}})$$

243 where RMS is the root-mean-square sound pressure of either the re-recordings of the boat  
244 sounds in the mesocosm or the recording of background noise.

245 In the aquaria without boat noise and to encompass the 1-h acclimatization period and  
246 the 40-min exposure period, we used a 100-min audio track of background noise previously  
247 recorded in the center of one mesocosm from the no noise – no fish treatment. We adjusted  
248 sound level to match that of the mesocosms. In the aquaria with boat noise, we used the 100-  
249 min audio track of background noise to which we added twelve boat sounds randomly  
250 selected from those broadcasted in the mesocosms. We randomly distributed the sounds over  
251 the 40-min exposure period and adjusted their level to match the range of SNR values we had

252 in the mesocosms (approx. 4.81 to 27 dB). In terms of boat traffic, this acoustic regime was  
253 representative of the highest activity that roach experienced within a day in the mesocosms  
254 (Fig. 1B and Supp. Mat. 1).

255

## 256 2.5 Data analysis

257

258 All the statistics were performed using R [40] with a significance level of 0.05. We used the  
259 Principal Response Curve (PRC, *prc* function of the *vegan* R package [41]) to study how the  
260 planktonic communities exposed to roach, boat noise, or both, have diverged over time  
261 compared to control communities (i.e. from the no fish – no noise treatment). PRC is a  
262 special case of redundancy analysis including time-series data particularly suited to the study  
263 of community dynamics in mesocosms [42]. It typically results in a diagram with one curve  
264 for each treatment, the time on the x-axis, the first major component of the community effects  
265 on the left y-axis and the weights of the taxa on the right y-axis. The more the weight  
266 deviates from zero the more the corresponding taxon contributes to the deviation from the  
267 control. We used Hellinger-transformed taxa (square root of the relative abundance) to reduce  
268 the influence of both rare (low abundances and/or many zeros) and abundant taxa [43].  
269 Significance in the PRC was tested using a permutation test (*anova.cca* function of the *vegan*  
270 R package) accounting for the non-independence of data due to repeated measurements on  
271 the same mesocosm. Significance in the difference between each treatment and the control  
272 was assessed with a multiple comparison test (*multiconstrained* function of the *BiodiversityR*  
273 R package).

274 Roach' growth rate ( $G$ ) was computed using the formulae:

$$275 \quad G = (L_{\text{final}} - L_{\text{initial}}) / L_{\text{initial}} * 100$$

276 where  $L_{\text{final}}$  and  $L_{\text{initial}}$  are the final and initial SL of roach, respectively.

277 Because growth data met the normality and homoscedasticity assumptions (Shapiro-Wilk and  
278 Bartlett tests, all  $p$  values  $> 0.05$ ), we used a linear mixed-effect model (*lme4* R package [44])  
279 with the noise condition as fixed factor and the mesocosm as random factor to test for  
280 significance of the difference in growth rate between the treatments.

281 The effects of noise and pre-exposure to noise on roach predation were assessed in  
282 two ways. First, we used a generalized linear mixed-effect model assuming a Poisson  
283 distribution to explain the total number of prey eaten as a function of the noise condition in  
284 the mesocosm, the noise condition in the aquarium and their interaction as fixed factors, and  
285 the mesocosm ID as random factor. Second, we estimated the preference of roach for  
286 *Daphnia* over *Chaoborus* larvae using the Manly's alpha ( $\alpha$ ) preference index [45,46]:

$$287 \quad \alpha_{daphnia} = \ln(50 - N_{daphnia}) / (\ln(50 - N_{daphnia}) + \ln(50 - N_{chaoborus}))$$

288 where 50 is the initial number of each prey, and  $N_{daphnia}$  and  $N_{chaoborus}$  the numbers of daphnia  
289 and *Chaoborus* larvae eaten. The Manly's alpha accounts for prey depletion during the  
290 predation test and ranges from zero when only the alternative prey (here *Chaoborus* larvae) is  
291 eaten to one when only the focal prey (here *Daphnia*) is eaten. The value of 0.5 indicates a  
292 lack of preference. As recommended by [47], we compared obtained values to the theoretical  
293 value of 0.5 using  $t$  tests except for the "no fish – noise" treatment where we used a Wilcoxon  
294 test to deal with the non-normality of data.

295 Roach behaviour was analyzed with model averaging and an information-theory  
296 approach. We used linear mixed-effect models to model each of the three response variables  
297 (cumulative swimming distance, distance to the speaker and area of the group) as a function  
298 of the noise condition in the mesocosm, the noise condition in the aquarium, the time, and  
299 taking the mesocosm ID as random factor as several groups came from the same mesocosm.  
300 Because the noise condition that roach have experienced in the mesocosm might have  
301 changed their response to boat noise in the aquarium and because the effect of time may vary

302 with the noise condition, we also included the interactions between the two noise treatments  
303 and between each noise treatment and time in the predictors. All predictors were centered and  
304 scaled using the *standardization* function of the *arm* R package. We ranked all the submodels  
305 based on small sampled-corrected AIC values ( $AIC_c$ , *dredge* and *get.models* functions of the  
306 *MuMIn* Rpackage [48]) and performed model averaging on a confidence set of models using  
307 a cut-off of 10  $AIC_c$  (*model.avg* function of the *AICcmodavg* R package). The predictors  
308 whose parameter estimate had a 95% confidence interval (CI) that included the value of zero  
309 were considered as having no significant effect.

310

### 311 **3. RESULTS**

312

313 The pelagic zooplankton communities of the mesocosms included four cladoceran families  
314 (Bosminidae, Daphniidae, Sididae and Chydoridae), cyclopoid and calanoid copepods,  
315 dipteran larvae of the genus *Chaoborus*, and some ostracods captured in the pelagic zone  
316 although being mainly benthic organisms. The diagram of the PRC analysis illustrates how  
317 adding roach, boat noise or both make the planktonic communities gradually deviate over  
318 time from those of the no fish – no noise treatment (i.e., control) considered as the baseline  
319 (Fig. 2). Adding boat noise made the communities deviate from the control and adding roach  
320 induced a larger deviation without variation between the two noise conditions (i.e., similar  
321 trajectories, Fig. 2). Table 1A shows that 30% of total variance was attributed to time and  
322 34% to the treatment regime, including its interaction with time. On the basis of the  
323 permutation tests, the treatment regime as well as time and their interaction had a significant  
324 influence on the community dynamics (Table 1B). The pairwise comparisons revealed that  
325 the difference between the two treatments with roach (with or without noise) was the only to

326 be not significant (Table 1C). Bosminidae and in a lesser extent Chydoridae, both copepod  
327 taxa and green algae are indicated with a positive taxon weight in the PRC, suggesting they  
328 were expected to increase in abundance with the treatments relative to the control and in  
329 proportion to their weight. On the other hand, Daphniidae and, to a lesser extent ostracod,  
330 Sididae and *Chaoborus* larvae exhibited negative species weights and were expected to  
331 decrease in abundance with the treatments. The taxa weights of diatoms and cyanobacteria  
332 were the smallest and close to zero (Fig. 2).

333 Individual fish growth did not significantly differ between the noise conditions ( $\chi_1^2 =$   
334 1.4813 and  $p = 0.2236$ , Fig. 3). In the absence of roach, prey survival in the aquaria was  
335 100% for both prey in the absence of boat noise, and 100% for *Chaoborus* larvae and 98%  
336 for *Daphnia* in the presence of boat noise. We therefore considered prey mortality during the  
337 predation tests to be the result of fish predation only. The effect of noise on the total number  
338 of consumed prey depended on the noise condition in the mesocosms, with significantly less  
339 prey consumed only for roach coming from the noiseless mesocosms ( $\chi_1^2 = 18.36$  and  $p <$   
340 0.001 for the interaction between the two noise conditions, Fig. 4A). Whatever the noise  
341 condition in the mesocosm, the Manly's alpha index did not differ from the theoretical value  
342 of 0.5 in noiseless aquaria ( $t = 1.36$  and  $p = 0.22$  for ambient noise,  $t = -0.32$  and  $p = 0.76$  for  
343 boat noise) but was significantly higher with boat noise ( $V = 27$  and  $p = 0.03$  for ambient  
344 noise,  $t = 3.10$  and  $p = 0.02$  for boat noise, Fig. 4B). Concerning the cumulative swimming  
345 distance and the distance to the speaker, the 95% CI of the parameter estimate included the  
346 value of zero for all the predictors. Concerning the area occupied by the group, boat noise in  
347 the aquarium and time were the only predictors whose parameter estimate 95% CI did not  
348 include the value of zero, with significantly positive values (Fig. 5).



349

#### 350 **4. DISCUSSION**

351

352 Exposure to anthropogenic noise is known to elicit physiological or behavioural responses in  
353 individual organisms [8,11–13,22]. But to what extent these alterations spread across  
354 ecological interactions to alter community dynamics and ecosystem functions is not clear. We  
355 conducted a mesocosm investigation to study the impact of chronic exposure to motorboat  
356 noise on the dynamics of a zooplankton – phytoplankton system either alone or dominated by  
357 a planktivorous fish. Although we detected alterations in fish feeding and behaviour, the  
358 strength of top-down control and its consequences on the structure of the planktonic  
359 communities were resilient to motorboat noise. This suggests that individual responses to  
360 noise do not necessarily result in ecological effects at the level of communities.

361         The pelagic mesoplankton communities of our mesocosms were dominated by  
362 cladocerans and copepods, two major groups of herbivorous microcrustaceans widespread in  
363 freshwater bodies. In smaller proportions, they also included ostracods (coming from the  
364 benthic areas of the mesocosms), and predatory larvae of the *Chaoborus* genus, known to  
365 feed on small zooplankton [49]. In fishless mesocosms, daphnid cladocerans gradually  
366 became the most abundant taxa. Compared to copepods, cladocerans have higher  
367 reproduction rates. Moreover, because daphnids are the largest cladocerans, they suffer  
368 smaller predation risk by *Chaoborus* larvae than the other cladocerans [50]. The presence of  
369 roach made the planktonic communities gradually deviate from those of the fishless  
370 communities with a shift in the dominant taxon of zooplankton from daphnids to bosminids  
371 whose abundance greatly increased. Visual-feeding fish like roach tend to prefer large

372 zooplankton [51] and it might be that selective predation on the two largest taxa: *Chaoborus*  
373 larvae and daphnids, has released bosminids from predation and competition. Alteration in  
374 the daphnids – bosminids balance is symptomatic of fish presence [52]. To a lesser extent,  
375 copepods and Chydoridae have also benefited from the roach-induced decrease in daphnids.  
376 This might be explained by the greater availability of food resources like green algae, which  
377 slightly increased in the presence of roach, but also rotifers that represent another important  
378 taxon of freshwater zooplankton. Due to their small size, we did not count the number of  
379 rotifers but they are known to increase in the presence of fish because of the removal of large  
380 cladocerans [53]. The slight increase in green algae in the presence of roach is consistent with  
381 the trophic cascade hypothesis: fish have a negative direct effect on zooplankton (here  
382 daphnids) and indirectly benefit phytoplankton that is released from grazing [34]. Another  
383 way roach can influence the planktonic communities is through the modulation of diel  
384 migration patterns. Indeed, some taxa migrate to the bottom under chemical cues by predators  
385 and become less frequent in the pelagic realm [54].

386         Motorboat noise did not alter the top-down structuring effect of roach on the  
387 planktonic communities and particularly the shift from daphnids to bosminids. This suggests  
388 that chronic exposure to noise had no effect on the feeding behaviour of roach, which is  
389 consistent with the absence of difference in growth rate between the two noise conditions.  
390 This is also consistent with the total number of prey eaten recorded during the predation tests,  
391 which was significantly reduced by motorboat noise for the roach that never experienced boat  
392 noise before but not for those pre-exposed to boat noise in the mesocosms. Weakening of the  
393 response to noise after repeated exposure has been reported in other fish species [38,55,56],  
394 and might reflect habituation through associative learning: naïve animals first allocate

395 attention to noise at the expense of other activities like feeding, and then resume normal  
396 behaviour as they learn that it is not associated with any threat. However, when looking  
397 closer to what has been eaten, we found motorboat noise to elicit selective preference for  
398 daphnids over *Chaoborus* larvae even for roach pre-exposed to boat noise in the mesocosm.  
399 This persistent response could find its origin in behaviour. Concerning invertebrates,  
400 although we did not record their behaviour, we know from past investigations that motorboat  
401 noise did not alter the mobility of daphnids [27] but triggers body rotations in *Chaoborus*  
402 larvae [38], interpreted as an anti-predatory response [57,58] that could have driven the  
403 choice of roach towards daphnids. Concerning roach behaviour, we found no alteration in  
404 mobility and no evidence for any avoidance of the sound source, but the area occupied by the  
405 three individuals was larger under motorboat noise. This effect seems to be persistent as it  
406 was also observed with the roach pre-exposed to boat noise in the mesocosms. Similarly,  
407 playback of pile driving was found to make juveniles of seabass less cohesive [59]. Noise  
408 could mask the perception of nearest neighbours' movements through the lateral line or  
409 impair the ability to process sensory information as a consequence of stress and/or distraction  
410 [59]. Compared to stress or distraction, masking does not weaken with repeated exposure.  
411 This could explain why the reduced group cohesion was also observed in the roach that  
412 experienced motorboat noise in the mesocosms. Disruption of group cohesion could  
413 ultimately compromise the benefits of grouping associated with the dilution and confusion  
414 effects [60]. Regarding feeding, we can expect the strength of intra-specific competition to  
415 decrease with the distance between individuals. Together with the lesser catchability of  
416 moving *Chaoborus* larvae, this could explain why the roach showed selective preference for  
417 daphnids under motorboat noise. At the level of communities, a selective preference for

418 daphnids, which were the main grazers, should have strengthened the trophic cascade, what  
419 we did not observe. The change in feeding we found in the aquaria may not have been strong  
420 enough to be detected in the mesocosms or maybe does not occur in a larger and more  
421 complex environment where other prey items are available.

422         In the fishless mesocosms, adding motorboat noise induced a small but detectable  
423 deviation from the control communities. This is interesting but also tricky to interpret since  
424 very little is known on the response of freshwater plankton to chronic anthropogenic noise.  
425 *Chaoborus* larvae occupied the highest trophic level of the fishless communities and we  
426 know that they are sensitive to motorboat sounds with more body rotations [38], interpreted  
427 as an anti-predatory response [58]. If noise also interferes with prey processing and reduces  
428 the capture efficiency of *Chaoborus* larvae, then it could be beneficial to small zooplankton.  
429 Noise could also trigger vertical migration to the bottom, as chemical cues from predators do  
430 [54], making some taxa like ostracods less detectable in the pelagic realm. Additional long-  
431 term investigations in mesocosms but also *in situ* are needed to better understand the response  
432 of planktonic communities to chronic anthropogenic noise.

433         Our investigation illustrates how extrapolating the impact of anthropogenic noise  
434 from individual responses to complex communities is far from obvious. Although we  
435 observed persistent alterations in roach behaviour with less group cohesion and altered  
436 feeding preference, these effects did not propagate downward along the food chain through  
437 trait-mediated cascading effects. A valuable perspective would be to study the dynamics of  
438 roach under chronic anthropogenic noise to test whether the behavioural responses we  
439 observed ultimately decrease survival and/or reproductive success [61], and result in density-  
440 mediated cascading effects.

441

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447

## 448 **ETHIC STATEMENTS**

449 All the procedures were conducted in accordance with appropriate European (*Directive*  
450 2010/63/EU) and French national guidelines, permits, and regulations regarding animal care  
451 and experimental use (Approval no. C42-218-0901).

452

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457 (Transnational Access).

458

## 459 **CONFLICT OF INTEREST**

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

461

## 462 **DATA AVAILABILITY**

463 The data that support the findings of this study are open available in Zenodo at

464 <https://doi.org/10.5281/zenodo.6760791>.

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466

## 467 **FIGURE LEGENDS**

468

469 **Figure 1:** Sound spectra of the two noise conditions (control: dashed lines, boat noise: one  
470 solid lines for each hour from 9 am to 6 pm) broadcasted in A) the mesocosms and B) the  
471 aquaria. Spectra were made from 1-hour recordings in the mesocosms and 20-min recordings  
472 in the aquaria.

473

474 **Figure 2:** Principal Response Curve (PRC) showing the effects of adding fish (squares),  
475 motorboat noise (dots) or both (triangles) on freshwater plankton communities compared to  
476 control communities (no fish – no noise, horizontal line, see text for further detail). Species  
477 weights are on the left axis (bos: Bosminidae, cyclo: cyclopoid copepods, cala: calanoid  
478 copepods, chydo: Chydoridae, green: green algae, diat: diatoms, cyano: cyanobacteria, sidi:  
479 Sididae, chao: *Chaoborus* larvae, ostra: ostracods, daph: Daphniidae). See Table 1 for the  
480 percentages of variance accounted for and the significance levels.

481

482 **Figure 3:** Fish growth rates (medians and interquartile ranges) in the mesocosms depending  
483 on the noise condition (white box: ambient, grey box: boat noise,  $n = 48$  per condition).

484

485 **Figure 4:** Results of the predation tests in aquaria with A) the total number of prey eaten *per*  
486 group of three fish (n=7 groups per acoustic mesocosm-aquarium treatment) presented to 50  
487 *Daphnia* and 50 *Chaoborus* larvae and B) the Manly's alpha preference index for *Daphnia*  
488 over *Chaoborus* larvae (medians and interquartile ranges) as a function of the noise condition  
489 previously experienced in the mesocosms and the noise condition in the aquaria (white box:  
490 ambient, grey box: boat noise).

491

492 **Figure 5:** Model-averaged coefficient estimates and 95% confidence intervals for the  
493 predictors included in the confidence set of models explaining the behaviour of roach *Rutilus*  
494 *rutilus* in groups of three individuals when feeding on *Daphnia* and *Chaoborus* larvae during  
495 the predation tests in aquaria. We used as response variables A) the area of the group, B) the  
496 cumulative swimming distance and C) the distance to the speaker. Predictors correspond to  
497 the noise condition in the mesocosms (boat noise or ambient noise as control), the noise  
498 condition in the aquaria of the predation tests (boat noise or ambient noise as control), the  
499 time, and the two-way interactions between time and the noise condition in the two  
500 experimental units and between the noise conditions of the two experimental units.

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515 **TABLE**

516

517 **Table 1:** Results of the Principal Response Curve (PRC) for the effect of motorboat noise

518 (absence / presence) and fish (absence / presence, for a total of four treatments) on freshwater

519 planktonic communities. A) Proportion of the total variance explained by the constraints:

520 time, treatment, and their interaction, captured by the canonical 1st axis of the PRC. B)

521 Significance of the PRC diagram on the basis on the permutation test for Constrained

522 Correspondence Analysis (CCA, 999 permutations). C) Pairwise comparisons for all the

523 possible treatment combinations following a CCA analysis.

524

525 A)

	Inertia	Proportion	Rank
Total	0.236	1	
Conditional (% of the total variance explained by time)	0.071	0.30	12
Constrained (% of the total variance explained by time*treatment)	0.085	0.36	11
Unconstrained	0.080	0.34	11



(% of the total variance not explained by predictors)			
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526

527 B)

	Df	Variance	F	Pr(>F)
Treatment	3	0.04	19.28	0.001 ***
Time	1	0.06	77.32	0.001 ***
Treatment*Time	3	0.02	8.98	0.001 ***

528

529 C)

Pairwise comparison	Df	Sum of Sqs	F	Pr(>F)
no fish - no noise fish - no noise	1	0.054	23.856	0.001 ***
no fish - no noise no fish - noise	1	0.011	4.801	0.003 **
no fish - no noise fish - noise	1	0.059	22.593	0.001 ***
fish - no noise no fish - noise	1	0.022	8.902	0.001 ***
fish - no noise fish - noise	1	0.005	1.624	0.177
no fish - noise fish - noise	1	0.027	9.523	0.001 ***

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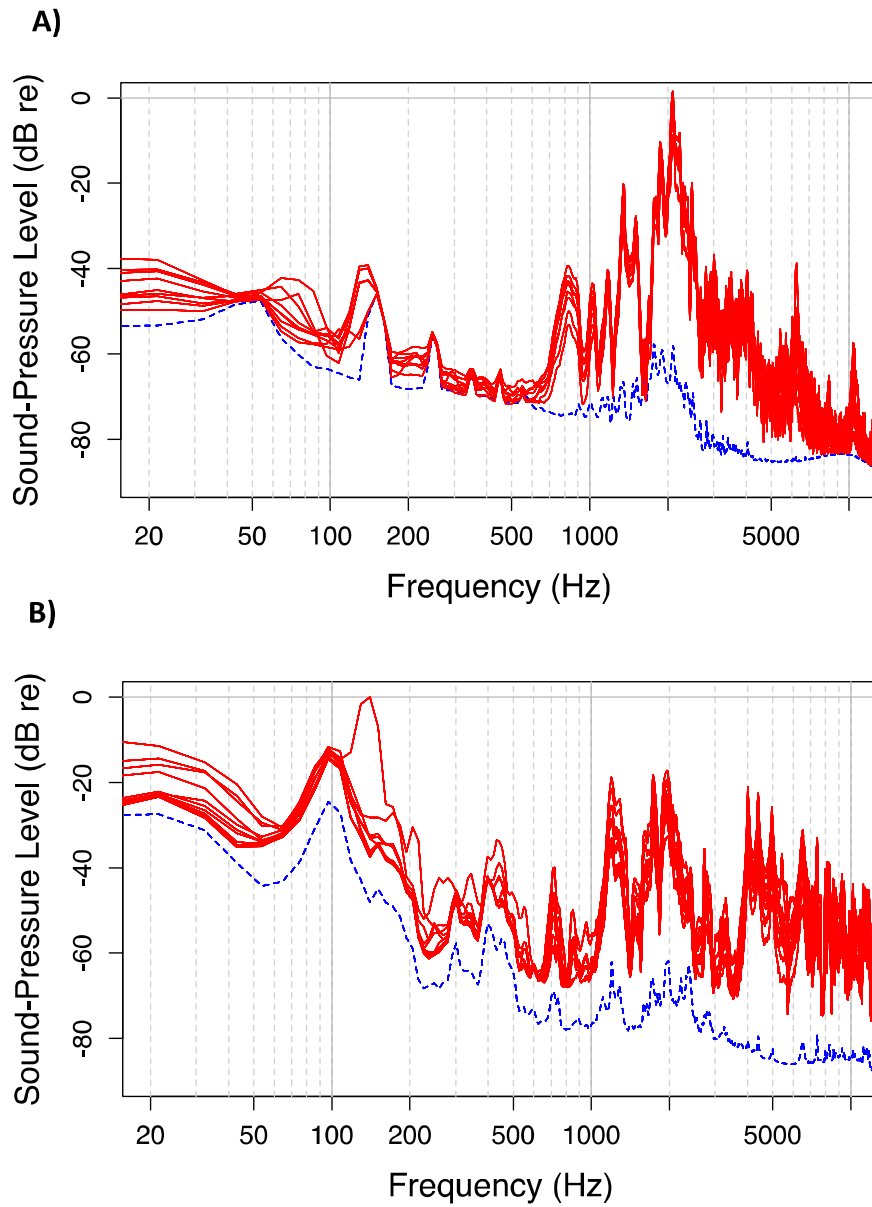
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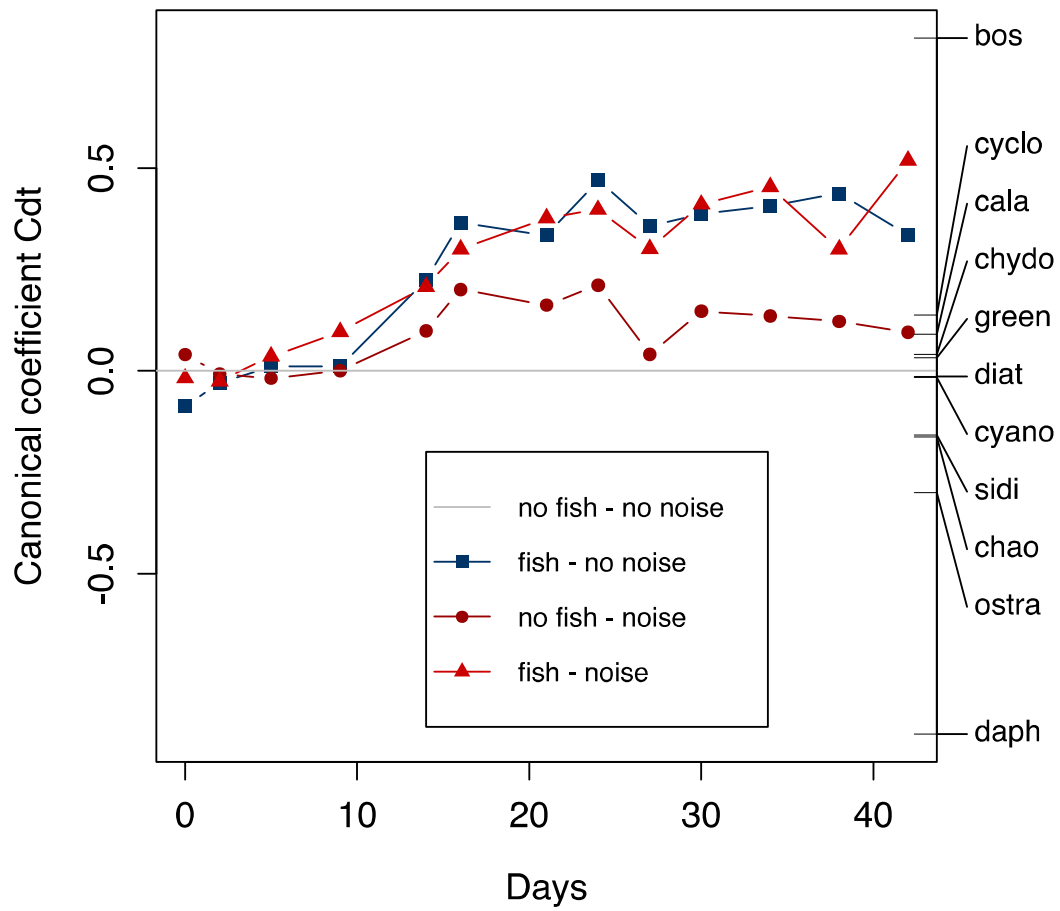


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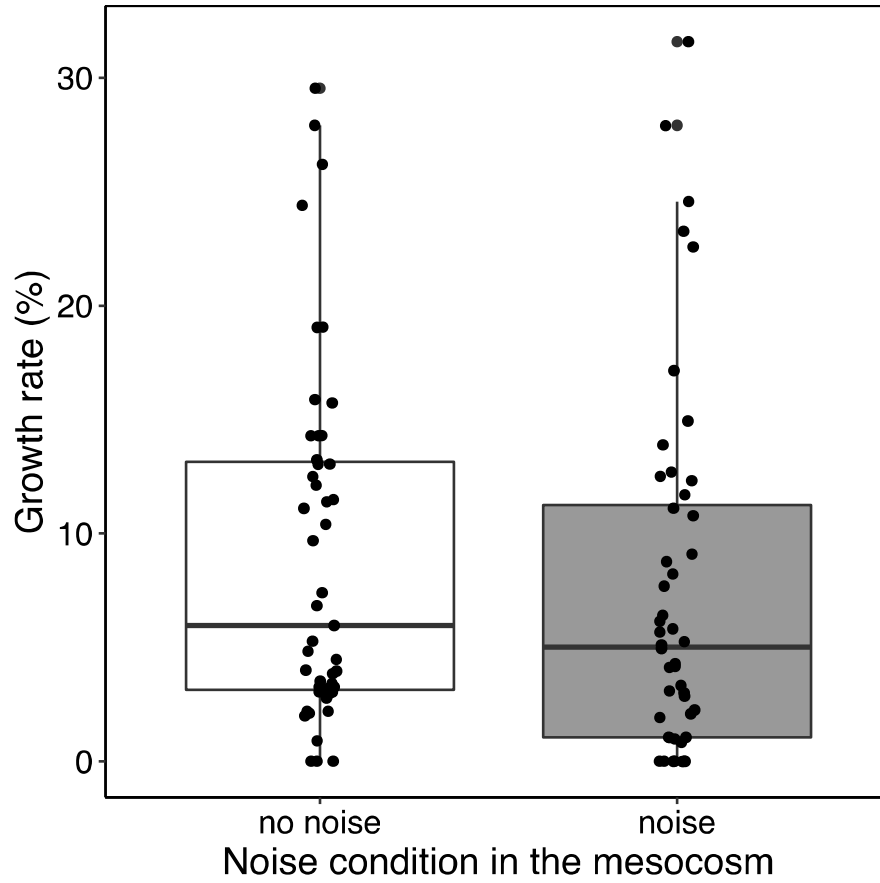
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Fig. 2



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**Fig. 3**

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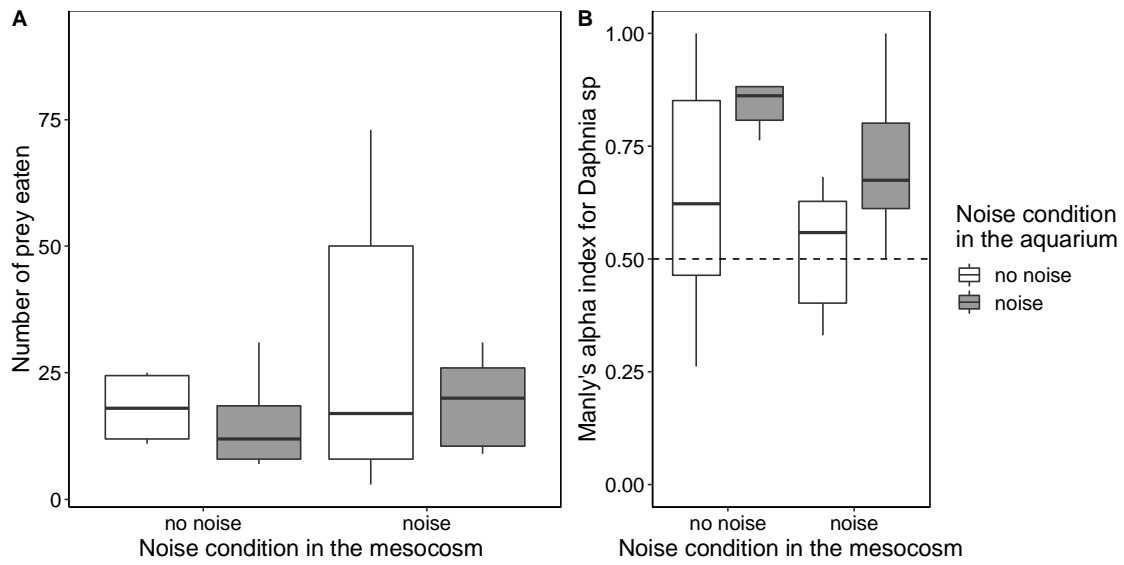
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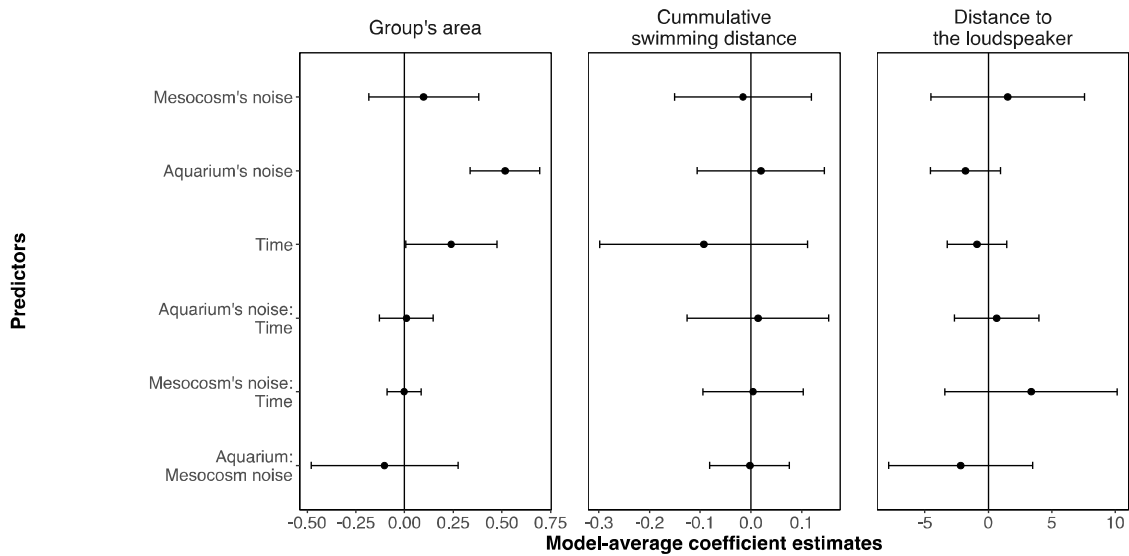
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**Fig. 4**



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**Fig. 5**