Noise-induced reduction in the attack rate of a planktivorous freshwater fish revealed by functional response analysis

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1 **How noise can alter predation: insights from the functional response**

2 **Running title:** Noise-modified functional response

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26 **KEYWORDS**

27 anthropogenic noise, behaviour, freshwater ecosystems, functional response, *Phoxinus*

28 *phoxinus*

29

30 **Abstract**

31 1. Anthropogenic noise can affect animals physically, physiologically and behaviourally.

32 Although individual responses to noise are well documented, the consequences in terms of

33 community structure, species coexistence and ecosystem functioning remain fairly unknown.

34 2. The impact of noise on predation has received a growing interest and alterations in trophic

35 links are observed when animals shift from foraging to stress-related behaviours, are

36 distracted by noise, or because of acoustic masking. However, the experimental procedures

37 classically used to quantify predation do not inform on the potential demographic impact on

38 prey.

39 3. We derived the relationship between resource use and availability (the functional response)

40 for European minnows (*Phoxinus phoxinus*) feeding on dipteran larvae (*Chaoborus* sp.) under

41 two noise conditions: ambient noise and ambient noise supplemented with motorboat noise.

42 The shape and magnitude of the functional response are powerful indicators of population

43 outcomes and predator – prey dynamics. We also recorded fish behaviour to identify some

44 proximate determinants of altered predation.

45 4. For both noise conditions, fish displayed a saturating (type II) functional response whose

46 shape depends on two parameters: attack rate and handling time. Boat noise did not affect

47 handling time but significantly reduced attack rate, resulting in a functional response curve of

48 the same height but with a less steep initial slope. Fish exhibited a stress-related response to

49 noise including an increased swimming distance and an altered spatial distribution.

50   5. Our study shows the usefulness of the functional response approach to study the ecological

51   impacts of noise and illustrates how behavioural responses of predators to noise can modify

52   the demographic pressure on prey. It also suggests that prey availability might mediate the

53   negative effect of noise on predation. Community outcomes are expected if the reduced

54   consumption of the main food sources goes with the overconsumption of alternative food

55   sources, changing the distribution pattern of interaction strengths. Predation release could also

56   trigger a trophic cascade, propagating the effect of noise to lower trophic levels.

57

58   **1 INTRODUCTION**

59

60   Anthropogenic (man-made) noise is recognized as a pervasive pollutant, changing the

61   soundscape of many ecosystems. It has been found to affect the anatomy, physiology and/or

62   behaviour of both invertebrates and vertebrates in several ways, with consequences ranging

63   from discrete, short-term behavioural adjustments to fitness reduction through decreased

64   reproduction or survival (Popper & Hastings, 2009; Kight & Swaddle, 2011; Shannon et al.,

65   2016). Noise is therefore likely to alter key ecological interactions like competition,

66   parasitism or predation, with potential consequences on species coexistence, community

67   stability and ecosystem-level processes (Kunc et al., 2016; Sabet et al., 2016). Although

68   large-scale effects are highly expected, documented impacts rarely exceed individual

69   responses.

70   By driving energy through food webs and affecting biodiversity, trophic interactions

71   influence ecosystem functioning. Noise is likely to alter the strength of a trophic interaction

72   and hence energy flow in many ways. A common reaction is that predators are stressed by

73   noise and shift from feeding to other activities like hiding, escaping or interacting with

74   conspecifics (Cox et al., 2018). Energy flow can also decrease when the auditory cues used to

3

75   locate prey are masked (Schaub et al., 2008), or when prey perceive noise as predation risk

76   and become more vigilant (Rabin et al., 2006). Alternatively, energy flow can increase when

77   prey are distracted and become more vulnerable to predation (Chan et al., 2010), or when

78   noise masks the acoustic cues involved in predator recognition (Kern & Radford, 2016).

79   Despite the increasing number of experimental studies reporting noise-modified trophic

80   interactions, predicting their ecological significance in terms of population dynamic and

81   species coexistence remains difficult. This comes partly from the experimental designs and

82   the predominant use of 'snapshot' predation tests, typically when a predator either alone or in

83   group is presented to a single prey density. Although snapshot predation tests provide a rapid

84   and effective method to quantify predation, they do not inform on the potential demographic

85   impact on the prey and, so importantly, results can depend on the prey density chosen (see

86   Fig. 2 in Dick et al., 2014).

87   Deriving the functional response (FR), which is the relationship between resource use

88   and availability (Solomon, 1949; Holling, 1959a), offers an alternative and complementary

89   approach to snapshot predation tests. Interestingly, the shape and magnitude of the

90   relationship (i.e. the FR curve) are powerful indicators of the strength of top-down control.

91   *Per capita* predation rate typically increases with prey availability and three broad shapes of

92   FR are frequently observed: the linear type I, the saturating type II with a decelerating

93   increase up to predator saturation, and the sigmoidal type III with acceleration first at low

94   prey densities and then deceleration towards saturation (Holling, 1959a). In terms of predator

95   – prey stability, type II FRs are characterized by a high proportional consumption at low prey

96   densities that can lead to unstable boom-burst population dynamics whereas the S-shape of

97   type III FRs offers low-density refugia for prey, which prevents such unstable dynamics

98   (Murdoch & Oaten, 1975; Juliano, 2001; Gentleman & Neuheimer, 2008; Kalinkat et al.,

99   2013). The FR approach provides an experimental framework to test context dependencies in

100 consumer – resource interactions. It has received a growing interest in the fields of

101 fundamental ecology, parasitology and invasion ecology, but remains largely ignored by the

102 ecologists interested in the ecological impact of anthropogenic noise. Very recently,

103 Villalobos-Jiménez et al. (2017) reported decreased magnitude in the FR of damselfly larvae

104 (*Ischnura elegans*) towards cladoceran prey with underwater noise compared to more silent

105 conditions, but no such investigations have been carried out in vertebrates.

106   Our aim was to test the effect of anthropogenic noise on the shape and magnitude of

107 the FR of a freshwater fish, the European minnow *Phoxinus phoxinus*, feeding on dipteran

108 prey. European minnows have a wide distribution range throughout the Palaearctic region and

109 inhabit the cold and well-oxygenated waters of fast-flowing mountain streams, large lowland

110 rivers and lakes (Kottelat & Freyhof, 2007; Vucić et al., 2018). Consequently, they can be

111 exposed to a wide range of anthropogenic noise including recreational shipping in small lakes

112 and industrial noise in large rivers (Voellmy et al. 2014). In our study, fish were presented to

113 six prey densities under conditions of ambient or motorboat noise, and we measured

114 swimming distance, spatial distribution and social interactions to link changes in predation

115 with changes in behaviour. We expected the FR of minnows to be of type II, which is the FR

116 type usually displayed by fish in low-complexity environments (i.e. no shelter provided,

117 Alexander et al., 2014, 2015; Laverty et al., 2017). The two key parameters of a type II FR are

118 the attack rate *a* and the handling time *h*. Attack rate is a measure of predator's efficiency at

119 low prey densities and defines the shape of the FR curve: the higher the attack rate, the

120 steeper the initial slope. Handling time is defined as the time during which the predator stops

121 searching for prey after a capture (Holling, 1959b). It includes successive stages like prey

122 handling and ingestion and defines the height of the FR curve: the lower the handling time,

123 the higher the asymptote. Using another experimental approach, Voellmy et al. (2014)

124 reported that *P. phoxinus* exposed to the additional noise produced by shipping consumed

125 significantly fewer live *Daphnia magna* and exhibited stress-related behaviours, including

126 increased inactivity and more social interactions. Accordingly, we expected the FR of *P.*

127 *phoxinus* to be negatively influenced by anthropogenic noise, with a greater effect on attack

128 rate than on handling time. Indeed, under the assumption of noise-induced increased

129 inactivity, a smaller swimming distance would decrease the probability of encountering prey,

130 especially at low densities when they are scarce, resulting in a smaller attack rate. Handling

131 time has a behavioural component but also depends on morphological and physiological

132 constraints. If the noise minnows were exposed to is unlikely to alter their anatomy or

133 physiology, it could distract them during prey handling and ingestion, resulting in an

134 increased handling time. We therefore expected a slight decrease in the height of the FR curve

135 and a more pronounced change in its shape at low prey densities, with either a less steep type

136 II or a shift towards the S-shape of the type III.

137

138 **2 METHODS**

139

140 **2.1 Animal collection and maintenance**

141

142 In March 2018, 70 *Phoxinus phoxinus* (body length = 5.5 ± 0.6 cm) were collected with

143 electrofishing from the Volvon, a small tributary of the Coise river, at Veauche

144 (45°34'12.4''N, 4°18'21.3''E, Loire, France), and transported to a breeding room of ENES

145 Laboratory thermoregulated at 17°C with a 12:12 light:dark regime. We considered this

146 population as naïve regarding motorboat noise. We did not control for sex and there was no

147 gravid female at this period of the year. Fish were housed for 20 days in a 300 L plastic tank

148 (housing tank) filled with continuously filtered and aerated dechlorinated tap water, and

149 equipped with shelters. They were fed daily with commercial fish pellets and starved for 24 h

150   prior to experimentation. We used *Chaoborus* sp. larvae as prey. In addition to being part of

151   the diet of *P. phoxinus* (Frost 1943), they are pelagic and do not form aggregates in

152   aquariums, which makes them good candidate prey items for functional response experiments

153   (Médoc et al., 2013, 2015). *Chaoborus* sp larvae were purchased from a commercial supplier

154   (www.aquaplante.fr) and maintained in 25 L aquaria under the same conditions than the fish.

155

156   **2.2 Experimental design and protocol**

157

158   Experiments took place in the breeding room thermoregulated at 17°C with a 12:12 light:dark

159   regime to keep animals under the same conditions. One single fish starved for 24 h was

160   placed in a glass aquarium (60 cm long x 30 cm wide x 32 cm high) filled with ≈ 50 L of

161   filtered and aerated dechlorinated tap water (28 cm water height) and containing a 2-cm layer

162   of Loire sand. Three sides were covered with black foam rubber panels (15 mm thick) to limit

163   acoustic reverberation whilst one side in the length was left transparent to film the

164   experiment. We inserted an underwater speaker (Electro-Voice UW30, 0.1 to 10 kHz) in the

165   center of the acoustic panel covering the left end of the aquarium (when facing the transparent

166   side). The center of the speaker was 11 cm below the water surface. At the opposite (right)

167   end, we spaced the acoustic panel from the aquarium wall and placed a hydrophone (Aquarian

168   Audio H2A-XLR Hydrophone, frequency response from 10 Hz to 100 KHz) connected to a

169   ZOOM H4next Handy recorder between them to control the sound signal during the

170   experiment. *P. phoxinus* being naturally gregarious (Frost 1943), we provided a companion

171   fish to the focal individual to promote normal behaviour. Companion fish were minnows of

172   standard size (4.7 ± 0.3 cm) used only for this purpose and kept apart from the other minnows

173   in the housing tank. We placed the companion in the center of the aquarium inside a

174   transparent plastic tube (8 cm diameter) to allow visual communication and prevent chemical

175 exchange, and changed it every six experiments. To avoid unexpected sounds that might

176 disturb the experiments, we placed the aquarium inside an acoustic box ('silent box', 89 cm

177 long x 78.5 cm wide x 75 cm high) with acoustic foam covering the inner surface, a diffuse

178 light source centered on the aquarium 34.5 cm above the water surface (875 lux light intensity

179 at the water surface, Lux Meter for android devices), one camera (HD-TVI ABUS

180 TVVR33418) facing the transparent side of the aquarium and another one filming from above

181 for behavioural measurements (see below).

182   Once the focal fish introduced and after a 30-min acclimatization period, the

183 experiment started with the introduction of *Chaoborus* sp. larvae at a single time using a 250-

184 ml glass beaker, trying to cover the entire surface of the aquarium to homogenize prey

185 distribution. Fish resumed their normal behaviour within the three minutes following prey

186 introduction (personal observations) and were allowed to forage for one hour. We tested six

187 prey densities (N_0 = 8, 16, 32, 64, 128 and 256) with four replicates per density (n = 4) and

188 two noise conditions (see below), which needed 48 fish (plus eight companions) for the whole

189 investigation. Prey densities and experiment duration were fixed based on preliminary

190 experiments in a way to reach predator saturation, avoid predator satiation, avoid total prey

191 consumption, and promote fitting of the functional response models especially at low prey

192 densities. To verify that *Chaoborus* sp. mortality during the experiments was the result of fish

193 predation only, we did four replicates (two per noise condition) of the highest density (N_0 =

194 256) without fish. At the end of each experiment, the focal fish was gently removed with a

195 hand net, measured for fork length and returned to the housing tank separately from the others

196 to prevent reuse. We counted the remaining *Chaoborus* sp. larvae to assess prey consumption

197 and changed the water every two experiments to remove the chemical signals that might have

198 been released by the animals.

199   The whole investigation needed 13 consecutive days with four successive experiments

200   per day. To balance the time effect, we distributed the experiments in a quasi-systematic way

201   regarding replicates, noise condition and prey densities. At the end of the whole investigation,

202   all the fish were returned to the Volvon.

203

204   **2.3 Noise conditions**

205

206   As the control noise condition, we played back the ambient noise the fish were exposed to for

207   20 days in the housing tank. The ambient noise was recorded before storing the fish, using the

208   Aquarian Audio H2A-XLR Hydrophone connected to the ZOOM H4next Handy recorder and

209   placed in the center of the housing tank 14 cm above the water surface (for a 28-cm water

210   height). After checking the recording to be sure there was no other sounds than water

211   agitation due to the external pump, we created a playback track of 90 min to encompass the

212   30-min acclimatization period and the 60-min foraging period.

213   For the anthropogenic noise condition, we supplemented the ambient-noise playback

214   track with motorboat noise at various Signal-to-Noise Ratios (SNRs) using Audacity®

215   software 2.2.1. The original boat recording was 45-sec long and corresponded to the passage

216   of a small fishing boat with an outboard engine (see Alves et al., 2016 for further detail). We

217   applied a linear fading on both ends of the boat noise to make it emerge from the ambient

218   noise. To provide a substantial acoustic stimulation, the boat noise was looped four times into

219   a 'noise sequence' of 3 min and we broadcasted eight noise sequences interspersed with

220   ambient noise over the 1-h foraging period. Within each noise sequence, we varied the SNR

221   between the four boat noises to mimic a fleet of four boats passing successively at various

222   distances. To avoid fish habituation to the noise or the rhythm, we varied the SNRs and the

223   time intervals between the noise sequences (Table 1).

224   The tracks were played back as WAV files using an audio player (VLC media player

225   1.1.8), an amplifier (Yamaha RX-V540RDS), and the underwater speaker. To calibrate sound

226   pressure within the aquarium, we placed the hydrophone used to record the ambient noise in

227   the center of the aquarium and adjusted the intensity of the amplifier to have the same Root-

228   Mean-Square (RMS) sound pressure than in the center of the housing tank. Then, to generate

229   the SNRs of 2, 4 and 8, we adjusted the RMS sound pressure of the boat noise to have 2, 4 or

230   8 times the RMS value of the ambient noise. Minnows have been shown to respond

231   behaviourally to tones up to 5 kHz (Dijkgraaf & Verheijen 1950, Voellmy et al., 2014), where

232   the frequency spectrums of the ambient noise and the boat noise differed (Fig. 1). We

233   therefore expected the minnows to respond differently to the two noise conditions.

234

235   **2.4 Behavioural measurements**

236

237   Behaviour was recorded over the 8 successive noise sequences, where fish experiencing the

238   anthropogenic noise condition were exposed to the boat noise while those experiencing the

239   control condition were exposed to the ambient noise. The swimming distance covered during

240   the 3 min of each noise sequence was assessed by visual tracking using a software

241   (Mousotron 12.1, Blacksun Software), a video player (VLC media player 1.1.8) and the above

242   camera. To measure spatial distribution, we used the front camera and virtually divided the

243   aquarium into two equal areas: left versus right to test noise aversion, the speaker being in the

244   left area, and bottom versus top for the position along the water column. Position was

245   recorded every 15 sec during the 3 min of each noise sequence and we assigned the value of

246   '0' when the fish was in the left or the bottom area, and the value of '1' for the right or the top

247   area. At the same time, we also measured the distance to the companion fish (head to head) to

248   assess social interactions.

249

2.5 Statistical analyses

251

252   We used the R software (version 3.5.1, R Development Core Team 2017) with a significance

253   level of 0.05 for all the statistical analyses. Fish size being not normally distributed for the

254   control noise condition (Wilk-Shapiro test, $P = 0.011$), we tested the difference in fish size

255   between the two noise conditions using a Wilcoxon-Mann-Whitney test.

256   Functional response (FR) analysis was done with the 'frair' package (Pritchard et al.,

257   2017). The first step was to investigate which FR model between the types I, II and II best

258   described our data using the 'frair_fit' function where the model is optimized using the

259   maximum likelihood estimation (MLE). The simple type I (or linear) FR ('fr_typeI' in 'frair')

260   is implemented as:

261        $N_e = aN_0T$

262   where N_e is the number of prey eaten, N_0 the initial prey density, a the attack rate and T the

263   total experimental time.

264   For the type II FR model, we used the Rogers' random predator equation ('fr_rogersII'

265   in 'frair'), which is a modified version of the Hollings' original type II FR dedicated to non-

266   replacement experiments. The number of prey eaten (N_e) follows the relationship:

267        $N_e = N_0 (1 - \exp (a(N_e h - T)))$

268   where N_0 is the initial prey density, a the attack rate, h the handling time and T the total

269   experimental time. Model fitting was achieved using the Lambert's transcendental equation

270   (Bolker, 2008, 'lambertW0' function from the 'lamW' package).

271   For the type III FR model, we used the Hassel's type III extension to the Roger's random

272   predator equation ('fr_hassIIInr' in 'frair'). The number of prey eaten (N_e) follows the same

273 relationship defined for the Rogers' type II model except that the attack rate (a) is assumed to

274 vary with prey density in the following hyperbolic relationship:

275     $a = bN_0 / (1 + cN_0)$

276 where b and c are coefficients to be fitted and N_0 the initial prey density.

277   We compared the fits using the second order Akaike criterion (AIC), considering that

278 the best model is the one having the lowest AIC and that a delta AIC lower than 2 between

279 two fits means that both corresponding models perform as well (Nakaya et al., 2005). In

280 addition to the AIC approach, we also used the 'frair_test' function to specifically decide

281 between the type II and type III models. The idea is to fit a polynomial logistic function to the

282 proportion of prey consumed, a logistic regression being more able than a non-linear curve to

283 detect the subtle difference in curve shape at low prey densities between the type II and type

284 III models (Juliano, 2001; Pritchard et al., 2017). A type II FR is characterized by a

285 significantly negative first order term and a type III FR by a significantly positive first order

286 term followed by a significantly negative second order term (Juliano, 2001).

287 Once the best model identified, the second step was to generate 95% confidence intervals

288 (CIs) of the FR parameter estimates. This was done by non-parametric bootsrapping (n =

289 2000) with the 'frair_boot' function.

290   Finally, the third step was to test the between-treatment difference in the FR fit. The

291 type II FR being the best model for both treatments, the FR comparison came down to a

292 comparison of its two constituent parameters: attack rate a and handling time h. This allowed

293 us to use the delta (or difference) method provided by the 'frair_compare' function that tests

294 whether Da and Dh (the differences in attack rates and handling times) significantly differ

295 from zero (Juliano, 2001; Pritchard et al., 2017). In addition to the delta method, we inspected

296 the overlapping of the CIs of a and h provided by the 'frair_boot' function. To compare the

297 FRs at intermediate prey densities where a difference would not be detected by the delta

298   method (see Pritchard et al., 2017), we inspected the overlapping of the 95% CIs when plotted

299   on the entire FR curves with the 'drawpoly' function.

300   Generalized linear models were used to model the response variables of fish behaviour

301   (i.e. swimming distance, horizontal location, vertical location and distance to the companion

302   fish) as a function of the noise treatment taking individual fish as a random factor.

303   Measurement period (i.e. the eight successive noise sequences), fish size and prey density

304   were treated as covariates that potentially affect fish behaviour. Trends in fish behaviour

305   during the course of the experiment can change under the effect of noise. This was modeled

306   by including a *Treatment × Period* interaction term in the model. The most complete model

307   we fitted was on the form:

308        $Y_{[0/1]ij} = Treatment_{[0/1]} + b_{[0/1]} Period_j + c\ FishSize_i + d\ PreyDensity_k + (ID)_i + \varepsilon_{ijk},$

309   where *Y* is the response variable, *Treatment* is the treatment effect including ambient noise [0]

310   and boat noise [1], *Period* denotes the change in behaviour through time quantified by a slope

311   coefficient *b* possibly different between treatments (i.e. $b_0 \neq b_1$ quantifies the *Treatment* x

312   *Period* interaction), *FishSize* and *PreyDensity* are covariates whose effects are quantified with

313   their respective coefficients (*c* and *d*), *ID* is a random factor for fish identity, and ε is the

314   within individual residual variation. The intercept of the model was fixed at the average of the

315   control group. We assumed a Gaussian response for the swimming distance and the distance

316   to the companion and a binomial response for the horizontal (the sound coming from the left

317   side) and vertical positions.

318   A preliminary step of model selection based on small-sample-corrected AIC values

319   (AICc) was used to select for the most likely model and repeated each response variable.

320   Models were fitted by maximum likelihood in the *lme4* R package (Bates et al., 2015). When

321   the models were competing (i.e. ΔAICc < 2), the most parsimonious model was selected

322   (Burnham & Anderson, 2003). The predictor variables *FishSize* and *PreyDensity* were log-

323   scaled in order to standardize their variance and ease model convergence while keeping a

324   biologically meaningful scale (Houle et al., 2011).

325

326   **3 RESULTS**

327

328   All the *Chaoborus* sp. larvae survived in the replicates without fish, suggesting that larvae

329   removal during the experiments was the result of fish predation. There was no significant

330   difference in fish size between the two noise conditions (Wilcoxon-Mann-Whitney test, $P =$

331   0.214). Based on the AIC values and for both noise conditions, the type II and type III

332   functional response (FR) models performed as well (ΔAIC < 2) and better than the type I

333   (Table 2). Using the logistic regression of the proportion of prey consumed against prey

334   density, the first order term was significantly negative for both noise conditions (ambient

335   noise: 1st order term = -0.030, z = -2.968, P = 0.003; boat noise: 1st order term = -0.024, z = -

336   2.433, P = 0.015), which suggested to choose the type II over the type III (Fig. 2). Based on

337   the delta method, there was no significant difference in the handling time h between the two

338   noise conditions (Dh = 0.001, z = 0.166, P = 0.868) but the attack rate a was significantly

339   lower with the boat noise compared to the ambient noise (Da = 0.835, z = 2.815, P = 0.005).

340   Consistently, the confidence intervals (CIs) fully overlapped for handling time and partly

341   overlapped for attack rate (Fig. 3). When looking at the CIs of the fitted curves (Fig. 2),

342   variability was higher with boat noise compared to ambient noise.

343   According to a model retaining the measurement period as a covariate (Supplementary

344   table 1), fish exposed to boat noise (3.48 ±0.24 m for a 3-min measurement period) tended to

345   move more than those exposed to ambient noise only (3.09 ±0.24 m, difference = 0.39 m, χ^2 =

346   320, p < 0.001). The swimming distance did not change through time among the two noise

347   conditions (χ^2 = 0.01, p = 0.94). The best model explaining the distance to the companion as

348   well as horizontal fish position included fish size as a covariate (Supplementary tables 2 and

349   3). The distance to the companion was not affected by noise ($\chi^2 = 0.91$, $p = 0.339$) but

350   increased with fish size ($\chi^2 = 6.19$, $p = 0.013$). Regarding the horizontal position, fish tended

351   to be more often on the right side of the aquarium, at the opposite of the sound source ($\chi^2 = $

352   15.38, $p < 0.001$). Vertical fish position was best explained by a model including

353   measurement period as a covariate (Supplementary table 4). Fish exposed to boat noise were

354   found more frequently in the top area of the aquarium than fish from the control group ($\chi^2 = $

355   199.32, $p < 0.001$).

356

357   **4. DISCUSSION**

358

359   We used the functional response (FR) approach to test the effect of anthropogenic noise on

360   the trophic interaction between the European minnow *Phoxinus phoxinus* and one of its

361   potential prey, the dipteran larva *Chaoborus* sp.. Beyond the quantification of predation, this

362   approach explicitly considers the demographic consequences for prey populations. As

363   expected and consistently with the FR displayed by other fish species in shelter-free

364   experimental arenas (Alexander et al., 2014, 2015; Laverty et al., 2017), the FR of *P.*

365   *phoxinus* for both noise conditions was found to be of type II, in which predation rate rises

366   with prey density at a decelerating rate to an upper asymptote. Type II FRs are considered

367   destabilizing because of the high proportion of prey consumed at low densities, potentially

368   leading to prey exclusion. However, more realistic conditions like predator learning, the

369   presence of alternative prey with prey switching, or habitat complexity with predator – free

370   areas can decrease predator's efficiency at low prey densities and generate the less

371   destabilizing type III FR (Alexander et al. 2013; Barrios-O'Neill et al., 2015). We therefore

372 cannot claim the FR of *P. phoxinus* towards *Chaoborus* sp. larvae to be also of type II in the

373 field.

374   Adding motorboat noise to ambient noise did not change handling time and therefore

375 maximum feeding rate (1/*h*), resulting in the same asymptote, but decreased attack rate,

376 resulting in a less steep initial slope. This is consistent with our assumption of a greater effect

377 on attack rate than on handling time, the former depending mainly on behaviour and the latter

378 more on physiological and morphological constraints. This also suggests that minnows,

379 conversely to other species like the three-spined stickleback (*Gasterosteus aculeatus*) (Purser

380 & Radford, 2011) or the fathead minnow (*Pimephales promelas*) (Hasan et al., 2018), were

381 not distracted by noise and consequently did not take more time to handle and ingest their

382 prey. Noise did not affect the distance to the companion fish, used to estimate social

383 interactions, but significantly increased the swimming distance and changed the spatial

384 distribution, fish having been found more often at the opposite side of the speaker and in the

385 top area of the aquarium than under ambient noise. Increase in movements is a common

386 response to anthropogenic noise (Cox et al., 2018), and transposed to our experimental

387 context, this could have theoretically increase the likelihood of encountering prey items,

388 especially at low prey densities. Despite this, attack rate was lower with noise, suggesting a

389 reduced foraging motivation. Consistently, *P. phoxinus* has been found to make fewer feeding

390 attempts on *Daphnia magna* when exposed to elevated noise levels (Voellmy et al., 2014).

391 When considered together, the behavioural changes we observed suggest a more general

392 stress-related response whereby fish move to avoid the areas of elevated noise level, which

393 can be at the expense of feeding depending on prey availability. Both swimming and foraging

394 are costly and the cost of foraging is high when prey are scarce. Therefore, at low prey

395 densities, stressed fish might have allocated less time to foraging to offset the additional cost

396   of increased swimming. At the opposite, when prey were abundant, the cost of foraging was

397   low and stressed fish might have been able to engage in both activities concurrently.

398   Between-individual variability in behaviours was higher with boat noise than with

399   ambient noise as revealed by the wider confidence intervals of the FR parameters and the FR

400   curves. Personality differences are a common feature of animal populations (Wolf &

401   Weissing, 2012) and individuals often vary along a shyness – boldness continuum. It could be

402   that personality differences are exacerbated by the stress induced by anthropogenic noise.

403   Our setup did not allow us to record and analyze the behaviour of *Chaoborus* larvae

404   and their reaction to noise could have driven the observed decrease in attack rate.

405   Invertebrates can perceive and use sounds (e.g. Solé et al., 2016) and their susceptibility to

406   anthropogenic noise raises a growing interest (Morley et al., 2014). For instance, elevated

407   sound level has been found to differentially affect the abundance of terrestrial arthropods

408   (Bunkley et al., 2017). When exposed to playback of ship noise, the shore crab *Carcinus*

409   *maenas* shows disrupted feeding and antipredator behaviours (Wale et al., 2013a), and stress-

410   related physiological responses (Wale et al., 2013b). Conversely, Sabet et al. (2016) did not

411   find evidence for a negative effect of elevated sound level on the swimming behaviour of

412   water fleas (*Daphnia magna*). In the present study, *Chaoborus* larvae could have change their

413   spatial distribution and/or increase their vigilance in response to noise, resulting in a lowered

414   encounter rate at low densities.

415   Whatever the underlying mechanisms driving the change in FR, our finding suggests

416   that anthropogenic noise has potential do decrease the strength of trophic links, which might

417   have population and community outcomes. From the predator's perspective, less energy input

418   would ultimately induce a fitness cost, which can be offset by adjusting foraging patterns. For

419   instance, the Mediterranean damselfish *Chromis chromis* was found to reallocate its foraging

420   effort during the periods of low traffic intensity (Bracciali et al., 2012). As suggested by the

421 avoidance of the speaker in the present study and as reported in the literature, predators can

422 also leave the foraging areas of elevated sound level to find more quiet feeding patches

423 (Miksis-Olds & Wagner, 2011), which can go with alterations in diet composition (Payne et

424 al., 2015). The distribution of interaction strengths within a community depends on

425 consumers' diet and influences stability. Theoretical investigations have indeed demonstrated

426 that a skewed distribution pattern with a few strong links (i.e. with a high predation rate) for a

427 majority of weak links, which is common in nature, promotes stability compared to a more

428 homogeneous distribution (McCann et al., 1998; Rooney & McCann, 2012). Further

429 experiments are needed to test the effect of anthropogenic noise on the distribution of

430 interaction strengths and stability. From the prey's perspective, predation release can

431 influence lower trophic levels depending on the position of the prey along the food chain. For

432 instance, *Chaoborus* sp. larvae are natural predators of water fleas (Pastorok, 1981) and the

433 reduced vulnerability to fish predation under elevated noise level might have a negative

434 indirect effect on water fleas. Very recently, Barton et al. (2018) have experimentally

435 demonstrated the cascading effect of noise pollution along a beetle – aphid – plant tri-trophic

436 food chain but, to our knowledge, this is the only study that formally addressed this issue.

437   To conclude, our study provides additional evidence for the negative effect of

438 anthropogenic noise on predation and shows the usefulness of the functional response

439 approach to study the ecological impact of noise. We need further experiments involving

440 more interacting species and designed under the conceptual frameworks of community

441 ecology and food-web theory to decipher how individual responses to noise spread through

442 community to ultimately alter ecosystem properties. Chronic-exposure investigations are also

443 welcome to test for the long-term effects of noise persist as some species have been shown to

444 habituate to noise (Jacobsen et al., 2014; Johansson et al., 2016; Magnhagen et al., 2017).

445

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595   **FIGURE CAPTIONS**

596

597   Figure 1: Spectral density of the audio signals used to create the two noise conditions. The

598   original audio signals and their re-recordings in the experimental setup are represented with

599   discontinuous and solid lines, respectively. European minnows have been reported to react to

600   frequencies up to 5 KHz.

601

602   Figure 2: Number of prey eaten as a function of prey density (functional response) for

603   European minnows (*Phoxinus phoxinus*) feeding on dipteran larvae (*Chaoborus* sp.) in two

604   noise conditions: ambient noise alone (control treatment, in blue) or supplemented with

605   motorboat noise (anthropogenic noise treatment, in red). Dots are direct observations and

606   curves are the functional responses fitted with the 'frair' package (Pritchard et al., 2017).

607   Shaded areas represent bootstrapped (*n* = 2000) 95% confidence intervals.

608

609   Figure 3: Estimates of the functional response parameters: attack rate and handling time, for

610   European minnows (*Phoxinus phoxinus*) feeding on dipteran larvae (*Chaoborus* sp.) in two

611   noise conditions: ambient noise alone (control treatment) or supplemented with motorboat

612   noise (anthropogenic noise treatment). Error bars represent bootstrapped (*n* = 2000) 95%
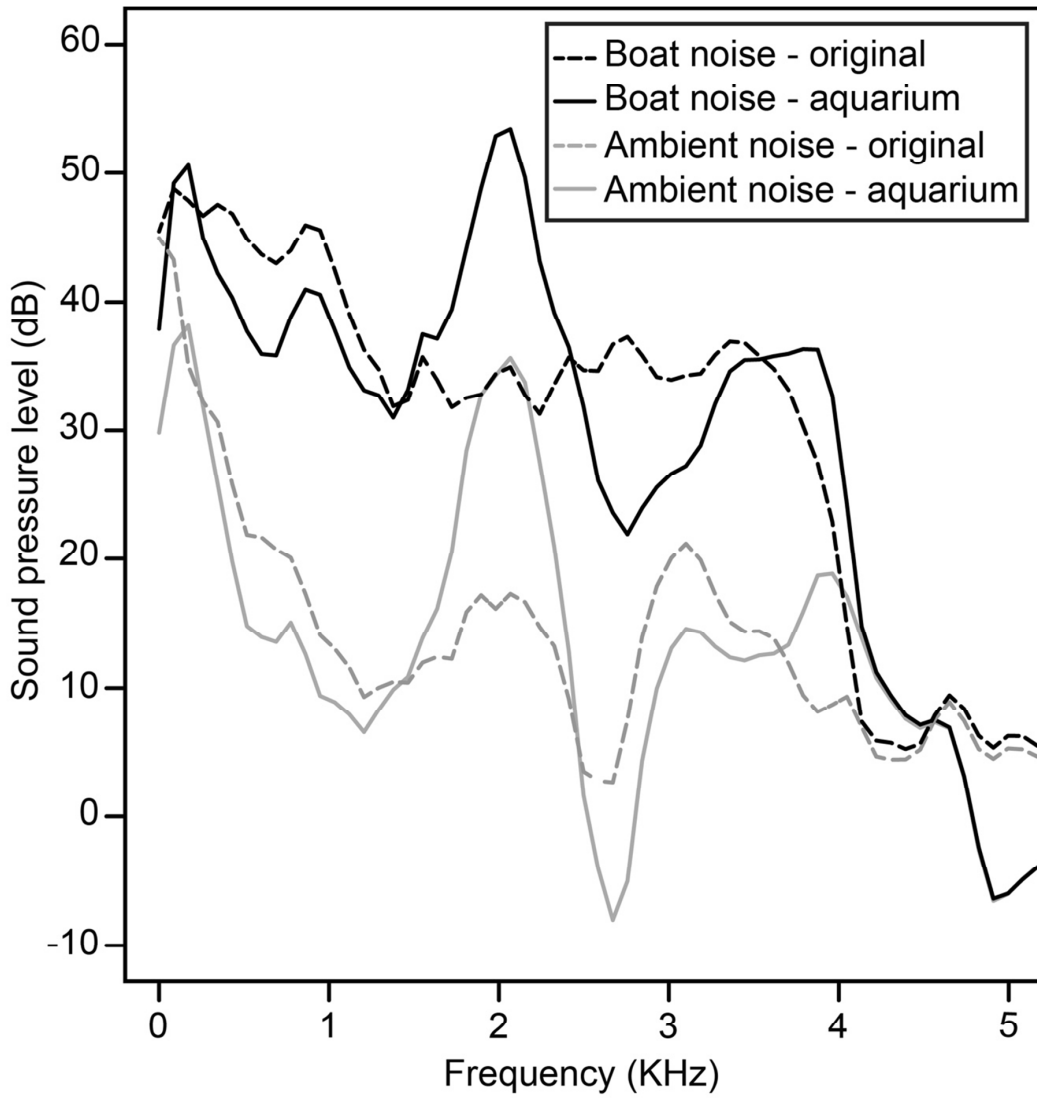
613   confidence intervals.

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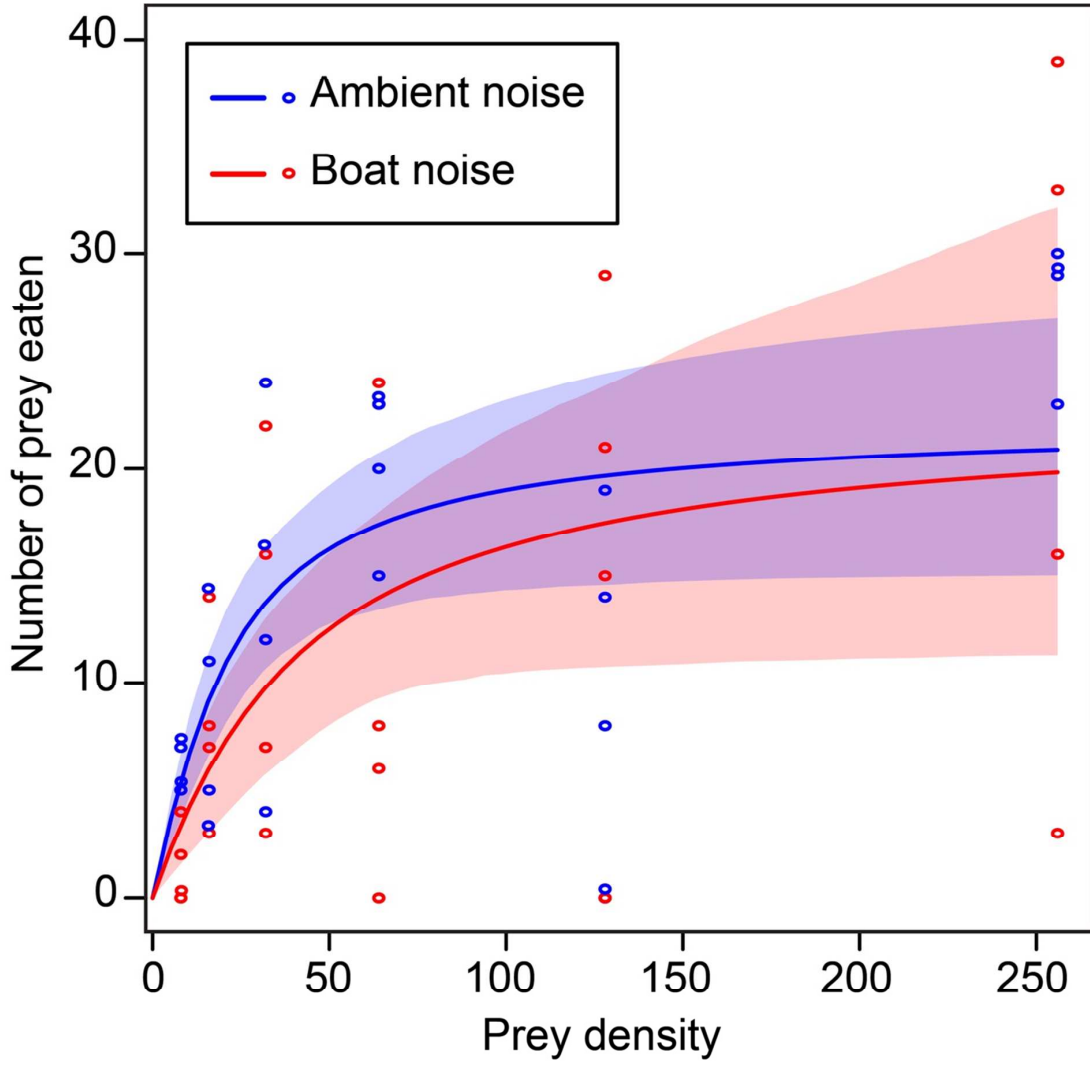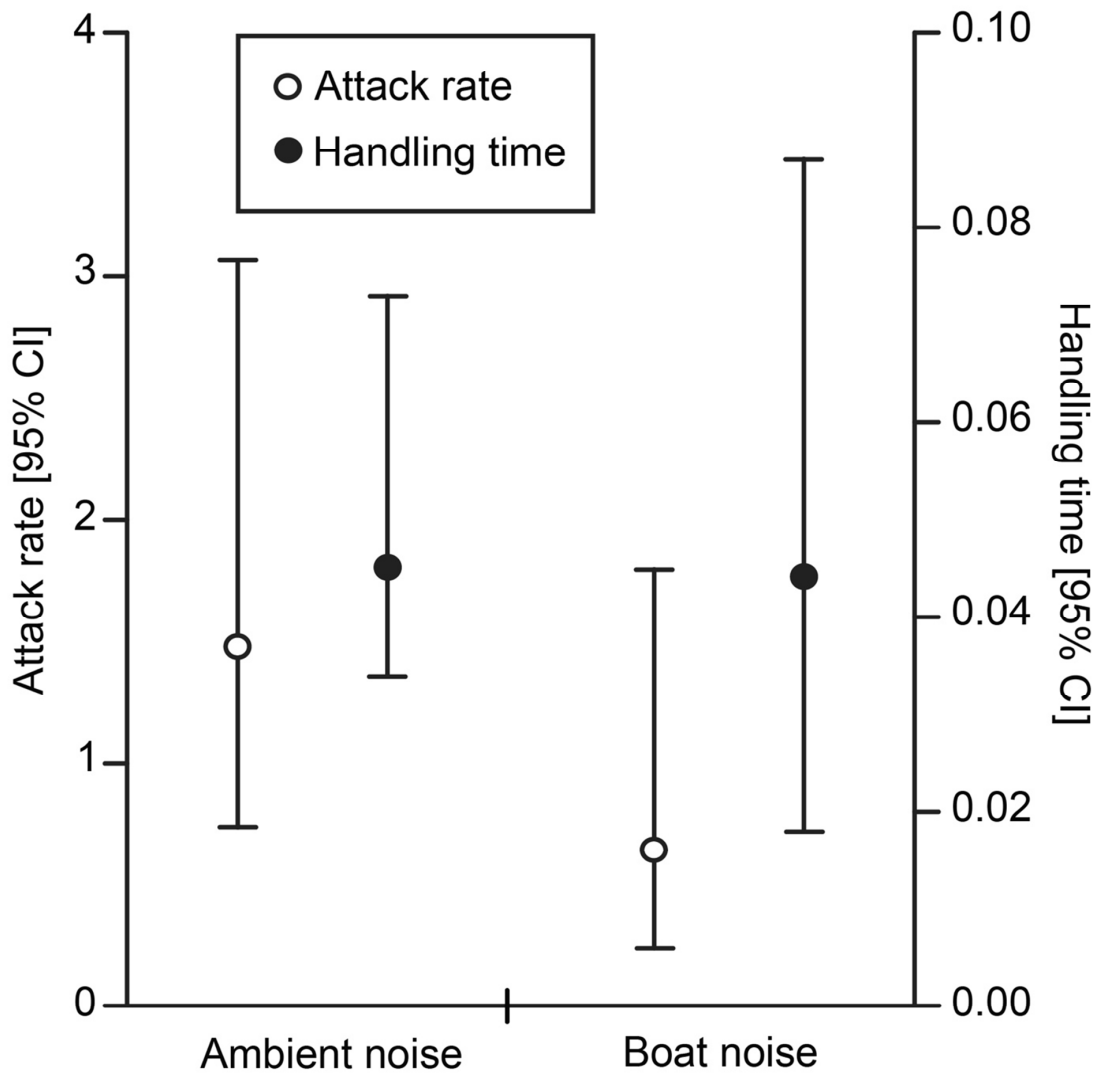47
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Fig. 1

Fig. 2

Fig. 3

Table 1: Playback track used in the anthropogenic noise condition with first 30 min of ambient noise during the acclimatizing period and then ambient noise and boat noise alternatively during the 1-h foraging period. During the 3-min sequences of boat noise, the sound made by a boat passing was looped four times at three signal-to-noise ratios compared to ambient noise.

Duration	Type of noise (SNRs*)
30 min 00 sec	Ambient
4 min 13 sec	Ambient
3 min 00 sec	Boat (2, 4, 8, 4)
5 min 09 sec	Ambient
3 min 00 sec	Boat (8, 2, 4, 8)
4 min 23 sec	Ambient
3 min 00 sec	Boat (4, 2, 8, 4)
4 min 44 sec	Ambient
3 min 00 sec	Boat (2, 4, 2, 8)
3 min 54 sec	Ambient
3 min 00 sec	Boat (2, 8, 4, 2)
5 min 00 sec	Ambient
3 min 00 sec	Boat (4, 8, 2, 8)
3 min 33 sec	Ambient
3 min 00 sec	Boat (4, 2, 4, 8)
5 min 04 sec	Ambient
3 min 00 sec	Boat (8, 4, 2, 2)

*Signal-to-Noise Ratios

Table 2: Akaike criteria (AIC) for the three candidate functional response models and the two

noise conditions. Values in brackets correspond to ΔAIC: the difference between the AIC

value for the current model and the lowest AIC value (in bold) for a given noise condition.

Noise condition	Type I	Type II	Type III
Ambient	415.38 (199.97)	**215.41**	217.41 (2)
Boat	388.82 (95.78)	**293.04**	294.25 (1.21)

Supplementary table 1: Model comparison based on ΔAICc for the swimming distance. K

gives the number of parameters in the mixed model (including random effects).

Model #	Model	K	AICc	ΔAICc	AICc weight	log-Likelihood
2	~ Treatment + Period + FishSizeLS + PreyDensityLS	7	1261.21	0.00	0.18	-623.46
3	~ Treatment + Period + FishSizeLS	6	1262.01	0.80	0.12	-624.90
7	~ Treatment + FishSizeLS + PreyDensityLS	6	1262.12	0.91	0.11	-624.95
5	~ Treatment + Period + PreyDensityLS	6	1262.47	1.26	0.10	-625.12
8	~ Treatment + Period	5	1262.93	1.72	0.08	-626.39
10	~ Treatment + FishSizeLS	5	1262.93	1.72	0.08	-626.39
1	~ Treatment + Period + FishSizeLS + PreyDensityLS + Treatment: Period	8	1263.29	2.08	0.06	-623.45
11	~ Treatment + PreyDensityLS	5	1263.39	2.18	0.06	-626.62
13	~ Constant	3	1263.55	2.34	0.06	-628.74
12	~ Treatment	4	1263.86	2.65	0.05	-627.88
4	~ Treatment + Period + FishSizeLS + Treatment: Period	7	1264.08	2.87	0.04	-624.89
6	~ Treatment + Period + PreyDensityLS + Treatment: Period	7	1264.54	3.33	0.03	-625.12
9	~ Treatment + Period + Treatment: Period	6	1264.99	3.78	0.03	-626.38

Supplementary table 2: Model comparison based on ΔAICc for the distance to the companion fish. *K* gives the number of parameters in the mixed model (including random effects).

Model #	Model	K	AICc	ΔAICc	AICc weight	log-Likelihood
10	~ Treatment + FishSizeLS	5	2174.49	0.00	0.35	-1082.17
7	~ Treatment + FishSizeLS + PreyDensityLS	6	2176.26	1.76	0.14	-1082.02
3	~ Treatment + Period + FishSizeLS	6	2176.49	2.00	0.13	-1082.13
13	~ Constant	3	2176.58	2.08	0.12	-1085.26
4	~ Treatment + Period + FishSizeLS + Treatment: Period	7	2177.89	3.40	0.06	-1081.80
2	~ Treatment + Period + FishSizeLS + PreyDensityLS	7	2178.26	3.77	0.05	-1081.98
12	~ Treatment	4	2178.27	3.77	0.05	-1085.08
1	~ Treatment + Period + FishSizeLS + PreyDensityLS + Treatment: Period	8	2179.68	5.18	0.03	-1081.65
11	~ Treatment + PreyDensityLS	5	2179.97	5.48	0.02	-1084.91
8	~ Treatment + Period	5	2180.25	5.76	0.02	-1085.05
9	~ Treatment + Period + Treatment: Period	6	2181.64	7.15	0.01	-1084.71
5	~ Treatment + Period + PreyDensityLS	6	2181.97	7.47	0.01	-1084.87
6	~ Treatment + Period + PreyDensityLS + Treatment:Period	7	2183.37	8.88	0.00	-1084.54

Supplementary table 3: Model comparison based on ΔAICc for the horizontal fish location. *K*

gives the number of parameters in the mixed model (including random effects).

Model #	Model	K	AICc	ΔAICc	AICc weight	log-Likelihood
10	~ Treatment + FishSizeLS	4	6148.38	0.00	0.36	-3070.19
3	~ Treatment + Period + FishSizeLS	5	6149.68	1.30	0.19	-3069.83
4	~ Treatment + Period + FishSizeLS + Treatment:Period	6	6149.98	1.60	0.16	-3068.98
7	~ Treatment + FishSizeLS + PreyDensityLS	5	6150.20	1.82	0.14	-3070.09
2	~ Treatment + Period + FishSizeLS + PreyDensityLS	6	6151.50	3.12	0.07	-3069.74
1	~ Treatment + Period + FishSizeLS + PreyDensityLS + Treatment: Period	7	6151.80	3.42	0.06	-3068.89
12	~ Treatment	3	6156.64	8.26	0.01	-3075.32
8	~ Treatment + Period	4	6157.94	9.56	0.00	-3074.97
9	~ Treatment + Period + Treatment:Period	5	6158.25	9.87	0.00	-3074.12
11	~ Treatment + PreyDensityLS	4	6158.40	10.02	0.00	-3075.20
13	~ Constant	2	6158.45	10.07	0.00	-3077.22
5	~ Treatment + Period + PreyDensityLS	5	6159.70	11.32	0.00	-3074.84
6	~ Treatment + Period + PreyDensityLS + Treatment:Period	6	6160.01	11.63	0.00	-3073.99

Supplementary table 4: Model comparison based on ΔAICc for the vertical fish location. K

gives the number of parameters in the mixed model (including random effects).

Model #	Model	K	AICc	ΔAICc	AICc weight	log-Likelihood
8	~ Treatment + Period	4	4619.36	0.00	0.28	-2305.67
9	~ Treatment + Period + Treatment:Period	5	4619.65	0.30	0.24	-2304.82
3	~ Treatment + Period + FishSizeLS	5	4621.25	1.89	0.11	-2305.62
5	~ Treatment + Period + PreyDensityLS	5	4621.33	1.97	0.11	-2305.66
4	~ Treatment + Period + FishSizeLS + Treatment:Period	6	4621.55	2.19	0.09	-2304.77
6	~ Treatment + Period + densityLS + Treatment:Period	6	4621.63	2.27	0.09	-2304.80
2	~ Treatment + Period + FishSizeLS + PreyDensityLS	6	4623.23	3.87	0.04	-2305.60
1	~ Treatment + Period + FishSizeLS + PreyDensityLS + Treatment:Period	7	4623.53	4.17	0.03	-2304.75
12	~ Treatment	3	4654.63	35.27	0.00	-2324.31
13	~ Constant	2	4654.66	35.31	0.00	-2325.33
10	~ Treatment + FishSizeLS	4	4656.52	37.16	0.00	-2324.26
11	~ Treatment + PreyDensityLS	4	4656.60	37.24	0.00	-2324.29
7	~ Treatment + FishSizeLS + PreyDensityLS	5	4658.50	39.14	0.00	-2324.24