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

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3 **1 How noise can alter predation: insights from the functional response**

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5 **2 Running title:** Noise-modified functional response

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3 26 **KEYWORDS**

4
5 27 anthropogenic noise, behaviour, freshwater ecosystems, functional response, *Phoxinus*

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7 28 *phoxinus*

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10
11 30 **Abstract**

12
13 31 1. Anthropogenic noise can affect animals physically, physiologically and behaviourally.

14
15 32 Although individual responses to noise are well documented, the consequences in terms of
16
17 33 community structure, species coexistence and ecosystem functioning remain fairly unknown.

18
19 34 2. The impact of noise on predation has received a growing interest and alterations in trophic

20
21 35 links are observed when animals shift from foraging to stress-related behaviours, are

22
23 36 distracted by noise, or because of acoustic masking. However, the experimental procedures

24
25 37 classically used to quantify predation do not inform on the potential demographic impact on

26
27 38 prey.

28
29 39 3. We derived the relationship between resource use and availability (the functional response)

30
31 40 for European minnows (*Phoxinus phoxinus*) feeding on dipteran larvae (*Chaoborus* sp.) under

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33 41 two noise conditions: ambient noise and ambient noise supplemented with motorboat noise.

34
35 42 The shape and magnitude of the functional response are powerful indicators of population

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37 43 outcomes and predator – prey dynamics. We also recorded fish behaviour to identify some

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39 44 proximate determinants of altered predation.

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41 45 4. For both noise conditions, fish displayed a saturating (type II) functional response whose

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43 46 shape depends on two parameters: attack rate and handling time. Boat noise did not affect

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45 47 handling time but significantly reduced attack rate, resulting in a functional response curve of

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47 48 the same height but with a less steep initial slope. Fish exhibited a stress-related response to

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

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3 50 5. Our study shows the usefulness of the functional response approach to study the ecological
4
5 51 impacts of noise and illustrates how behavioural responses of predators to noise can modify
6
7 52 the demographic pressure on prey. It also suggests that prey availability might mediate the
8
9 53 negative effect of noise on predation. Community outcomes are expected if the reduced
10
11 54 consumption of the main food sources goes with the overconsumption of alternative food
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13 55 sources, changing the distribution pattern of interaction strengths. Predation release could also
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15 56 trigger a trophic cascade, propagating the effect of noise to lower trophic levels.
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19 20 58 **1 INTRODUCTION**

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24 60 Anthropogenic (man-made) noise is recognized as a pervasive pollutant, changing the
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26 61 soundscape of many ecosystems. It has been found to affect the anatomy, physiology and/or
27
28 62 behaviour of both invertebrates and vertebrates in several ways, with consequences ranging
29
30 63 from discrete, short-term behavioural adjustments to fitness reduction through decreased
31
32 64 reproduction or survival (Popper & Hastings, 2009; Kight & Swaddle, 2011; Shannon et al.,
33
34 65 2016). Noise is therefore likely to alter key ecological interactions like competition,
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36 66 parasitism or predation, with potential consequences on species coexistence, community
37
38 67 stability and ecosystem-level processes (Kunc et al., 2016; Sabet et al., 2016). Although
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40 68 large-scale effects are highly expected, documented impacts rarely exceed individual
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42 69 responses.
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46 70 By driving energy through food webs and affecting biodiversity, trophic interactions
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48 71 influence ecosystem functioning. Noise is likely to alter the strength of a trophic interaction
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50 72 and hence energy flow in many ways. A common reaction is that predators are stressed by
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52 73 noise and shift from feeding to other activities like hiding, escaping or interacting with
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54 74 conspecifics (Cox et al., 2018). Energy flow can also decrease when the auditory cues used to
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3 75 locate prey are masked (Schaub et al., 2008), or when prey perceive noise as predation risk
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5 76 and become more vigilant (Rabin et al., 2006). Alternatively, energy flow can increase when
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7 77 prey are distracted and become more vulnerable to predation (Chan et al., 2010), or when
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9 78 noise masks the acoustic cues involved in predator recognition (Kern & Radford, 2016).
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11 79 Despite the increasing number of experimental studies reporting noise-modified trophic
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13 80 interactions, predicting their ecological significance in terms of population dynamic and
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15 81 species coexistence remains difficult. This comes partly from the experimental designs and
16
17 82 the predominant use of ‘snapshot’ predation tests, typically when a predator either alone or in
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19 83 group is presented to a single prey density. Although snapshot predation tests provide a rapid
20
21 84 and effective method to quantify predation, they do not inform on the potential demographic
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23 85 impact on the prey and, so importantly, results can depend on the prey density chosen (see
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25 86 Fig. 2 in Dick et al., 2014).

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29 87 Deriving the functional response (FR), which is the relationship between resource use
30
31 88 and availability (Solomon, 1949; Holling, 1959a), offers an alternative and complementary
32
33 89 approach to snapshot predation tests. Interestingly, the shape and magnitude of the
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35 90 relationship (i.e. the FR curve) are powerful indicators of the strength of top-down control.
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37 91 *Per capita* predation rate typically increases with prey availability and three broad shapes of
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39 92 FR are frequently observed: the linear type I, the saturating type II with a decelerating
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41 93 increase up to predator saturation, and the sigmoidal type III with acceleration first at low
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43 94 prey densities and then deceleration towards saturation (Holling, 1959a). In terms of predator
44
45 95 – prey stability, type II FRs are characterized by a high proportional consumption at low prey
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47 96 densities that can lead to unstable boom-burst population dynamics whereas the S-shape of
48
49 97 type III FRs offers low-density refugia for prey, which prevents such unstable dynamics
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51 98 (Murdoch & Oaten, 1975; Juliano, 2001; Gentleman & Neuheimer, 2008; Kalinkat et al.,
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53 99 2013). The FR approach provides an experimental framework to test context dependencies in
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3 100 consumer – resource interactions. It has received a growing interest in the fields of
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5 101 fundamental ecology, parasitology and invasion ecology, but remains largely ignored by the
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7 102 ecologists interested in the ecological impact of anthropogenic noise. Very recently,
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9 103 Villalobos-Jiménez et al. (2017) reported decreased magnitude in the FR of damselfly larvae
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11 104 (*Ischnura elegans*) towards cladoceran prey with underwater noise compared to more silent
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13 105 conditions, but no such investigations have been carried out in vertebrates.

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15
16 106 Our aim was to test the effect of anthropogenic noise on the shape and magnitude of
17
18 107 the FR of a freshwater fish, the European minnow *Phoxinus phoxinus*, feeding on dipteran
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20 108 prey. European minnows have a wide distribution range throughout the Palaearctic region and
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22 109 inhabit the cold and well-oxygenated waters of fast-flowing mountain streams, large lowland
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24 110 rivers and lakes (Kottelat & Freyhof, 2007; Vucić et al., 2018). Consequently, they can be
25
26 111 exposed to a wide range of anthropogenic noise including recreational shipping in small lakes
27
28 112 and industrial noise in large rivers (Voellmy et al. 2014). In our study, fish were presented to
29
30 113 six prey densities under conditions of ambient or motorboat noise, and we measured
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32 114 swimming distance, spatial distribution and social interactions to link changes in predation
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34 115 with changes in behaviour. We expected the FR of minnows to be of type II, which is the FR
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36 116 type usually displayed by fish in low-complexity environments (i.e. no shelter provided,
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38 117 Alexander et al., 2014, 2015; Laverty et al., 2017). The two key parameters of a type II FR are
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40 118 the attack rate a and the handling time h . Attack rate is a measure of predator's efficiency at
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42 119 low prey densities and defines the shape of the FR curve: the higher the attack rate, the
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44 120 steeper the initial slope. Handling time is defined as the time during which the predator stops
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46 121 searching for prey after a capture (Holling, 1959b). It includes successive stages like prey
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48 122 handling and ingestion and defines the height of the FR curve: the lower the handling time,
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50 123 the higher the asymptote. Using another experimental approach, Voellmy et al. (2014)
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52 124 reported that *P. phoxinus* exposed to the additional noise produced by shipping consumed
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3 125 significantly fewer live *Daphnia magna* and exhibited stress-related behaviours, including
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5 126 increased inactivity and more social interactions. Accordingly, we expected the FR of *P.*
6
7 127 *phoxinus* to be negatively influenced by anthropogenic noise, with a greater effect on attack
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9 128 rate than on handling time. Indeed, under the assumption of noise-induced increased
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11 129 inactivity, a smaller swimming distance would decrease the probability of encountering prey,
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13 130 especially at low densities when they are scarce, resulting in a smaller attack rate. Handling
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15 131 time has a behavioural component but also depends on morphological and physiological
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17 132 constraints. If the noise minnows were exposed to is unlikely to alter their anatomy or
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19 133 physiology, it could distract them during prey handling and ingestion, resulting in an
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21 134 increased handling time. We therefore expected a slight decrease in the height of the FR curve
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23 135 and a more pronounced change in its shape at low prey densities, with either a less steep type
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25 136 II or a shift towards the S-shape of the type III.
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31 138 **2 METHODS**

32 139 33 34 35 140 **2.1 Animal collection and maintenance**

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39 142 In March 2018, 70 *Phoxinus phoxinus* (body length = 5.5 ± 0.6 cm) were collected with
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41 143 electrofishing from the Volvon, a small tributary of the Coise river, at Veauche
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43 144 ($45^{\circ}34'12.4''N$, $4^{\circ}18'21.3''E$, Loire, France), and transported to a breeding room of ENES
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45 145 Laboratory thermoregulated at $17^{\circ}C$ with a 12:12 light:dark regime. We considered this
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47 146 population as naïve regarding motorboat noise. We did not control for sex and there was no
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49 147 gravid female at this period of the year. Fish were housed for 20 days in a 300 L plastic tank
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51 148 (housing tank) filled with continuously filtered and aerated dechlorinated tap water, and
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53 149 equipped with shelters. They were fed daily with commercial fish pellets and starved for 24 h
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3 150 prior to experimentation. We used *Chaoborus* sp. larvae as prey. In addition to being part of
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5 151 the diet of *P. phoxinus* (Frost 1943), they are pelagic and do not form aggregates in
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7 152 aquariums, which makes them good candidate prey items for functional response experiments
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9 153 (Médoc et al., 2013, 2015). *Chaoborus* sp larvae were purchased from a commercial supplier
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11 154 (www.aquaplante.fr) and maintained in 25 L aquaria under the same conditions than the fish.
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16 156 **2.2 Experimental design and protocol**

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20 158 Experiments took place in the breeding room thermoregulated at 17°C with a 12:12 light:dark
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22 159 regime to keep animals under the same conditions. One single fish starved for 24 h was
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24 160 placed in a glass aquarium (60 cm long x 30 cm wide x 32 cm high) filled with ≈ 50 L of
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26 161 filtered and aerated dechlorinated tap water (28 cm water height) and containing a 2-cm layer
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28 162 of Loire sand. Three sides were covered with black foam rubber panels (15 mm thick) to limit
29
30 163 acoustic reverberation whilst one side in the length was left transparent to film the
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32 164 experiment. We inserted an underwater speaker (Electro-Voice UW30, 0.1 to 10 kHz) in the
33
34 165 center of the acoustic panel covering the left end of the aquarium (when facing the transparent
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36 166 side). The center of the speaker was 11 cm below the water surface. At the opposite (right)
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38 167 end, we spaced the acoustic panel from the aquarium wall and placed a hydrophone (Aquarian
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40 168 Audio H2A-XLR Hydrophone, frequency response from 10 Hz to 100 KHz) connected to a
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42 169 ZOOM H4next Handy recorder between them to control the sound signal during the
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44 170 experiment. *P. phoxinus* being naturally gregarious (Frost 1943), we provided a companion
45
46 171 fish to the focal individual to promote normal behaviour. Companion fish were minnows of
47
48 172 standard size (4.7 ± 0.3 cm) used only for this purpose and kept apart from the other minnows
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50 173 in the housing tank. We placed the companion in the center of the aquarium inside a
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52 174 transparent plastic tube (8 cm diameter) to allow visual communication and prevent chemical
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3 175 exchange, and changed it every six experiments. To avoid unexpected sounds that might
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5 176 disturb the experiments, we placed the aquarium inside an acoustic box ('silent box', 89 cm
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7 177 long x 78.5 cm wide x 75 cm high) with acoustic foam covering the inner surface, a diffuse
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9 178 light source centered on the aquarium 34.5 cm above the water surface (875 lux light intensity
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11 179 at the water surface, Lux Meter for android devices), one camera (HD-TVI ABUS
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13 180 TVVR33418) facing the transparent side of the aquarium and another one filming from above
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15 181 for behavioural measurements (see below).
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18 182 Once the focal fish introduced and after a 30-min acclimatization period, the
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20 183 experiment started with the introduction of *Chaoborus* sp. larvae at a single time using a 250-
21
22 184 ml glass beaker, trying to cover the entire surface of the aquarium to homogenize prey
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24 185 distribution. Fish resumed their normal behaviour within the three minutes following prey
25
26 186 introduction (personal observations) and were allowed to forage for one hour. We tested six
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28 187 prey densities ($N_0 = 8, 16, 32, 64, 128$ and 256) with four replicates per density ($n = 4$) and
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30 188 two noise conditions (see below), which needed 48 fish (plus eight companions) for the whole
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32 189 investigation. Prey densities and experiment duration were fixed based on preliminary
33
34 190 experiments in a way to reach predator saturation, avoid predator satiation, avoid total prey
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36 191 consumption, and promote fitting of the functional response models especially at low prey
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38 192 densities. To verify that *Chaoborus* sp. mortality during the experiments was the result of fish
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40 193 predation only, we did four replicates (two per noise condition) of the highest density ($N_0 =$
41
42 194 256) without fish. At the end of each experiment, the focal fish was gently removed with a
43
44 195 hand net, measured for fork length and returned to the housing tank separately from the others
45
46 196 to prevent reuse. We counted the remaining *Chaoborus* sp. larvae to assess prey consumption
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48 197 and changed the water every two experiments to remove the chemical signals that might have
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50 198 been released by the animals.
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3 199 The whole investigation needed 13 consecutive days with four successive experiments
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5 200 per day. To balance the time effect, we distributed the experiments in a quasi-systematic way
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7 201 regarding replicates, noise condition and prey densities. At the end of the whole investigation,
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9 202 all the fish were returned to the Volvon.

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12 13 204 **2.3 Noise conditions**

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18 206 As the control noise condition, we played back the ambient noise the fish were exposed to for
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20 207 20 days in the housing tank. The ambient noise was recorded before storing the fish, using the
21
22 208 Aquarian Audio H2A-XLR Hydrophone connected to the ZOOM H4next Handy recorder and
23
24 209 placed in the center of the housing tank 14 cm above the water surface (for a 28-cm water
25
26 210 height). After checking the recording to be sure there was no other sounds than water
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28 211 agitation due to the external pump, we created a playback track of 90 min to encompass the
29
30 212 30-min acclimatization period and the 60-min foraging period.

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33 213 For the anthropogenic noise condition, we supplemented the ambient-noise playback
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35 214 track with motorboat noise at various Signal-to-Noise Ratios (SNRs) using Audacity®
36
37 215 software 2.2.1. The original boat recording was 45-sec long and corresponded to the passage
38
39 216 of a small fishing boat with an outboard engine (see Alves et al., 2016 for further detail). We
40
41 217 applied a linear fading on both ends of the boat noise to make it emerge from the ambient
42
43 218 noise. To provide a substantial acoustic stimulation, the boat noise was looped four times into
44
45 219 a ‘noise sequence’ of 3 min and we broadcasted eight noise sequences interspersed with
46
47 220 ambient noise over the 1-h foraging period. Within each noise sequence, we varied the SNR
48
49 221 between the four boat noises to mimic a fleet of four boats passing successively at various
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51 222 distances. To avoid fish habituation to the noise or the rhythm, we varied the SNRs and the
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53 223 time intervals between the noise sequences (Table 1).
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3 224 The tracks were played back as WAV files using an audio player (VLC media player
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5 225 1.1.8), an amplifier (Yamaha RX-V540RDS), and the underwater speaker. To calibrate sound
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7 226 pressure within the aquarium, we placed the hydrophone used to record the ambient noise in
8
9 227 the center of the aquarium and adjusted the intensity of the amplifier to have the same Root-
10
11 228 Mean-Square (RMS) sound pressure than in the center of the housing tank. Then, to generate
12
13 229 the SNRs of 2, 4 and 8, we adjusted the RMS sound pressure of the boat noise to have 2, 4 or
14
15 230 8 times the RMS value of the ambient noise. Minnows have been shown to respond
16
17 231 behaviourally to tones up to 5 kHz (Dijkgraaf & Verheijen 1950, Voellmy et al., 2014), where
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19 232 the frequency spectrums of the ambient noise and the boat noise differed (Fig. 1). We
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21 233 therefore expected the minnows to respond differently to the two noise conditions.
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27 235 **2.4 Behavioural measurements**

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31 237 Behaviour was recorded over the 8 successive noise sequences, where fish experiencing the
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33 238 anthropogenic noise condition were exposed to the boat noise while those experiencing the
34
35 239 control condition were exposed to the ambient noise. The swimming distance covered during
36
37 240 the 3 min of each noise sequence was assessed by visual tracking using a software
38
39 241 (Mousotron 12.1, Blacksun Software), a video player (VLC media player 1.1.8) and the above
40
41 242 camera. To measure spatial distribution, we used the front camera and virtually divided the
42
43 243 aquarium into two equal areas: left versus right to test noise aversion, the speaker being in the
44
45 244 left area, and bottom versus top for the position along the water column. Position was
46
47 245 recorded every 15 sec during the 3 min of each noise sequence and we assigned the value of
48
49 246 '0' when the fish was in the left or the bottom area, and the value of '1' for the right or the top
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51 247 area. At the same time, we also measured the distance to the companion fish (head to head) to
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53 248 assess social interactions.
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250 2.5 Statistical analyses

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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_hassIIIInr’ in ‘frair’). The number of prey eaten (N_e) follows the same

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3 273 relationship defined for the Rogers' type II model except that the attack rate (a) is assumed to
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5 274 vary with prey density in the following hyperbolic relationship:

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7 275
$$a = bN_0 / (1 + cN_0)$$

8
9 276 where b and c are coefficients to be fitted and N_0 the initial prey density.

10
11 277 We compared the fits using the second order Akaike criterion (AIC), considering that
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13 278 the best model is the one having the lowest AIC and that a delta AIC lower than 2 between
14
15 279 two fits means that both corresponding models perform as well (Nakaya et al., 2005). In
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17 280 addition to the AIC approach, we also used the 'frair_test' function to specifically decide
18
19 281 between the type II and type III models. The idea is to fit a polynomial logistic function to the
20
21 282 proportion of prey consumed, a logistic regression being more able than a non-linear curve to
22
23 283 detect the subtle difference in curve shape at low prey densities between the type II and type
24
25 284 III models (Juliano, 2001; Pritchard et al., 2017). A type II FR is characterized by a
26
27 285 significantly negative first order term and a type III FR by a significantly positive first order
28
29 286 term followed by a significantly negative second order term (Juliano, 2001).
30
31 287 Once the best model identified, the second step was to generate 95% confidence intervals
32
33 288 (CIs) of the FR parameter estimates. This was done by non-parametric bootstrapping ($n =$
34
35 289 2000) with the 'frair_boot' function.

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37
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39 290 Finally, the third step was to test the between-treatment difference in the FR fit. The
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41 291 type II FR being the best model for both treatments, the FR comparison came down to a
42
43 292 comparison of its two constituent parameters: attack rate a and handling time h . This allowed
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45 293 us to use the delta (or difference) method provided by the 'frair_compare' function that tests
46
47 294 whether Da and Dh (the differences in attack rates and handling times) significantly differ
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49 295 from zero (Juliano, 2001; Pritchard et al., 2017). In addition to the delta method, we inspected
50
51 296 the overlapping of the CIs of a and h provided by the 'frair_boot' function. To compare the
52
53 297 FRs at intermediate prey densities where a difference would not be detected by the delta
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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:

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

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* ×
 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. $\Delta AICc < 2$), the most parsimonious model was selected
 322 (Burnham & Anderson, 2003). The predictor variables *FishSize* and *PreyDensity* were log-

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3 323 scaled in order to standardize their variance and ease model convergence while keeping a
4
5 324 biologically meaningful scale (Houle et al., 2011).
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9 326 **3 RESULTS**

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13 328 All the *Chaoborus* sp. larvae survived in the replicates without fish, suggesting that larvae
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15 329 removal during the experiments was the result of fish predation. There was no significant
16
17 330 difference in fish size between the two noise conditions (Wilcoxon-Mann-Whitney test, $P =$
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19 331 0.214). Based on the AIC values and for both noise conditions, the type II and type III
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21 332 functional response (FR) models performed as well ($\Delta AIC < 2$) and better than the type I
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23 333 (Table 2). Using the logistic regression of the proportion of prey consumed against prey
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25 334 density, the first order term was significantly negative for both noise conditions (ambient
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27 335 noise: 1st order term = -0.030, $z = -2.968$, $P = 0.003$; boat noise: 1st order term = -0.024, $z = -$
28
29 336 2.433, $P = 0.015$), which suggested to choose the type II over the type III (Fig. 2). Based on
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31 337 the delta method, there was no significant difference in the handling time h between the two
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33 338 noise conditions ($Dh = 0.001$, $z = 0.166$, $P = 0.868$) but the attack rate a was significantly
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35 339 lower with the boat noise compared to the ambient noise ($Da = 0.835$, $z = 2.815$, $P = 0.005$).
36
37 340 Consistently, the confidence intervals (CIs) fully overlapped for handling time and partly
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39 341 overlapped for attack rate (Fig. 3). When looking at the CIs of the fitted curves (Fig. 2),
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41 342 variability was higher with boat noise compared to ambient noise.
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46 343 According to a model retaining the measurement period as a covariate (Supplementary
47
48 344 table 1), fish exposed to boat noise (3.48 ± 0.24 m for a 3-min measurement period) tended to
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50 345 move more than those exposed to ambient noise only (3.09 ± 0.24 m, difference = 0.39 m, $\chi^2 =$
51
52 346 320, $p < 0.001$). The swimming distance did not change through time among the two noise
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54 347 conditions ($\chi^2 = 0.01$, $p = 0.94$). The best model explaining the distance to the companion as
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3 348 well as horizontal fish position included fish size as a covariate (Supplementary tables 2 and
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5 349 3). The distance to the companion was not affected by noise ($\chi^2 = 0.91, p = 0.339$) but
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7 350 increased with fish size ($\chi^2 = 6.19, p = 0.013$). Regarding the horizontal position, fish tended
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9 351 to be more often on the right side of the aquarium, at the opposite of the sound source ($\chi^2 =$
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11 352 15.38, $p < 0.001$). Vertical fish position was best explained by a model including
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13 353 measurement period as a covariate (Supplementary table 4). Fish exposed to boat noise were
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15 354 found more frequently in the top area of the aquarium than fish from the control group ($\chi^2 =$
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17 355 199.32, $p < 0.001$).

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357 4. DISCUSSION

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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; Lavery 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

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3 372 cannot claim the FR of *P. phoxinus* towards *Chaoborus* sp. larvae to be also of type II in the
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5 373 field.

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7 374 Adding motorboat noise to ambient noise did not change handling time and therefore
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9 375 maximum feeding rate ($1/h$), resulting in the same asymptote, but decreased attack rate,
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11 376 resulting in a less steep initial slope. This is consistent with our assumption of a greater effect
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13 377 on attack rate than on handling time, the former depending mainly on behaviour and the latter
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15 378 more on physiological and morphological constraints. This also suggests that minnows,
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17 379 conversely to other species like the three-spined stickleback (*Gasterosteus aculeatus*) (Purser
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19 380 & Radford, 2011) or the fathead minnow (*Pimephales promelas*) (Hasan et al., 2018), were
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21 381 not distracted by noise and consequently did not take more time to handle and ingest their
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23 382 prey. Noise did not affect the distance to the companion fish, used to estimate social
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25 383 interactions, but significantly increased the swimming distance and changed the spatial
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27 384 distribution, fish having been found more often at the opposite side of the speaker and in the
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29 385 top area of the aquarium than under ambient noise. Increase in movements is a common
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31 386 response to anthropogenic noise (Cox et al., 2018), and transposed to our experimental
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33 387 context, this could have theoretically increase the likelihood of encountering prey items,
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35 388 especially at low prey densities. Despite this, attack rate was lower with noise, suggesting a
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37 389 reduced foraging motivation. Consistently, *P. phoxinus* has been found to make fewer feeding
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39 390 attempts on *Daphnia magna* when exposed to elevated noise levels (Voellmy et al., 2014).
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41 391 When considered together, the behavioural changes we observed suggest a more general
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43 392 stress-related response whereby fish move to avoid the areas of elevated noise level, which
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45 393 can be at the expense of feeding depending on prey availability. Both swimming and foraging
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47 394 are costly and the cost of foraging is high when prey are scarce. Therefore, at low prey
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49 395 densities, stressed fish might have allocated less time to foraging to offset the additional cost
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3 396 of increased swimming. At the opposite, when prey were abundant, the cost of foraging was
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5 397 low and stressed fish might have been able to engage in both activities concurrently.

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7 398 Between-individual variability in behaviours was higher with boat noise than with
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9 399 ambient noise as revealed by the wider confidence intervals of the FR parameters and the FR
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11 400 curves. Personality differences are a common feature of animal populations (Wolf &
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13 401 Weissing, 2012) and individuals often vary along a shyness – boldness continuum. It could be
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15 402 that personality differences are exacerbated by the stress induced by anthropogenic noise.

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17 403 Our setup did not allow us to record and analyze the behaviour of *Chaoborus* larvae
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19 404 and their reaction to noise could have driven the observed decrease in attack rate.
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21 405 Invertebrates can perceive and use sounds (e.g. Solé et al., 2016) and their susceptibility to
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23 406 anthropogenic noise raises a growing interest (Morley et al., 2014). For instance, elevated
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25 407 sound level has been found to differentially affect the abundance of terrestrial arthropods
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27 408 (Bunkley et al., 2017). When exposed to playback of ship noise, the shore crab *Carcinus*
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29 409 *maenas* shows disrupted feeding and antipredator behaviours (Wale et al., 2013a), and stress-
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31 410 related physiological responses (Wale et al., 2013b). Conversely, Sabet et al. (2016) did not
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33 411 find evidence for a negative effect of elevated sound level on the swimming behaviour of
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35 412 water fleas (*Daphnia magna*). In the present study, *Chaoborus* larvae could have change their
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37 413 spatial distribution and/or increase their vigilance in response to noise, resulting in a lowered
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39 414 encounter rate at low densities.

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43 415 Whatever the underlying mechanisms driving the change in FR, our finding suggests
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45 416 that anthropogenic noise has potential do decrease the strength of trophic links, which might
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47 417 have population and community outcomes. From the predator's perspective, less energy input
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49 418 would ultimately induce a fitness cost, which can be offset by adjusting foraging patterns. For
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51 419 instance, the Mediterranean damselfish *Chromis chromis* was found to reallocate its foraging
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53 420 effort during the periods of low traffic intensity (Bracciali et al., 2012). As suggested by the
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3 421 avoidance of the speaker in the present study and as reported in the literature, predators can
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5 422 also leave the foraging areas of elevated sound level to find more quiet feeding patches
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7 423 (Miksis-Olds & Wagner, 2011), which can go with alterations in diet composition (Payne et
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9 424 al., 2015). The distribution of interaction strengths within a community depends on
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11 425 consumers' diet and influences stability. Theoretical investigations have indeed demonstrated
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13 426 that a skewed distribution pattern with a few strong links (i.e. with a high predation rate) for a
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15 427 majority of weak links, which is common in nature, promotes stability compared to a more
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17 428 homogeneous distribution (McCann et al., 1998; Rooney & McCann, 2012). Further
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19 429 experiments are needed to test the effect of anthropogenic noise on the distribution of
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21 430 interaction strengths and stability. From the prey's perspective, predation release can
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23 431 influence lower trophic levels depending on the position of the prey along the food chain. For
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25 432 instance, *Chaoborus* sp. larvae are natural predators of water fleas (Pastorok, 1981) and the
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27 433 reduced vulnerability to fish predation under elevated noise level might have a negative
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29 434 indirect effect on water fleas. Very recently, Barton et al. (2018) have experimentally
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31 435 demonstrated the cascading effect of noise pollution along a beetle – aphid – plant tri-trophic
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33 436 food chain but, to our knowledge, this is the only study that formally addressed this issue.

37 To conclude, our study provides additional evidence for the negative effect of
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39 438 anthropogenic noise on predation and shows the usefulness of the functional response
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41 439 approach to study the ecological impact of noise. We need further experiments involving
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43 440 more interacting species and designed under the conceptual frameworks of community
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45 441 ecology and food-web theory to decipher how individual responses to noise spread through
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47 442 community to ultimately alter ecosystem properties. Chronic-exposure investigations are also
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49 443 welcome to test for the long-term effects of noise persist as some species have been shown to
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51 444 habituate to noise (Jacobsen et al., 2014; Johansson et al., 2016; Magnhagen et al., 2017).

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450 **REFERENCES**

- 451
- 452 Alexander, M. E., Dick, J. T., Weyl, O. L., Robinson, T. B., & Richardson, D. M. (2014).
453 Existing and emerging high impact invasive species are characterized by higher functional
454 responses than natives. *Biology Letters*, **10**(2), 20130946.
- 455 Alexander, M. E., Dick, J. T., & O'Connor, N. E. (2013). Trait-mediated indirect interactions
456 in a marine intertidal system as quantified by functional responses. *Oikos*, **122**(11), 1521-
457 1531.
- 458 Alexander, M. E., Kaiser, H., Weyl, O. L. F., & Dick, J. T. A. (2015). Habitat simplification
459 increases the impact of a freshwater invasive fish. *Environmental Biology of Fishes*, **98**(2),
460 477-486.
- 461 Alves, D., Amorim, M. C. P., & Fonseca, P. J. (2016). Boat noise reduces acoustic active
462 space in the lusitanian toadfish *Halobatrachus didactylus*. In *Proceedings of Meetings on*
463 *Acoustics 4ENAL* (Vol. 27, No. 1, p. 010033). ASA.
- 464 Barrios-O'Neill, D., Dick, J. T., Emmerson, M. C., Ricciardi, A., & MacIsaac, H. J. (2015).
465 Predator-free space, functional responses and biological invasions. *Functional Ecology*, **29**(3),
466 377-384.
- 467 Barton, B. T., Hodge, M. E., Speights, C. J., Autrey, A. M., Lashley, M. A., & Klink, V. P.
468 (2018). Testing the AC/DC hypothesis: Rock and roll is noise pollution and weakens a trophic
469 cascade. *Ecology and Evolution*. DOI :10.002/ece3.4273.

- 1
2
3 470 Bates, D., Mächler, M., Bolker, B., & Walker, S. (2014). Fitting linear mixed-effects models
4
5 471 using lme4. arXiv:1406.5823.
6
7 472 Bolker, B. M. (2008). *Ecological models and data in R*. Princeton University Press.
8
9 473 Chan, A. A. Y. H., Giraldo-Perez, P., Smith, S., & Blumstein, D. T. (2010). Anthropogenic
10
11 474 noise affects risk assessment and attention: the distracted prey hypothesis. *Biology Letters*, **6**,
12
13 475 458-461.
14
15 476 Bracciali, C., Campobello, D., Giacomini, C., & Sara, G. (2012). Effects of nautical traffic and
16
17 477 noise on foraging patterns of Mediterranean damselfish (*Chromis chromis*). *PloS one*, **7**(7),
18
19 478 e40582.
20
21 479 Bunkley, J. P., McClure, C. J., Kawahara, A. Y., Francis, C. D., & Barber, J. R. (2017).
22
23 480 Anthropogenic noise changes arthropod abundances. *Ecology and Evolution*, **7**(9), 2977-
24
25 481 2985.
26
27 482 Burnham, K. P., & Anderson, D. R. (2003). *Model selection and multimodel inference: a*
28
29 483 *practical information-theoretic approach*. Springer Science & Business Media.
30
31 484 Dick, J. T. A., Alexander, M. E., Jeschke, J. M., Ricciardi, A., MacIsaac, H. J., Robinson, T.,
32
33 485 ... Richardson, D. M. (2014). Advancing impact prediction and hypothesis testing in invasion
34
35 486 ecology using a comparative functional response approach. *Biological Invasions*, **16**, 735-
36
37 487 753.
38
39 488 Dijkgraaf, S., & Verheijen, F. (1950). Recent tests on tone differentiation capacity in the
40
41 489 minnow. *Zeitschrift für vergleichende Physiologie*, **32**(3), 248-256.
42
43 490 Frost, W. E. (1943). The natural history of the minnow, *Phoxinus phoxinus*. *The Journal of*
44
45 491 *Animal Ecology*, **12**(2), 139-162.
46
47 492 Gentleman, W. C., & Neuheimer, A. B. (2008). Functional responses and ecosystem
48
49 493 dynamics: How clearance rates explain the influence of satiation, food-limitation and
50
51 494 acclimation. *Journal of Plankton Research*, **30**, 1215-1231.
52
53
54
55
56
57
58
59
60

- 1
2
3 495 Hasan, M. R., Crane, A. L., Ferrari, M. C., & Chivers, D. P. (2018). A cross-modal effect of
4
5 496 noise: the disappearance of the alarm reaction of a freshwater fish. *Animal Cognition*, **21**(3),
6
7 497 419-424.
- 8
9 498 Holling, C. S. (1959a). Some characteristics of simple types of predation and parasitism. *The*
10
11 499 *Canadian Entomologist*, **91**, 385–398.
- 12
13 500 Holling, C. S. (1959b). The components of predation as revealed by a study of small-mammal
14
15 501 predation of the european pine sawfly. *The Canadian Entomologist*, **91**:293–320.
- 16
17 502 Houle, D., Pélabon, C., Wagner, G. P., & Hansen, T. F. (2011). Measurement and meaning in
18
19 503 biology. *The Quarterly Review of Biology*, **86**(1), 3-34.
- 20
21 504 Jacobsen, L., Baktoft, H., Jepsen, N., Aarestrup, K., Berg, S., & Skov, C. (2014). Effect of
22
23 505 boat noise and angling on lake fish behaviour. *Journal of Fish Biology*, **84**(6), 1768-1780.
- 24
25 506 Johansson, K., Sigray, P., Backström, T., & Magnhagen, C. (2016). Stress response and
26
27 507 habituation to motorboat noise in two coastal fish species in the Bothnian Sea. In *The Effects*
28
29 508 *of Noise on Aquatic Life II* (pp. 513-521). New York, Springer.
- 30
31 509 Juliano, S. A. (2001). Non-linear curve fitting: predation and functional response curves. In
32
33 510 Scheiner, S. M., & Gurevitch, J. *Design and analysis of ecological experiments* (pp. 178–
34
35 511 196). Oxford University Press.
- 36
37 512 Kalinkat, G., Schneider, F. D., Digel, C., Guill, C., Rall, B. C., & Brose, U. (2013). Body
38
39 513 masses, functional responses and predator-prey stability. *Ecology Letters*, **16**, 1126–1134.
- 40
41 514 Kern, J. M., & Radford, A. N. (2016). Anthropogenic noise disrupts use of vocal information
42
43 515 about predation risk. *Environmental Pollution*, **218**, 988-995.
- 44
45 516 Kight, C. R., & Swaddle, J. P. (2011). How and why environmental noise impacts animals:
46
47 517 An integrative, mechanistic review. *Ecology Letters*, **14**, 1052–1061.
- 48
49 518 Kottelat, M., & Freyhof, J. (2007). *Handbook of European freshwater fishes*. Publications
50
51 519 Kottelat.
- 52
53
54
55
56
57
58
59
60

- 1
2
3 520 Kunc, H. P., McLaughlin, K. E., & Schmidt, R. (2016). Aquatic noise pollution: implications
4
5 521 for individuals, populations, and ecosystems. *Proceedings of the Royal Society B*, **283**(1836),
6
7 522 20160839.
- 8
9 523 Laverty, C., Green, K. D., Dick, J. T., Barrios-O'Neill, D., Mensink, P. J., Médoc, V., ...
10
11 524 Britton, J. R. (2017). Assessing the ecological impacts of invasive species based on their
12
13 525 functional responses and abundances. *Biological Invasions*, **19**(5), 1653-1665.
- 14
15 526 Magnhagen, C., Johansson, K., & Sigray, P. (2017). Effects of motorboat noise on foraging
16
17 527 behaviour in Eurasian perch and roach: A field experiment. *Marine Ecology Progress*
18
19 528 *Series*, **564**, 115-125.
- 20
21 529 McCann, K., Hastings, A., & Huxel, G. R. (1998). Weak trophic interactions and the balance
22
23 530 of nature. *Nature*, **395**, 794-798.
- 24
25 531 Médoc, V., Albert, H., & Spataro, T. (2015). Functional response comparisons among
26
27 532 freshwater amphipods: ratio-dependence and higher predation for *Gammarus pulex* compared
28
29 533 to the non-natives *Dikerogammarus villosus* and *Echinogammarus berilloni*. *Biological*
30
31 534 *Invasions*, **17**, 3625–3637.
- 32
33 535 Médoc, V., Spataro, T., & Arditi, R. (2013). Prey: Predator ratio dependence in the functional
34
35 536 response of a freshwater amphipod. *Freshwater Biology*, **58**, 858–865.
- 36
37 537 Morley, E. L., Jones, G., & Radford, A. N. (2014). The importance of invertebrates when
38
39 538 considering the impacts of anthropogenic noise. *Proceedings of the Royal Society*
40
41 539 *B*, **281**(1776), 20132683.
- 42
43 540 Miksis-Olds, J. L., & Wagner, T. (2011). Behavioral response of manatees to variations in
44
45 541 environmental sound levels. *Marine Mammal Science*, **27**(1), 130-148.
- 46
47 542 Murdoch, W. W., Oaten, A. (1975). Predation and population stability. *Advances In*
48
49 543 *Ecological Research*, **9**, 1–131.
- 50
51
52
53
54
55
56
57
58
59
60

- 1
2
3 544 Nakaya, T., Fotheringham, A. S., Brunson, C., & Charlton, M. (2005). Geographically
4
5 545 weighted Poisson regression for disease association mapping. *Statistics in Medicine*, **24**(17),
6
7 546 2695-2717.
- 8
9 547 Pastorok, R. A. (1981). Prey vulnerability and size selection by *Chaoborus* larvae.
10
11 548 *Ecology*, **62**(5), 1311-1324.
- 12
13 549 Payne, N. L., van der Meulen, D. E., Suthers, I. M., Gray, C. A., & Taylor, M. D. (2015).
14
15 550 Foraging intensity of wild mulloway *Argyrosomus japonicus* decreases with increasing
16
17 551 anthropogenic disturbance. *Marine Biology*, **162**(3), 539-546.
- 18
19 552 Popper, A. N., & Hastings, M. C. (2009) The effects of anthropogenic sources of sound on
20
21 553 fishes. *Journal of Fish Biology*, **75**, 455-489.
- 22
23 554 Pritchard, D. W., Paterson, R. A., Bovy, H. C., & Barrios-O'Neill, D. (2017). Frair: an R
24
25 555 package for fitting and comparing consumer functional responses. *Methods in Ecology and*
26
27 556 *Evolution*, **8**(11), 1528-1534.
- 28
29 557 Purser, J., & Radford, A. N. (2011). Acoustic noise induces attention shifts and reduces
30
31 558 foraging performance in three-spined sticklebacks (*Gasterosteus aculeatus*). *PLoS One*, **6**(2),
32
33 559 e17478.
- 34
35 560 Rabin, L. A., Coss, R. G., & Owings, D. H. (2006). The effects of wind turbines on
36
37 561 antipredator behavior in California ground squirrels (*Spermophilus beecheyi*). *Biological*
38
39 562 *Conservation*, **131**, 410-420.
- 40
41 563 Rooney, N., & McCann, K. S. (2012). Integrating food web diversity, structure and
42
43 564 stability. *Trends in Ecology & Evolution*, **27**(1), 40-46.
- 44
45 565 Sabet, S. S., Neo, Y. Y., & Slabbekoorn, H. (2016). Impact of anthropogenic noise on aquatic
46
47 566 animals: from single species to community-level effects. In *The Effects of Noise on Aquatic*
48
49 567 *Life II* (pp. 957-961). New York, Springer.
- 50
51
52
53
54
55
56
57
58
59
60

- 1
2
3 568 Solé, M., Lenoir, M., Fortuño, J. M., Durfort, M., Van der Schaar, M., & André, M. (2016).
4
5 569 Evidence of Cnidarians sensitivity to sound after exposure to low frequency underwater
6
7 570 sources. *Scientific Reports*, **6**, 37979.
8
9 571 Solomon, M. E. (1949). The natural control of animal populations. *Journal of Animal*
10
11 572 *Ecology*, **18**, 1–35
12
13 573 Shannon, G., McKenna, M. F., Angeloni, L. M., Crooks, K. R., Fristrup, K. M., Brown, E., ...
14
15 574 McFarland, S. (2016). A synthesis of two decades of research documenting the effects of
16
17 575 noise on wildlife. *Biological Reviews* **91**(4), 982–1005.
18
19 576 Schaub, A., Ostwald, J., & Siemers, B. M. (2008). Foraging bats avoid noise. *Journal of*
20
21 577 *Experimental Biology*, **211**, 3174–3180.
22
23 578 Villalobos-Jiménez, G., Dunn, A. M., & Hassall, C. (2017). Environmental noise reduces
24
25 579 predation rate in an aquatic invertebrate. *Journal of Insect Conservation*, **21**, 839–847.
26
27 580 Voellmy, I. K., Purser, J., Flynn, D., Kennedy, P., Simpson, S. D., & Radford, A. N. (2014).
28
29 581 Acoustic noise reduces foraging success in two sympatric fish species via different
30
31 582 mechanisms. *Animal Behaviour*, **89**, 191–198.
32
33 583 Vucić, M., Jelić, D., Žutinić, P., Grandjean, F., & Jelić, M. (2018). Distribution of Eurasian
34
35 584 minnows (Phoxinus: Cypriniformes) in the Western Balkans. *Knowledge & Management of*
36
37 585 *Aquatic Ecosystems*, **419**, 11.
38
39
40 586 Wale, M. A., Simpson, S. D., & Radford, A. N. (2013a). Noise negatively affects foraging
41
42 587 and antipredator behaviour in shore crabs. *Animal Behaviour*, **86**(1), 111–118.
43
44 588 Wale, M. A., Simpson, S. D., & Radford, A. N. (2013b). Size-dependent physiological
45
46 589 responses of shore crabs to single and repeated playback of ship noise. *Biology letters*, **9**(2),
47
48 590 20121194.
49
50 591 Wolf, M., & Weissing, F. J. (2012). Animal personalities: consequences for ecology and
51
52 592 evolution. *Trends in Ecology & Evolution*, **27**(8), 452–461.
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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.

614

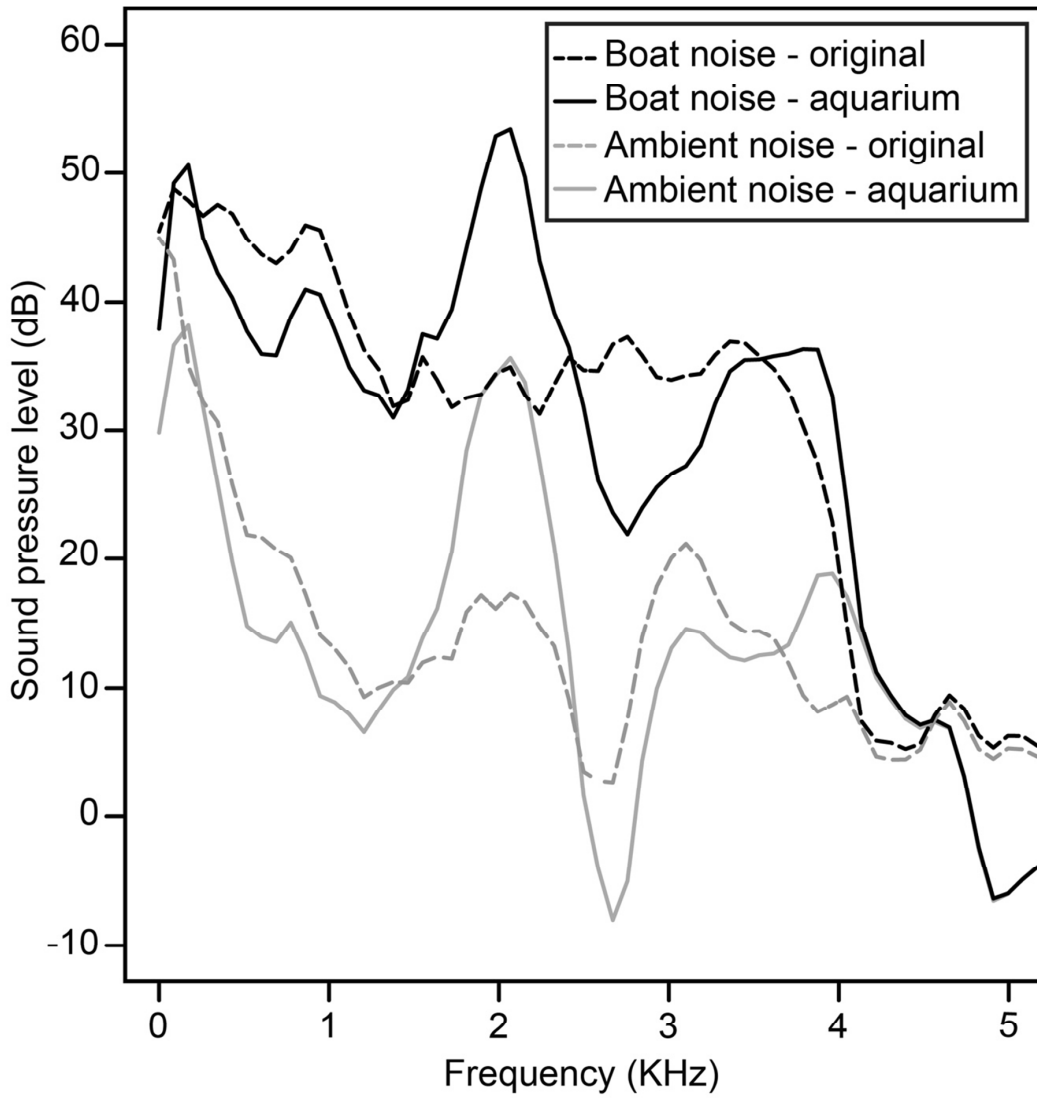


Fig. 1

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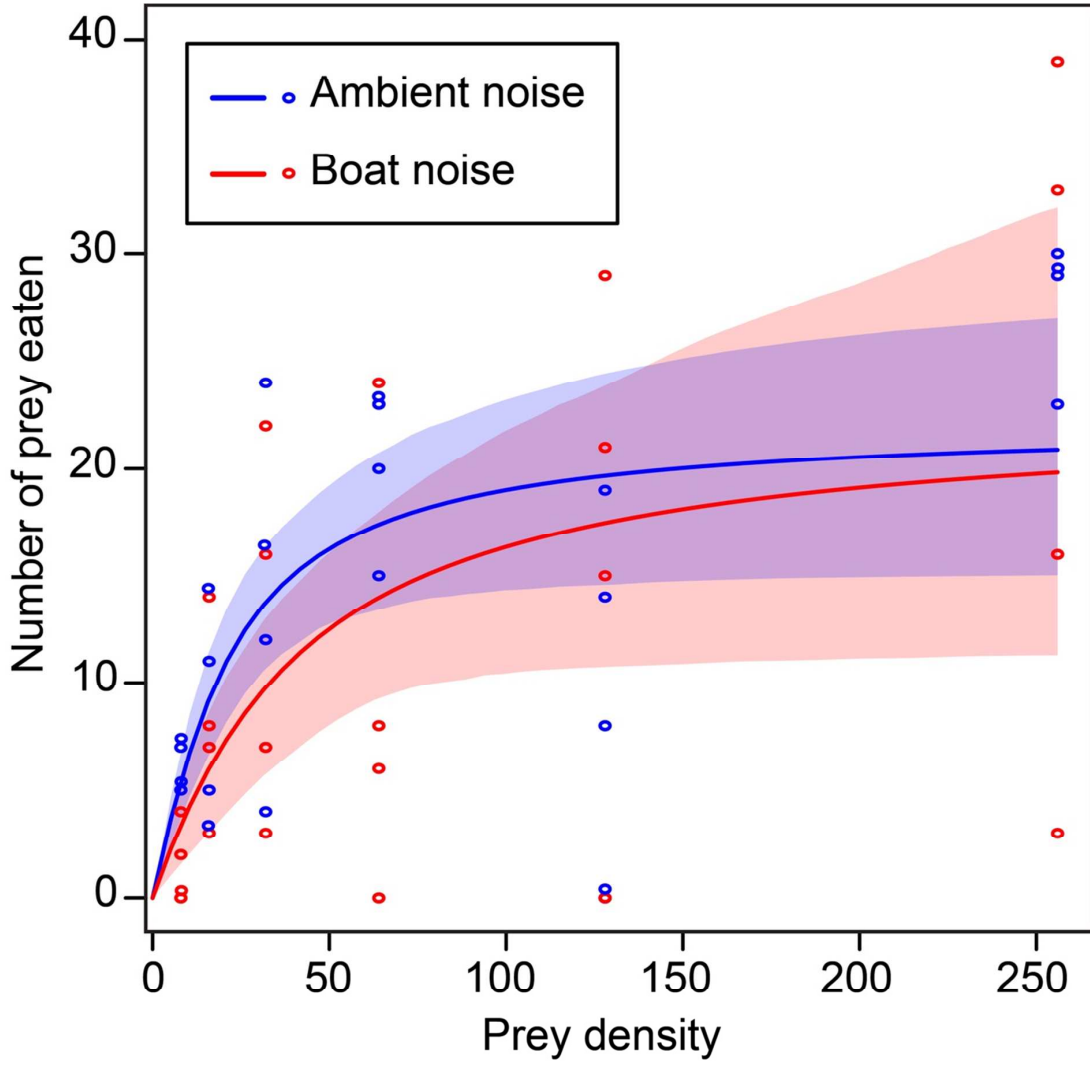


Fig. 2

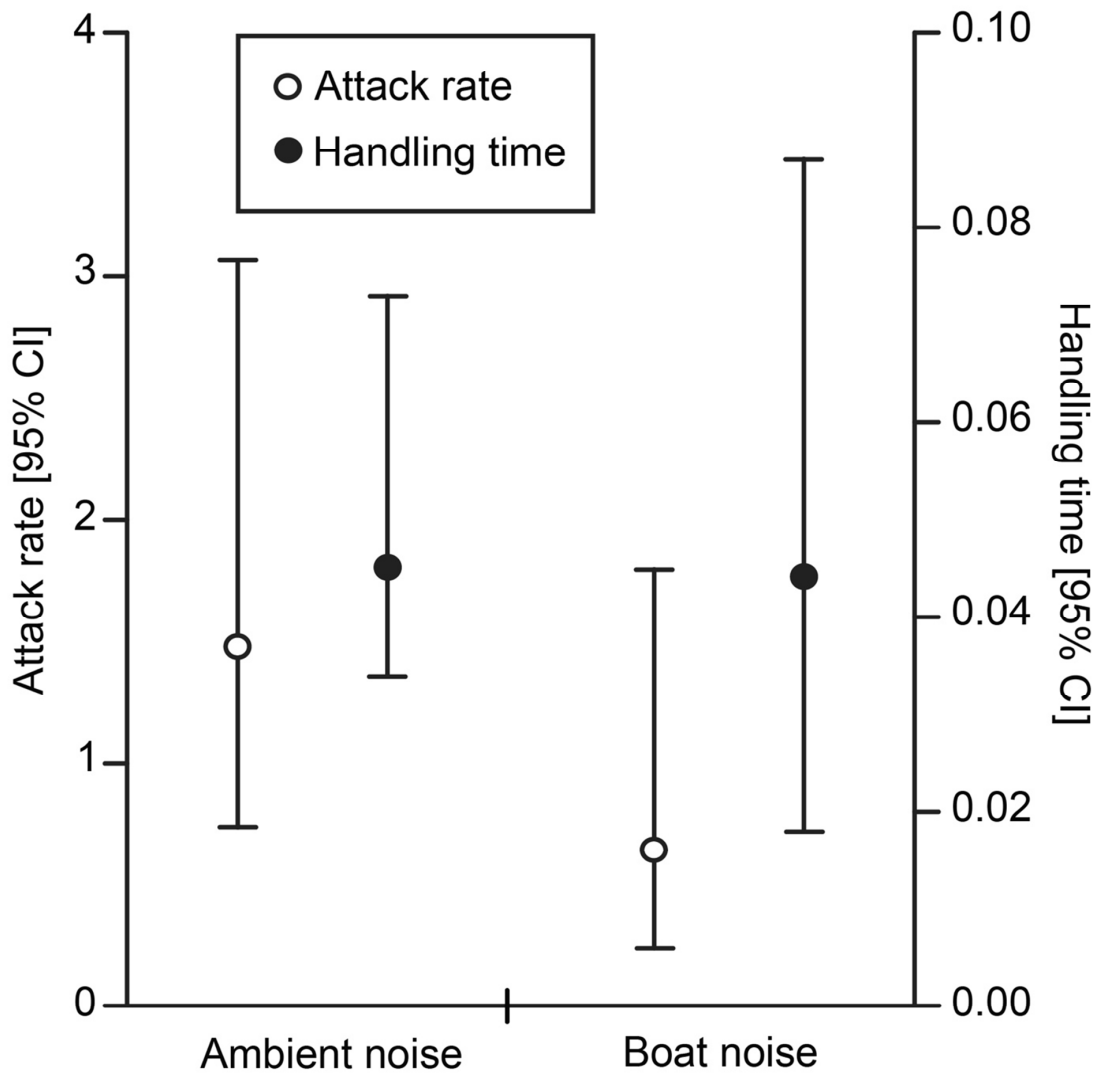


Fig. 3

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

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5 Table 2: Akaike criteria (AIC) for the three candidate functional response models and the two
6
7 noise conditions. Values in brackets correspond to ΔAIC : the difference between the AIC
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9 value for the current model and the lowest AIC value (in bold) for a given noise condition.
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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)

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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 $\Delta AICc$ for the distance to the companion fish. K gives the number of parameters in the mixed model (including random effects).

Model #	Model	K	AICc	$\Delta AICc$	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 $\Delta AICc$ for the horizontal fish location. K gives the number of parameters in the mixed model (including random effects).

Model #	Model	K	AICc	$\Delta AICc$	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 $\Delta AICc$ for the vertical fish location. K gives the number of parameters in the mixed model (including random effects).

Model #	Model	K	AICc	$\Delta AICc$	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