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

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## How noise can alter predation: insights from the functional response

Running title: Noise-modified functional response

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## KEYWORDS

anthropogenic noise, behaviour, freshwater ecosystems, functional response, Phoxinus phoxinus

Abstract

1. Anthropogenic noise can affect animals physically, physiologically and behaviourally. Although individual responses to noise are well documented, the consequences in terms of community structure, species coexistence and ecosystem functioning remain fairly unknown. 2. The impact of noise on predation has received a growing interest and alterations in trophic links are observed when animals shift from foraging to stress-related behaviours, are distracted by noise, or because of acoustic masking. However, the experimental procedures classically used to quantify predation do not inform on the potential demographic impact on prey.
2. We derived the relationship between resource use and availability (the functional response) for European minnows (Phoxinus phoxinus) feeding on dipteran larvae (Chaoborus sp.) under two noise conditions: ambient noise and ambient noise supplemented with motorboat noise. The shape and magnitude of the functional response are powerful indicators of population outcomes and predator - prey dynamics. We also recorded fish behaviour to identify some proximate determinants of altered predation.
3. For both noise conditions, fish displayed a saturating (type II) functional response whose shape depends on two parameters: attack rate and handling time. Boat noise did not affect handling time but significantly reduced attack rate, resulting in a functional response curve of the same height but with a less steep initial slope. Fish exhibited a stress-related response to noise including an increased swimming distance and an altered spatial distribution.
4. Our study shows the usefulness of the functional response approach to study the ecological impacts of noise and illustrates how behavioural responses of predators to noise can modify the demographic pressure on prey. It also suggests that prey availability might mediate the negative effect of noise on predation. Community outcomes are expected if the reduced consumption of the main food sources goes with the overconsumption of alternative food sources, changing the distribution pattern of interaction strengths. Predation release could also trigger a trophic cascade, propagating the effect of noise to lower trophic levels.

## 1 INTRODUCTION

Anthropogenic (man-made) noise is recognized as a pervasive pollutant, changing the soundscape of many ecosystems. It has been found to affect the anatomy, physiology and/or behaviour of both invertebrates and vertebrates in several ways, with consequences ranging from discrete, short-term behavioural adjustments to fitness reduction through decreased reproduction or survival (Popper \& Hastings, 2009; Kight \& Swaddle, 2011; Shannon et al., 2016). Noise is therefore likely to alter key ecological interactions like competition, parasitism or predation, with potential consequences on species coexistence, community stability and ecosystem-level processes (Kunc et al., 2016; Sabet et al., 2016). Although large-scale effects are highly expected, documented impacts rarely exceed individual responses.

By driving energy through food webs and affecting biodiversity, trophic interactions influence ecosystem functioning. Noise is likely to alter the strength of a trophic interaction and hence energy flow in many ways. A common reaction is that predators are stressed by noise and shift from feeding to other activities like hiding, escaping or interacting with conspecifics (Cox et al., 2018). Energy flow can also decrease when the auditory cues used to
locate prey are masked (Schaub et al., 2008), or when prey perceive noise as predation risk and become more vigilant (Rabin et al., 2006). Alternatively, energy flow can increase when prey are distracted and become more vulnerable to predation (Chan et al., 2010), or when noise masks the acoustic cues involved in predator recognition (Kern \& Radford, 2016). Despite the increasing number of experimental studies reporting noise-modified trophic interactions, predicting their ecological significance in terms of population dynamic and species coexistence remains difficult. This comes partly from the experimental designs and the predominant use of 'snapshot' predation tests, typically when a predator either alone or in group is presented to a single prey density. Although snapshot predation tests provide a rapid and effective method to quantify predation, they do not inform on the potential demographic impact on the prey and, so importantly, results can depend on the prey density chosen (see Fig. 2 in Dick et al., 2014).

Deriving the functional response (FR), which is the relationship between resource use and availability (Solomon, 1949; Holling, 1959a), offers an alternative and complementary approach to snapshot predation tests. Interestingly, the shape and magnitude of the relationship (i.e. the FR curve) are powerful indicators of the strength of top-down control. Per capita predation rate typically increases with prey availability and three broad shapes of FR are frequently observed: the linear type I, the saturating type II with a decelerating increase up to predator saturation, and the sigmoidal type III with acceleration first at low prey densities and then deceleration towards saturation (Holling, 1959a). In terms of predator - prey stability, type II FRs are characterized by a high proportional consumption at low prey densities that can lead to unstable boom-burst population dynamics whereas the S-shape of type III FRs offers low-density refugia for prey, which prevents such unstable dynamics (Murdoch \& Oaten, 1975; Juliano, 2001; Gentleman \& Neuheimer, 2008; Kalinkat et al., 2013). The FR approach provides an experimental framework to test context dependencies in
consumer - resource interactions. It has received a growing interest in the fields of fundamental ecology, parasitology and invasion ecology, but remains largely ignored by the ecologists interested in the ecological impact of anthropogenic noise. Very recently, Villalobos-Jiménez et al. (2017) reported decreased magnitude in the FR of damselfly larvae (Ischnura elegans) towards cladoceran prey with underwater noise compared to more silent conditions, but no such investigations have been carried out in vertebrates.

Our aim was to test the effect of anthropogenic noise on the shape and magnitude of the FR of a freshwater fish, the European minnow Phoxinus phoxinus, feeding on dipteran prey. European minnows have a wide distribution range throughout the Palaearctic region and inhabit the cold and well-oxygenated waters of fast-flowing mountain streams, large lowland rivers and lakes (Kottelat \& Freyhof, 2007; Vucić et al., 2018). Consequently, they can be exposed to a wide range of anthropogenic noise including recreational shipping in small lakes and industrial noise in large rivers (Voellmy et al. 2014). In our study, fish were presented to six prey densities under conditions of ambient or motorboat noise, and we measured swimming distance, spatial distribution and social interactions to link changes in predation with changes in behaviour. We expected the FR of minnows to be of type II, which is the FR type usually displayed by fish in low-complexity environments (i.e. no shelter provided, Alexander et al., 2014, 2015; Laverty et al., 2017). The two key parameters of a type II FR are the attack rate $a$ and the handling time $h$. Attack rate is a measure of predator's efficiency at low prey densities and defines the shape of the FR curve: the higher the attack rate, the steeper the initial slope. Handling time is defined as the time during which the predator stops searching for prey after a capture (Holling, 1959b). It includes successive stages like prey handling and ingestion and defines the height of the FR curve: the lower the handling time, the higher the asymptote. Using another experimental approach, Voellmy et al. (2014) reported that $P$. phoxinus exposed to the additional noise produced by shipping consumed
significantly fewer live Daphnia magna and exhibited stress-related behaviours, including increased inactivity and more social interactions. Accordingly, we expected the FR of $P$. phoxinus to be negatively influenced by anthropogenic noise, with a greater effect on attack rate than on handling time. Indeed, under the assumption of noise-induced increased inactivity, a smaller swimming distance would decrease the probability of encountering prey, especially at low densities when they are scarce, resulting in a smaller attack rate. Handling time has a behavioural component but also depends on morphological and physiological constraints. If the noise minnows were exposed to is unlikely to alter their anatomy or physiology, it could distract them during prey handling and ingestion, resulting in an increased handling time. We therefore expected a slight decrease in the height of the FR curve and a more pronounced change in its shape at low prey densities, with either a less steep type II or a shift towards the S-shape of the type III.

## 2 METHODS

### 2.1 Animal collection and maintenance

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

### 2.2 Experimental design and protocol

Experiments took place in the breeding room thermoregulated at $17^{\circ} \mathrm{C}$ with a $12: 12$ light:dark regime to keep animals under the same conditions. One single fish starved for 24 h was placed in a glass aquarium ( 60 cm long $\times 30 \mathrm{~cm}$ wide $\times 32 \mathrm{~cm}$ high) filled with $\approx 50 \mathrm{~L}$ of filtered and aerated dechlorinated tap water ( 28 cm water height) and containing a $2-\mathrm{cm}$ layer of Loire sand. Three sides were covered with black foam rubber panels ( 15 mm thick) to limit acoustic reverberation whilst one side in the length was left transparent to film the experiment. We inserted an underwater speaker (Electro-Voice UW30, 0.1 to 10 kHz ) in the center of the acoustic panel covering the left end of the aquarium (when facing the transparent side). The center of the speaker was 11 cm below the water surface. At the opposite (right) end, we spaced the acoustic panel from the aquarium wall and placed a hydrophone (Aquarian Audio H2A-XLR Hydrophone, frequency response from 10 Hz to 100 KHz ) connected to a ZOOM H4next Handy recorder between them to control the sound signal during the experiment. P. phoxinus being naturally gregarious (Frost 1943), we provided a companion fish to the focal individual to promote normal behaviour. Companion fish were minnows of standard size $(4.7 \pm 0.3 \mathrm{~cm})$ used only for this purpose and kept apart from the other minnows in the housing tank. We placed the companion in the center of the aquarium inside a transparent plastic tube ( 8 cm diameter) to allow visual communication and prevent chemical
exchange, and changed it every six experiments. To avoid unexpected sounds that might disturb the experiments, we placed the aquarium inside an acoustic box ('silent box', 89 cm long $\times 78.5 \mathrm{~cm}$ wide $\times 75 \mathrm{~cm}$ high) with acoustic foam covering the inner surface, a diffuse light source centered on the aquarium 34.5 cm above the water surface ( 875 lux light intensity at the water surface, Lux Meter for android devices), one camera (HD-TVI ABUS TVVR33418) facing the transparent side of the aquarium and another one filming from above for behavioural measurements (see below).

Once the focal fish introduced and after a $30-\mathrm{min}$ acclimatization period, the experiment started with the introduction of Chaoborus sp. larvae at a single time using a 250 ml glass beaker, trying to cover the entire surface of the aquarium to homogenize prey distribution. Fish resumed their normal behaviour within the three minutes following prey introduction (personal observations) and were allowed to forage for one hour. We tested six prey densities ( $N_{0}=8,16,32,64,128$ and 256) with four replicates per density $(n=4)$ and two noise conditions (see below), which needed 48 fish (plus eight companions) for the whole investigation. Prey densities and experiment duration were fixed based on preliminary experiments in a way to reach predator saturation, avoid predator satiation, avoid total prey consumption, and promote fitting of the functional response models especially at low prey densities. To verify that Chaoborus sp. mortality during the experiments was the result of fish predation only, we did four replicates (two per noise condition) of the highest density ( $N_{0}=$ 256) without fish. At the end of each experiment, the focal fish was gently removed with a hand net, measured for fork length and returned to the housing tank separately from the others to prevent reuse. We counted the remaining Chaoborus sp. larvae to assess prey consumption and changed the water every two experiments to remove the chemical signals that might have been released by the animals.

The whole investigation needed 13 consecutive days with four successive experiments per day. To balance the time effect, we distributed the experiments in a quasi-systematic way regarding replicates, noise condition and prey densities. At the end of the whole investigation, all the fish were returned to the Volvon.

### 2.3 Noise conditions

As the control noise condition, we played back the ambient noise the fish were exposed to for 20 days in the housing tank. The ambient noise was recorded before storing the fish, using the Aquarian Audio H2A-XLR Hydrophone connected to the ZOOM H4next Handy recorder and placed in the center of the housing tank 14 cm above the water surface (for a $28-\mathrm{cm}$ water height). After checking the recording to be sure there was no other sounds than water agitation due to the external pump, we created a playback track of 90 min to encompass the $30-\mathrm{min}$ acclimatization period and the $60-\mathrm{min}$ foraging period.

For the anthropogenic noise condition, we supplemented the ambient-noise playback track with motorboat noise at various Signal-to-Noise Ratios (SNRs) using Audacity® software 2.2.1. The original boat recording was 45 -sec long and corresponded to the passage of a small fishing boat with an outboard engine (see Alves et al., 2016 for further detail). We applied a linear fading on both ends of the boat noise to make it emerge from the ambient noise. To provide a substantial acoustic stimulation, the boat noise was looped four times into a 'noise sequence' of 3 min and we broadcasted eight noise sequences interspersed with ambient noise over the 1-h foraging period. Within each noise sequence, we varied the SNR between the four boat noises to mimic a fleet of four boats passing successively at various distances. To avoid fish habituation to the noise or the rhythm, we varied the SNRs and the time intervals between the noise sequences (Table 1).

The tracks were played back as WAV files using an audio player (VLC media player 1.1.8), an amplifier (Yamaha RX-V540RDS), and the underwater speaker. To calibrate sound pressure within the aquarium, we placed the hydrophone used to record the ambient noise in the center of the aquarium and adjusted the intensity of the amplifier to have the same Root-Mean-Square (RMS) sound pressure than in the center of the housing tank. Then, to generate the SNRs of 2,4 and 8 , we adjusted the RMS sound pressure of the boat noise to have 2,4 or 8 times the RMS value of the ambient noise. Minnows have been shown to respond behaviourally to tones up to 5 kHz (Dijkgraaf \& Verheijen 1950, Voellmy et al., 2014), where the frequency spectrums of the ambient noise and the boat noise differed (Fig. 1). We therefore expected the minnows to respond differently to the two noise conditions.

### 2.4 Behavioural measurements

Behaviour was recorded over the 8 successive noise sequences, where fish experiencing the anthropogenic noise condition were exposed to the boat noise while those experiencing the control condition were exposed to the ambient noise. The swimming distance covered during the 3 min of each noise sequence was assessed by visual tracking using a software (Mousotron 12.1, Blacksun Software), a video player (VLC media player 1.1.8) and the above camera. To measure spatial distribution, we used the front camera and virtually divided the aquarium into two equal areas: left versus right to test noise aversion, the speaker being in the left area, and bottom versus top for the position along the water column. Position was recorded every 15 sec during the 3 min of each noise sequence and we assigned the value of ' 0 ' when the fish was in the left or the bottom area, and the value of ' 1 ' for the right or the top area. At the same time, we also measured the distance to the companion fish (head to head) to assess social interactions.

### 2.5 Statistical analyses

We used the R software (version 3.5.1, R Development Core Team 2017) with a significance level of 0.05 for all the statistical analyses. Fish size being not normally distributed for the control noise condition (Wilk-Shapiro test, $P=0.011$ ), we tested the difference in fish size between the two noise conditions using a Wilcoxon-Mann-Whitney test.

Functional response (FR) analysis was done with the 'frair' package (Pritchard et al., 2017). The first step was to investigate which FR model between the types I, II and II best described our data using the 'frair_fit' function where the model is optimized using the maximum likelihood estimation (MLE). The simple type I (or linear) FR ('fr_typel' in 'frair') is implemented as:

$$
N_{e}=a N_{0} T
$$

where $N_{e}$ is the number of prey eaten, $N_{0}$ the initial prey density, $a$ the attack rate and $T$ the total experimental time.

For the type II FR model, we used the Rogers' random predator equation ('fr_rogersII' in 'frair'), which is a modified version of the Hollings' original type II FR dedicated to nonreplacement experiments. The number of prey eaten $\left(N_{e}\right)$ follows the relationship:

$$
N_{e}=N_{o}\left(1-\exp \left(a\left(N_{e} h-\mathrm{T}\right)\right)\right)
$$

where $N_{0}$ is the initial prey density, $a$ the attack rate, $h$ the handling time and $T$ the total experimental time. Model fitting was achieved using the Lambert's transcendental equation (Bolker, 2008, 'lambertW0' function from the 'lamW' package).

For the type III FR model, we used the Hassel's type III extension to the Roger's random predator equation ('fr_hassIIInr' in 'frair'). The number of prey eaten $\left(N_{e}\right)$ follows the same
relationship defined for the Rogers' type II model except that the attack rate (a) is assumed to vary with prey density in the following hyperbolic relationship:

$$
a=b N_{0} /\left(1+c N_{0}\right)
$$

where $b$ and $c$ are coefficients to be fitted and $N_{0}$ the initial prey density.
We compared the fits using the second order Akaike criterion (AIC), considering that the best model is the one having the lowest AIC and that a delta AIC lower than 2 between two fits means that both corresponding models perform as well (Nakaya et al., 2005). In addition to the AIC approach, we also used the 'frair_test' function to specifically decide between the type II and type III models. The idea is to fit a polynomial logistic function to the proportion of prey consumed, a logistic regression being more able than a non-linear curve to detect the subtle difference in curve shape at low prey densities between the type II and type III models (Juliano, 2001; Pritchard et al., 2017). A type II FR is characterized by a significantly negative first order term and a type III FR by a significantly positive first order term followed by a significantly negative second order term (Juliano, 2001).

Once the best model identified, the second step was to generate $95 \%$ confidence intervals (CIs) of the FR parameter estimates. This was done by non-parametric bootsrapping ( $n=$ 2000) with the 'frair_boot' function.

Finally, the third step was to test the between-treatment difference in the FR fit. The type II FR being the best model for both treatments, the FR comparison came down to a comparison of its two constituent parameters: attack rate $a$ and handling time $h$. This allowed us to use the delta (or difference) method provided by the 'frair_compare' function that tests whether $D a$ and $D h$ (the differences in attack rates and handling times) significantly differ from zero (Juliano, 2001; Pritchard et al., 2017). In addition to the delta method, we inspected the overlapping of the CIs of $a$ and $h$ provided by the 'frair_boot' function. To compare the FRs at intermediate prey densities where a difference would not be detected by the delta
method (see Pritchard et al., 2017), we inspected the overlapping of the $95 \%$ CIs when plotted on the entire FR curves with the 'drawpoly' function.

Generalized linear models were used to model the response variables of fish behaviour (i.e. swimming distance, horizontal location, vertical location and distance to the companion fish) as a function of the noise treatment taking individual fish as a random factor.

Measurement period (i.e. the eight successive noise sequences), fish size and prey density were treated as covariates that potentially affect fish behaviour. Trends in fish behaviour during the course of the experiment can change under the effect of noise. This was modeled by including a Treatment $\times$ Period interaction term in the model. The most complete model we fitted was on the form:

$$
\mathrm{Y}_{[0 / 1] \mathrm{ij}}=\text { Treatment }_{[0 / 1]}+b_{[0 / 1]} \text { Period }_{j}+c \text { FishSize }_{i}+\text { PreyDensity }_{k}+(\text { ID })_{i}+\varepsilon_{i j k}
$$

where $Y$ is the response variable, Treatment is the treatment effect including ambient noise [0] and boat noise [1], Period denotes the change in behaviour through time quantified by a slope coefficient $b$ possibly different between treatments (i.e. $\mathrm{b}_{0} \neq \mathrm{b}_{1}$ quantifies the Treatment x Period interaction), FishSize and PreyDensity are covariates whose effects are quantified with their respective coefficients ( $c$ and $d$ ), $I D$ is a random factor for fish identity, and $\varepsilon$ is the within individual residual variation. The intercept of the model was fixed at the average of the control group. We assumed a Gaussian response for the swimming distance and the distance to the companion and a binomial response for the horizontal (the sound coming from the left side) and vertical positions.

A preliminary step of model selection based on small-sample-corrected AIC values (AICc) was used to select for the most likely model and repeated each response variable. Models were fitted by maximum likelihood in the lme 4 R package (Bates et al., 2015). When the models were competing (i.e. $\Delta \mathrm{AICc}<2$ ), the most parsimonious model was selected (Burnham \& Anderson, 2003). The predictor variables FishSize and PreyDensity were log-
scaled in order to standardize their variance and ease model convergence while keeping a biologically meaningful scale (Houle et al., 2011).

## 3 RESULTS

All the Chaoborus sp. larvae survived in the replicates without fish, suggesting that larvae removal during the experiments was the result of fish predation. There was no significant difference in fish size between the two noise conditions (Wilcoxon-Mann-Whitney test, $P=$ 0.214). Based on the AIC values and for both noise conditions, the type II and type III functional response (FR) models performed as well ( $\Delta \mathrm{AIC}<2$ ) and better than the type I (Table 2). Using the logistic regression of the proportion of prey consumed against prey density, the first order term was significantly negative for both noise conditions (ambient noise: $1^{\text {st }}$ order term $=-0.030, z=-2.968, P=0.003$; boat noise: $1^{\text {st }}$ order term $=-0.024, z=-$ 2.433, $P=0.015$ ), which suggested to choose the type II over the type III (Fig. 2). Based on the delta method, there was no significant difference in the handling time $h$ between the two noise conditions ( $D h=0.001, z=0.166, P=0.868$ ) but the attack rate $a$ was significantly lower with the boat noise compared to the ambient noise ( $D a=0.835, z=2.815, P=0.005$ ). Consistently, the confidence intervals (CIs) fully overlapped for handling time and partly overlapped for attack rate (Fig. 3). When looking at the CIs of the fitted curves (Fig. 2), variability was higher with boat noise compared to ambient noise.

According to a model retaining the measurement period as a covariate (Supplementary table 1), fish exposed to boat noise ( $3.48 \pm 0.24 \mathrm{~m}$ for a 3-min measurement period) tended to move more than those exposed to ambient noise only $\left(3.09 \pm 0.24 \mathrm{~m}\right.$, difference $=0.39 \mathrm{~m}, \chi^{2}=$ $320, p<0.001$ ). The swimming distance did not change through time among the two noise conditions ( $\chi^{2}=0.01, p=0.94$ ). The best model explaining the distance to the companion as
well as horizontal fish position included fish size as a covariate (Supplementary tables 2 and 3). The distance to the companion was not affected by noise ( $\chi^{2}=0.91, p=0.339$ ) but increased with fish size $\left(\chi^{2}=6.19, p=0.013\right)$. Regarding the horizontal position, fish tended to be more often on the right side of the aquarium, at the opposite of the sound source $\left(\chi^{2}=\right.$ 15.38, $p<0.001$ ). Vertical fish position was best explained by a model including measurement period as a covariate (Supplementary table 4). Fish exposed to boat noise were found more frequently in the top area of the aquarium than fish from the control group $\left(\chi^{2}=\right.$ 199.32, $p<0.001$ ).

## 4. DISCUSSION

We used the functional response (FR) approach to test the effect of anthropogenic noise on the trophic interaction between the European minnow Phoxinus phoxinus and one of its potential prey, the dipteran larva Chaoborus sp.. Beyond the quantification of predation, this approach explicitly considers the demographic consequences for prey populations. As expected and consistently with the FR displayed by other fish species in shelter-free experimental arenas (Alexander et al., 2014, 2015; Laverty et al., 2017), the FR of $P$. phoxinus for both noise conditions was found to be of type II, in which predation rate rises with prey density at a decelerating rate to an upper asymptote. Type II FRs are considered destabilizing because of the high proportion of prey consumed at low densities, potentially leading to prey exclusion. However, more realistic conditions like predator learning, the presence of alternative prey with prey switching, or habitat complexity with predator - free areas can decrease predator's efficiency at low prey densities and generate the less destabilizing type III FR (Alexander et al. 2013; Barrios-O’Neill et al., 2015). We therefore
cannot claim the FR of $P$. phoxinus towards Chaoborus sp. larvae to be also of type II in the field.

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

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

Our setup did not allow us to record and analyze the behaviour of Chaoborus larvae and their reaction to noise could have driven the observed decrease in attack rate. Invertebrates can perceive and use sounds (e.g. Solé et al., 2016) and their susceptibility to anthropogenic noise raises a growing interest (Morley et al., 2014). For instance, elevated sound level has been found to differentially affect the abundance of terrestrial arthropods (Bunkley et al., 2017). When exposed to playback of ship noise, the shore crab Carcinus maenas shows disrupted feeding and antipredator behaviours (Wale et al., 2013a), and stressrelated physiological responses (Wale et al., 2013b). Conversely, Sabet et al. (2016) did not find evidence for a negative effect of elevated sound level on the swimming behaviour of water fleas (Daphnia magna). In the present study, Chaoborus larvae could have change their spatial distribution and/or increase their vigilance in response to noise, resulting in a lowered encounter rate at low densities.

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

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

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## FIGURE CAPTIONS

Figure 1: Spectral density of the audio signals used to create the two noise conditions. The original audio signals and their re-recordings in the experimental setup are represented with discontinuous and solid lines, respectively. European minnows have been reported to react to frequencies up to 5 KHz .

Figure 2: Number of prey eaten as a function of prey density (functional response) for European minnows (Phoxinus phoxinus) feeding on dipteran larvae (Chaoborus sp.) in two noise conditions: ambient noise alone (control treatment, in blue) or supplemented with motorboat noise (anthropogenic noise treatment, in red). Dots are direct observations and curves are the functional responses fitted with the 'frair' package (Pritchard et al., 2017). Shaded areas represent bootstrapped $(n=2000) 95 \%$ confidence intervals.

Figure 3: Estimates of the functional response parameters: attack rate and handling time, for European minnows (Phoxinus phoxinus) feeding on dipteran larvae (Chaoborus sp.) in two noise conditions: ambient noise alone (control treatment) or supplemented with motorboat noise (anthropogenic noise treatment). Error bars represent bootstrapped ( $n=2000$ ) $95 \%$ confidence intervals.


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*) |
| :---: | :---: |
| $30 \min 00 \mathrm{sec}$ | 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 $\triangle$ AIC: 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 | $415.38(199.97)$ | $\mathbf{2 1 5 . 4 1}$ | $217.41(2)$ |
| Boat | $388.82(95.78)$ | $\mathbf{2 9 3 . 0 4}$ | $294.25(1.21)$ |

Supplementary table 1 : Model comparison based on $\triangle \mathrm{AICc}$ for the swimming distance. K gives the number of parameters in the mixed model (including random effects).

| $\begin{gathered} \hline \text { Model } \\ \# \end{gathered}$ | Model | K | AICc | $\Delta \mathrm{AICc}$ | AICc weight | log- <br> Likelihood |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| 2 | Treatment + Period + <br> FishSizeLS + PreyDensityLS | 7 | 1261.21 | 0.00 | 0.18 | -623.46 |
| 3 | $\sim$ Treatment + Period + FishSizeLS | 6 | 1262.01 | 0.80 | 0.12 | -624.90 |
| 7 | $\sim$ Treatment + FishSizeLS + PreyDensityLS | 6 | 1262.12 | 0.91 | 0.11 | -624.95 |
| 5 | $\sim$ Treatment + Period + PreyDensityLS | 6 | 1262.47 | 1.26 | 0.10 | -625.12 |
| 8 | $\sim$ Treatment + Period | 5 | 1262.93 | 1.72 | 0.08 | -626.39 |
| 10 | $\sim$ Treatment + FishSizeLS | 5 | 1262.93 | 1.72 | 0.08 | -626.39 |
| 1 | $\sim$ Treatment + Period + <br> FishSizeLS + PreyDensityLS + Treatment: Period | 8 | 1263.29 | 2.08 | 0.06 | -623.45 |
| 11 | $\sim$ Treatment + PreyDensityLS | 5 | 1263.39 | 2.18 | 0.06 | -626.62 |
| 13 | $\sim$ Constant | 3 | 1263.55 | 2.34 | 0.06 | -628.74 |
| 12 | $\sim$ 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 | $\sim$ Treatment + Period + PreyDensityLS + Treatment: | 7 | 1264.54 | 3.33 | 0.03 | -625.12 |
| 9 | $\sim$ Treatment + Period + Treatment: Period | 6 | 1264.99 | 3.78 | 0.03 | -626.38 |

Supplementary table 2: Model comparison based on $\triangle \mathrm{AICc}$ for the distance to the companion fish. $K$ gives the number of parameters in the mixed model (including random effects).

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

Supplementary table 3: Model comparison based on $\triangle \mathrm{AICc}$ for the horizontal fish location. $K$ gives the number of parameters in the mixed model (including random effects).

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

Supplementary table 4: Model comparison based on $\triangle$ AICc for the vertical fish location. K gives the number of parameters in the mixed model (including random effects).

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

