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Anthropogenic noise does not strengthen multiple predator effects in a freshwater invasive fish

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ABSTRACT

Anthropogenic noise has potential to alter community dynamics by modifying the strength of nested ecological interactions like predation. Direct effects of noise on per capita predation rates have received much attention but the context in which predation occurs is often oversimplified. For instance, many animals interact with conspecifics while foraging and these non-trophic interactions can positively or negatively influence per capita predation rates. These effects are often referred to as multiple-predator effects (MPEs). The extent to which noise can modulate MPEs and thereby indirectly alter per capita predation remains unknown. To address this question, we derived the relationship between per capita predation rate and prey density, namely the functional response (FR), of single and pairs of the invasive topmouth gudgeon *Pseudorasbora parva* when feeding on water fleas under two noise conditions: control ambient noise estimated at 95 dB re 1 μ Pa and ambient noise supplemented with motorboat sounds whose relative importance over ambient noise ranged from 4.81 to 27 dB. In addition, we used video recordings to track fish movements. To detect MPEs, we compared the observed group-level FRs to predicted group-level FRs inferred from the individual FRs and based on additive effects only. Regardless of the number of fish and the noise condition, the FR was always of type II, showing predation rate in a decelerating rise to an upper asymptote. Compared to the noiseless condition, the predation rate of single fish exposed to noise did not differ at high prey densities but was significantly lower at low prey densities, resulting in a FR with the same asymptote but a less steep initial slope. Noise also reduced fish mobility, which might explain the decrease in predation rate at low prey densities. Conspecific presence suppressed the individual response to noise, the FRs of two fish (observed group-level FRs) being perfectly similar between the two noise conditions. Although observed and predicted group-level FRs did not differ significantly, observed group-level FRs tended to fall in the low range of predicted group-level FRs suggesting antagonism and a negative effect of non-trophic interactions on individual foraging performance. Interestingly, the difference between predicted and observed group-level FRs was not greater with noise, which means that noise did not strengthen MPEs. Our results show that when considering the social context of foraging, here through the presence of a conspecific, anthropogenic noise does not compromise foraging in the invasive *P. parva*.

Keyword: Anthropogenic noise, *Daphnia pulex*, functional response, predator-predator interaction, *Pseudorasbora parva*

1. Introduction

Energy flow throughout communities, largely driven by trophic interactions, determines biomass distribution, species coexistence, stability and ultimately ecosystem processes (Abdala-Roberts et al., 2019). It follows that any environmental stressor likely to modulate the strength of trophic interactions may have huge ecological impacts. Anthropogenic (i.e., man-made) noise is considered a pervasive pollutant, inducing behavioural, physiological, and sometimes anatomical alterations in animals (Erbe et al., 2018; Popper & Hastings, 2009; Shannon et al., 2016). Noise pollution has been shown to mask the acoustic cues used for prey (Francis & Barber, 2013) or predator (Merrall & Evans, 2020) detection, and to distract prey when escaping predators (Chan et al., 2010; Wale et al., 2013) or predators when searching for prey (Allen et al., 2021; Rojas et al., 2021). Animals can leave resource-rich areas to avoid noise (Bayne et al., 2008; Blickley et al., 2012; Goodwin & Shriver, 2011) or exhibit behavioural stress responses at the expense of foraging (Francis et al., 2012; Hanache et al., 2020; Voellmy et al., 2014). However, understanding the ecological implications of noise-induced changes in *per capita* consumption rates needs to account for the context in which foraging occurs.

For many species, foraging has a social component as individuals do not forage alone in their environment. The *per capita* consumption rate of cooperative foragers will benefit from the presence of conspecifics whereas mutual interference usually reduces individual performance in non-cooperative foragers (Harpaz & Schneidman, 2020). The time spent interacting is indeed not allocated to foraging, this effect being even greater when non-trophic interactions include agonistic behaviors. Consumption rates by multiple predators can thus differ from what could be expected with the assumption of independent, additive effects of each single predator on prey survival, and these effects are often referred to as multiple-predator effects (MPEs) (Sentis et al., 2017).

There is growing evidence that anthropogenic noise can change the strength of non-trophic interactions. Brintjes & Radford (2013) found that aggressive and submissive behaviors between dominant pairs and their subordinates were increased under playback of boat noise in the cooperative breeding cichlid *Neolamprologus pulcher*. Pile-driving noise was shown to disrupt the coherence and coordination of shoals in juveniles of the sea bass *Dicentrarchus labrax* (Herbert-Read et al., 2017). Inter-individual distance is reduced by tonal signals (Currie et al., 2020) and motorboat noise (Hanache et al., 2020) in the Eurasian minnow *Phoxinus phoxinus*, a behavioural response that has been suspected to contribute to the decrease in attack rate on live dipteran larvae (Hanache et al., 2020). Anthropogenic noise may therefore alter *per capita* predation indirectly through the emergence of MPEs and ignoring the social context in which foraging occurs may lead to misestimate the effect of noise. To our knowledge, this issue has received no interest yet.

Functional response derivation offers an experimental framework to characterize the dynamic of predation under context-dependencies. The functional response (FR) describes how *per-capita* consumption rate varies with resource density (Holling, 1959), the shape and magnitude of this relationship providing mechanistic insight into consumer behaviour and the phenomenological consequences for resource populations (i.e., prey). For instance, saturating (type II) FRs, where predation rate increases with prey density at a decelerating rate towards an asymptote, are more likely to promote unstable boom-bust population dynamics than sigmoidal (type III) FRs, where prey experience reduced predation when scarce (Gentleman & Neuheimer, 2008; Juliano, 2001; Kalinkat et al., 2013; Murdoch & Oaten, 1975). Functional response derivation can be applied to single consumers as well as to conspecific or heterospecific groups of consumers (Michaelides et al., 2018; Wasserman et al., 2016) and comparing group-level FRs to what could be predicted from the additive effect of individual-level FRs allows the detection of MPEs (Kéfi et al., 2012; Sentis et al., 2017; Veselý et al., 2019; Wasserman et al., 2016). Synergism between consumers and risk

enhancement for the resource are expected when observed group-level FRs exceed predicted group-level FRs, whilst the reverse suggests antagonism and risk reduction.

In the present study, we investigated the effect of repeated daily exposure to motorboat noise (i.e., chronic noise) on the functional response (FR) and the behaviour of single individuals and pairs of the invasive topmouth gudgeon *Pseudorasbora parva*, listed as one of the top ten worst invasive species in Europe (Britton et al., 2007; Pinder et al., 2005). *Pseudorasbora parva* produces involuntary sounds while sucking in food items and it has a chain of Weberian ossicles that connect the swim bladder to the inner ear and improve hearing ability, with greatest sensitivity at 500 Hz (Scholz & Ladich, 2006). Prior to the FR experiments, *P. parva* were exposed to boat sounds as the response to noise was found to weaken with repeated exposure in some fish species (see Rojas et al., 2021 for an example in another freshwater invasive fish, the pumpkinseed sunfish *Lepomis gibbosus*). To detect MPEs, we compared for both noise conditions observed group-level FRs to predicted group-level FRs inferred from individual predation rates.

Based on published results on fish FR in shelter-free environments (Cuthbert et al., 2019; Dick et al., 2013; Hanache et al., 2020), we expected the FR of *P. parva* to be of type II (decelerating curve) where *per capita* predation is defined by two key parameters: the attack rate a that corresponds to the spatial pattern of prey searching *per* unit of time and fixes FR curve's initial slope (the higher the attack rate, the higher the slope), and the handling time h that is the average time spent on a caught prey item and determines FR curve's asymptote (the smaller the handling time, the higher the asymptote, Holling 1959). The inverse of handling time and therefore the asymptote also correspond to the maximum feeding rate. Because noise was found to promote conspecific interactions through reduced inter-individual distance in another cyprinid fish the Eurasian minnow *Phoxinus phoxinus* (Currie et al., 2020; Hanache et al., 2020), we expected higher MPEs and therefore a negative indirect effect on *per capita* predation.

2. Materials and Methods

2.1. Animal collection and husbandry

Pseudorasbora parva (7.144 ± 0.4 cm, no distinction of sex) were collected in November 2019 using net fishing from the Grandes Lèches pond at Saint-Nizier-le-Désert ($46^{\circ}03'27.8''N$, $5^{\circ}07'09.0''E$, Auvergne-Rhône-Alpes, France), whose water is drained once a year to harvest the fish for commercial purposes. Fish from this pond are expected to be naïve to motorboat noise as there is no anthropogenic activity. They were transported in aerated water tanks to a breeding room of the ENES laboratory (Saint-Etienne, France) thermoregulated at $18^{\circ}C$ with a 12:12 light: dark regime, and stored in two 110-L aquariums (community aquariums hereafter) at an average density of 0.5 fish.L⁻¹. The community aquariums were filled with dechlorinated tap water and equipped with an underwater speaker (Electro-Voice UW30, 0.1-10 kHz) inserted in the middle of a black foam rubber panel (15-mm thick), a 2-cm layer of Loire sand (Aquasand Nature, Zolux déco), artificial plants, an air pump, and an external filtering system (Tetra EX 600) whose power was calibrated to generate the same level of ambient noise among the two aquariums. Twenty-eight additional fish serving as companion fish in the functional response experiments (see 2.3) were stored in another 110-L aquarium (stock aquarium hereafter), equipped like the community aquariums but without speaker. Fish were fed daily with commercial food pellets (Tetra flakes, approximately 3 items *per* fish), preferred over live food to avoid habituation to a particular prey species and homogenize fish behaviour.

We used the water flea *Daphnia pulex* (Cladocera: Daphniidae) as prey species. They are widespread in freshwaters, represent an important food source for many species (Jurgens, n.d.; Persson et al., 2007), and are commonly used as prey items in laboratory experiments (Laverty et al., 2017; Priyadarshana et al., 2006). To promote vigor and survival, water fleas were purchased regularly from a commercial supplier (AQUARIUS, Andrézieux-Bouthéon, Auvergne-Rhône-Alpes, France) and used in the predation tests within 24 hours.

Once at the laboratory, they were transferred into a 54-L aquarium to acclimate them to the temperature of the experimental room.

2.2. Fish pre-exposure to noise

We used the same procedure as in Rojas et al. (2021). Briefly, we tried to mimic the daily activity of a small leisure lake by broadcasting from 9 am to 6 pm 150 sounds from recreational boats (from six to 25 *per* hour), previously generated from 15 original recordings made by V. Médoc in a surrounding lake (45°45'07.54"N, 4°25'56.47"E, Loire, France) at 1-m depth. We created five copies of each of the 15 original recordings, changing the amplitude between the copies. The resulting 75 (5*15) sounds were then duplicated to get the 150 sounds. Fish experienced the soundscape of their aquarium (ambient noise hereafter) between boat sounds and for the rest of the day. We looped continuously a 1-hr audio track of silence for control fish. On average, ambient noise level was 95 dB re 1 μ Pa RMS sound pressure level and resulted from the residual noise of the building and the electric equipment required for rearing. Rountree et al. (2020) investigated the soundscape composition of many freshwater habitats in North America. Our value of 95 dB belongs their lowest category of ambient noise level and is close to the average value of 98.7 dB obtained from 36 ponds and lakes. Our low level of ambient noise allowed us to make the boat sounds emerge from ambient noise without using high levels, with signal-to-noise ratios (SNR) ranging from 4.81 to 27 dB (SNR quantify the relative importance of boat sounds over ambient noise, see Rojas et al. 2021 for further detail on the playback track). The pre-exposure period lasted from 21 to 36 days depending on when fish experienced the predation test, a prolonged exposure period according to Magnhagen et al. (2017). Fish scheduled for the predation tests were starved for 24 hr to standardize hunger. A plastic canvas was fixed at the opposite side of the speaker to separate them from the other fish in the community aquariums. The audio tracks were played back as WAV files using a ZOOM H4next Handy Recorder, an amplifier (Dynavox CS-PA 1MK) and the UW30 underwater loudspeaker. Re-recordings for sound intensity calibration were made with an Aquarian Audio H2A-HLR hydrophone (frequency response from 10 to 100 kHz) connected to the ZOOM.

2.3. Functional response

Predation tests took place in an experimental room next to the breeding room, thermoregulated at 18°C. We used the same setup as in Rojas et al. (2021). One or two *P. parva* ($P = 1$ or 2) were placed in a 50-L glass aquarium containing a 2-cm layer of Loire sand, a UW30 speaker fixed at the left end, and a translucent plastic tube (11.5 cm diameter) going up to the water surface in the middle (see Figures S1b, c in Rojas et al. 2021). *Pseudorasbora parva* belongs to the minnow family (Cyprinidae) that mostly includes gregarious fishes (Pitcher, 1986, personal observation). We reared the fish in community aquariums during the pre-exposure period and expected that tests under solitary conditions would not reflect natural responses and induce additional stress that could mask the effect of noise. For these reasons, we introduced a companion fish (a *P. parva* of standard body length used only once and only for this purpose) into the plastic tube to promote normal behaviour in the single predator treatment ($P = 1$), the tube remaining empty when $P = 2$. To avoid external sounds, the aquarium was placed inside an acoustic box equipped with two cameras (HD-TVI ABUS TVVR33418, one facing the aquarium and another above) and a source of diffuse light delivering 185 lux at the water surface (Light Meter for Apple devices). We equipped the experimental room with two equivalent setups (aquarium + acoustic box) to run several tests concurrently and reduce the time needed to perform all the tests.

After a 30-min acclimatization period during which we played back the ambient noise recorded in the community aquariums, we introduced water fleas at a single time using a 250-ml glass beaker and with a circular hand movement to homogenize their spatial distribution. We tested seven initial prey densities (for $P = 1$: $N_0 = 4, 8, 16, 32, 64, 128$ and 256 ; for $P = 2$: $N_0 = 15, 25, 50, 100, 200, 300$ and 400) chosen based on previous studies (Laverty et al., 2017) so as to reach predator saturation (high densities) and to promote

model fitting and the type II versus type III discrimination (low densities). During the foraging period, fixed at 45 min to limit predation satiation, fish experienced the same ambient noise than during the acclimatization period supplemented or not (noisy and control conditions, respectively) with motorboat noise. We used the same playback track for all the tests performed under the same noise condition and the track of the noisy condition was made of 24 boat sounds randomly chosen from the 75 used for pre-exposure (see 2.2) and distributed over six consecutive “noise sequences” (two to six boat sound *per* sequence) separated by a few minutes of ambient noise (Figure.1, see Table 1 on Rojas et al 2021). Ambient noise and boat sounds were re-recorded and calibrated to have the same RMS sound pressure levels than is the community aquarium (see Rojas et al. 2021 for further detail on the playback tracks).

At the end of each predation test, the companion fish (for $P = 1$ only) was returned to the stock aquarium, the focal fish measured for fork length to the nearest mm and sacrificed using MS-222, and the remaining water fleas collected using a hand net and counted. Water was bubbled between tests to maintain oxygenation and changed after three consecutive tests to remove potential chemical cues. We ran four replicates *per* prey density, giving a total of 112 predation tests if we consider all the modalities regarding prey and predator densities, and noise conditions. For both noise conditions, we also ran four replicates without fish at the highest prey density ($N_0 = 400$) to control for mortality that would not result from *P. parva* predation. The whole experiment needed six consecutive days during which the predation tests were distributed in a quasi-systematic way to balance the effect of time among replicates, prey and predator densities, and noise conditions.

2.4. Behaviour

Fish behaviour was recorded over three minutes during the six successive noise sequences, where exposed fish experienced boat sounds and control fish ambient noise. We used the above camera, a video player (VLC media player 1.1.8) and visual tracking with Mousotron 12.1 (Blacksun Software) to measure swimming distance. As a proxy of the strength of non-trophic (i.e., social) interactions, we measured inter-individual distances (head-to-head): between focal fish and companion fish for $P = 1$ and between the two focal fish for $P = 2$. We measured the distance between focal fish (head) and the center of the speaker to assess noise avoidance. Both distances (between fish and to the speaker) were estimated every 15 sec during each 3-min period using the front camera and the PixelStick application (for Apple devices).

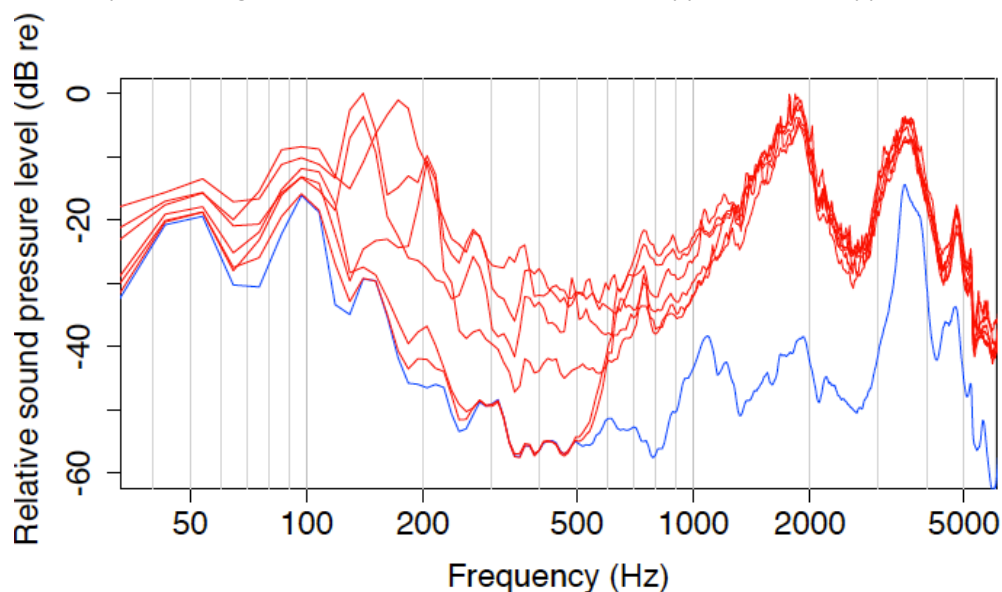


Figure 1: Spectral density of the motorboat noise (red lines, one *per* noise sequence, see text for further detail) and ambient noise (blue line) playback tracks used to assess the relationship between *per capita* predation rate and prey density (the functional response) in the invasive topmouth gudgeon *Pseudorasbora parva* feeding on the water flea *Daphnia pulex*.

We studied 108 water fleas to assess their mobility under both ambient (n=56) and boat noise (n=52 instead of 56 due to a technical issue) playlist used during functional response test (45-min). We used two 50-L glass aquaria with an underwater loudspeaker inserted in the middle of a black foam rubber panel (15-mm thick) fixed on the left end, and a lightning above for better visibility (185 lux light intensity at the water surface, Light Meter for Apple devices). Four individuals were assessed simultaneously in a 4-well dish (diameter 6 cm, depth 1.5 cm) placed above a brick in the middle of the aquarium. The water fleas were filmed using a GoPro Hera 4 Session camera and videos were analyzed using Kinovea software (0.9.1 beta).

2.5. Statistics

We used the R software (version 3.5.1, R Core Team, 2018) with a significance level of 0.05 for all the statistical analyses. We first controlled for the absence of difference in fish size (average value when $P = 2$) between the four experimental groups (two noise conditions for two fish densities) using a Wilcoxon test with single fish and an ANOVA for the tests with two fish as the data did not meet the assumptions of parametric statistics. FR analysis was done with the *frair* R package (Pritchard et al., 2017). Modelling the three categorical forms of FR (linear type I, Rogers' type II and Hassel's type III) by maximum likelihood estimation (Bolker, 2008) allowed us to exclude the linear type I whose Akaike Information Criterion (AIC) was significantly higher compared to that of types II and III ($\Delta AIC > 2$). To better discriminate between types II (decelerating) and III (sigmoidal) we fitted a polynomial logistic function to the proportion of prey eaten, with type II indicated by a significantly negative first order term and type III by a significantly positive first order term and negative second order term (Juliano, 2001). To account for the fact that we did not replace consumed water fleas and because the best model was always of type II (first order term \pm SE for one fish in ambient noise: -0.0072 ± 0.0005 , one fish in boat noise: -0.0039 ± 0.0005 , two fish in ambient noise: -0.0081 ± 0.0003 , two fish in boat noise: -0.0052 ± 0.0007 , all $p < 0.001$), we used a modified version of the Holling's original type II model through the Rogers' (1972) Random Predator Equation where the number of prey eaten (N_e) follows the relationship:

$$N_e = N_0(1 - e^{a(N_e h - T)})$$

with N_0 the initial prey density, a the attack rate, h the handling time and T the total experimental time.

Equation solving was achieved using the Lambert's transcendental equation (Bolker, 2008) and we used non-parametric bootstrapping ($n = 999$) to get multiple estimates of the FR curves and parameters, and generate bias corrected and accelerated (BCa) 95% confidence intervals (95% CIs hereafter), which account for the bias and skew as well as the bounded nature of a and h . All FRs being of the same categorical form (type II), pairwise FR comparison was possible with the delta method from the *frair* package. It tests the null hypothesis that differences in a (Da) and h (Dh) do not differ from zero making assumptions about their error structure. We also compared FRs visually, inspecting how the BCa intervals of a and h overlapped as recommended by (Pritchard et al., 2017).

To detect non-trophic interactions (i.e., MPEs), we compared for each noise condition the observed group-level FR obtained with two fish to a predicted group-level FR inferred from the FR of single fish and assuming the absence of MPEs. Following Sentis and Boukal (2018) and McCoy et al. (2012), we parameterized a population-dynamic model with the attack rate and handling time estimates obtained with one fish to predict how prey density would change with time as a function of initial prey density and predator density:

$$\frac{dN}{dt} = - \sum_{i=1}^n f_i(N) P_i$$

where N is the prey density, P_i the predator density ($i = 1, 2$) and $f_i(N)$ its FR. Compared to alternative approaches like the multiplicative risk model, the population-dynamic model has been shown to be more robust to infer MPEs and account for prey depletion (Sentis & Boukal, 2018). We generated four random FR parameter sets (to match with the number of replicates of our predation tests) considering the 95% CIs of

observed a and h via a Latin hypercube sampling algorithm (Soetaert et al., 2010) to account for uncertainty in the FR parameter estimates. Initial values of N were set at the experimental initial prey densities (i.e., 15, 25, 50, 100, 200, 300 and 400) to calculate predicted prey survival (and thus consumption) for the four parameter sets. As for observed FRs, we fitted a type-II FR that fitted best the 999 predicted values and compared their parameter estimates (a and h) to those of the corresponding observed FR using the delta method (*frair_compare* function). We repeated this procedure 999 times.

Variations in the three distances used to characterize fish behaviour (for each 3-min recording period: swimming distance, average inter-individual distance calculated from the 12 measures, average distance to the speaker calculated from the 12 measures when $P=1$ and 24 measures when $P=2$) were explained with linear mixed-effects models via the *lme4R* package (Bates et al., 2015), applying a square-root transformation to improve normality of the residuals when needed. Each response variable was modelled as a function of one qualitative predictor: *FR Noise* (i.e., the noise condition during FR derivation with ambient noise as control), three quantitative predictors: *Time* (implemented as the start position of the first boat sound for each noise sequence), *Prey density* and *Fish size*, and taking individual fish as random factor. We added one interaction terms: between *FR Noise* and *Time* as temporal variation in behaviour can change with noise. For $P=2$, we used the same global model. We performed AIC model selection using the *MuMIn* package (Barton, 2009) and ranked the models based on small sampled-corrected AIC values (AIC_c), choosing a ΔAIC_c cut-off of 3, a conservative threshold suggested by Bolker (2008).

A linear mixed-effects model was also used to explain the cumulative swimming distance of water fleas as a function of noise condition (ambient noise or boat noise) interacting with test duration and taking position in the 4-well box as a random factor.

2.6. Ethical notes

The capture and transport of *P. parva* have been approved by the Direction Départementale des Territoires de la Loire (DDT 42). We followed the European (Directive 2010/63/EU) and French national guidelines and got the permits (Approval no C42-218-0901, Direction Départementale de la Protection des Populations de la Loire, Préfecture du Rhône) to conduct experiments on animals.

3. Results

For both noise conditions, *Daphnia* survival was 100% in absence of fish demonstrating that mortality during FR tests was due to the predation by *P. parva*. Fish body length did not differ between the experimental groups (Wilcox test, for one fish: $W = 351.5$, $p = 0.51$; ANOVA for two fish, Sum-square =

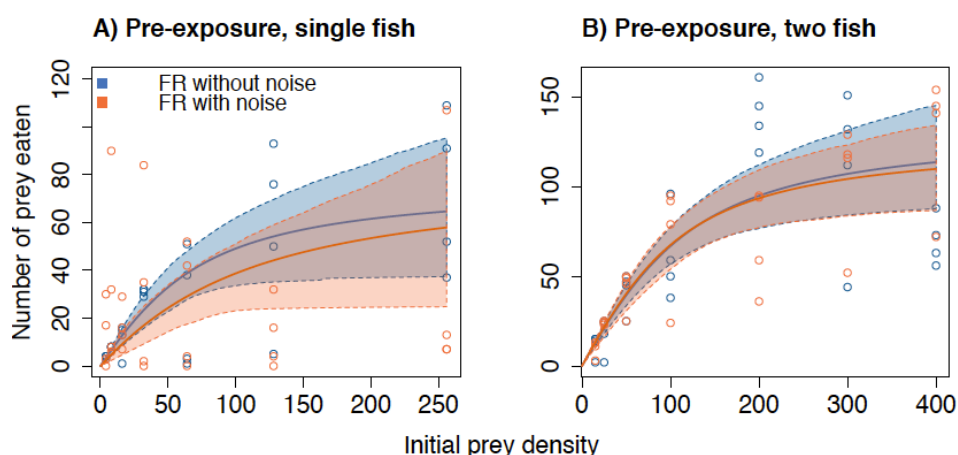


Figure 2: Type-II functional responses of (A) single and (B) two topmouth gudgeon (*Pseudorasbora parva*) feeding on *Daphnia pulex* under control ambient noise (blue solid line) and motorboat noise (orange solid line). Dots are raw data ($n = 4$ replicates *per* prey density) and shaded areas represent bootstrapped 95% confidence intervals.

Table 1: Results (*p* values) of the delta method used to compare both functional response (FR) parameters (attack rate and handling time) between the observed and predicted group-level FRs obtained for two noise condition (ambient noise and boat noise) in the topmouth gudgeon *Pseudorasbora parva* feeding on *Daphnia pulex*. *P* values are distributed according to the significance level of 5%. Positive values of *Da* indicate when the observed FR is above the predicted FR and positive values of *Dh* indicate when the observed FR are below the predicted FR.

	No boat Noise		With boat Noise	
	<i>p</i> value < 0.05	<i>p</i> value > 0.05	<i>p</i> value < 0.05	<i>p</i> value > 0.05
<i>Da</i> > 0	4	126	392	508
<i>Da</i> < 0	870		100	
<i>Dh</i> > 0	358	511	566	300
<i>Dh</i> < 0	131		134	

0.0112, *df* = 1, *F* = 0.699, *p* = 0.407). Whatever noise condition and predator density, the type-II FR was always the best model (Figure 2). When alone, fish exposed to chronic noise showed a significantly decreased attack rate compared to control (*Da*: estimate = -1.24, Standard Error = 0.31, *p* < 0.001) but no difference in handling time (*Dh*: estimate = -0.0003, SE = 0.001 *p* = 0.80), resulting in a less steep FR curve with a similar asymptote (Figure 2a). When they were two, both FRs matched perfectly and there was no difference in attack rate neither handling time between the two noise conditions (*Da*: estimate = 0.26, SE = 0.29, *p* = 0.38; *Dh*: estimate = 0.0003, SE = 0.0003, *p* = 0.28, Figure 2b).

Observed group-level FRs were in the low range of predicted group-level FRs for both noise conditions (Figure 3). Under ambient noise, *Da* was significantly negative 870 times over the 1000 iterations indicating that observed FR was less steep than predicted FR while *Dh* was not different from zero more than half the times suggesting relatively similar asymptotes (Table 1, Figure 3a). Under boat noise, *Da* did not differ from zero 508 times over the 1000 iterations, indicating similar slopes. *Dh* was significantly positive more than half the times suggesting higher asymptote in the predicted FR compared to the observed FR (Table 1, Figure 3b).

The swimming distance of solitary fish was significantly lower with noise than without noise (estimate = -3.58, SE = 1.62, *p* = 0.028; Figure 4), and the distance to the companion fish significantly decreased over time (estimate = -0.23, SE = 0.06, *p* < 0.001). No difference was observed in the distance to the loudspeaker between the two noise conditions (*p* = 0.610). In the presence of a conspecific, none of the predictors had

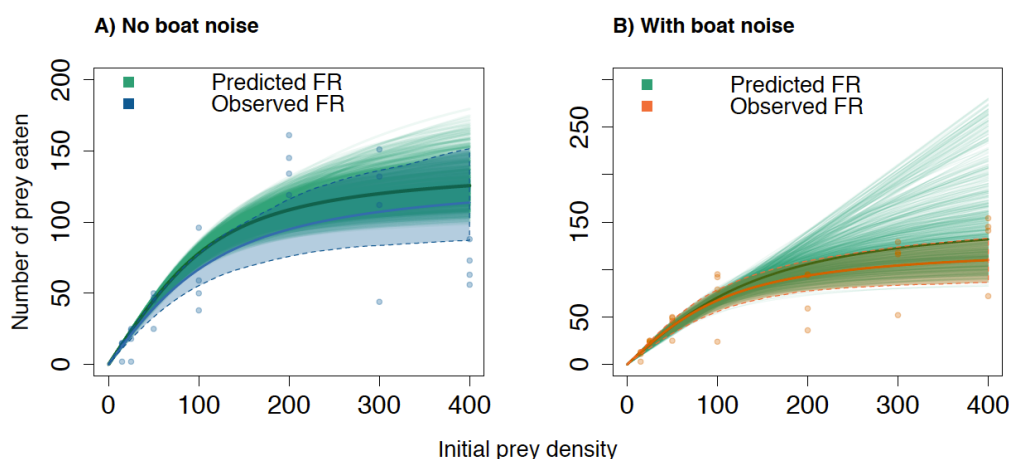


Figure 3: Predicted type-II functional responses (FRs, green solid lines, *n* = 1000) for two invasive topmouth gudgeon (*Pseudorasbora parva*) feeding on *Daphnia pulex* and inferred from the FRs obtained with single individuals under (A) control ambient noise and (B) motorboat noise. Predicted FRs are compared to those obtained with two fish feeding simultaneously under ambient (solid blue line) or boat (solid orange line) noise. Dots are raw data (*n* = 4 replicates *per* prey density) and shaded areas represent bootstrapped 95% confidence intervals.

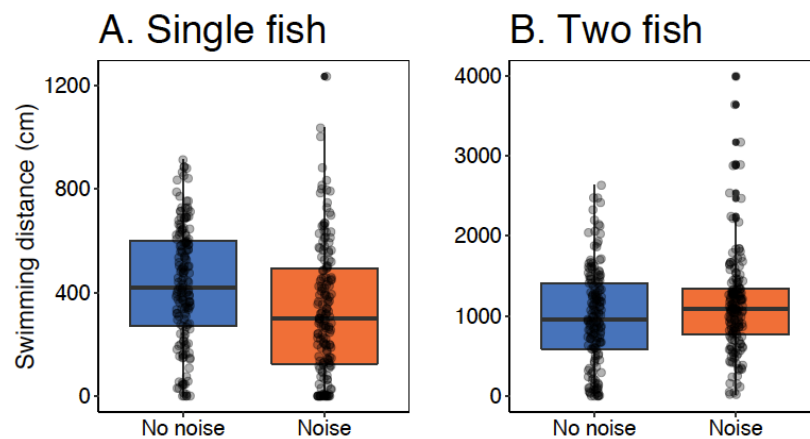


Figure 4: Boxplot of the total swimming distance (m) covered by (A) single and (B) pairs of the invasive topmouth gudgeon *Pseudorasbora parva* during the predation tests performed to derive their functional response towards water fleas (*Daphnia pulex*) under control ambient noise (blue) and motorboat noise (orange).

any significant effect on the distance to the speaker, the distance between fish and on swimming distance (all $p > 0.10$).

The cumulative swimming distance of water fleas increased over time ($\chi^2_1 = 8.69$ and $p = 0.003$) but did not differ between ambient and boat noise conditions ($\chi^2_1 = 0.74$ and $p = 0.39$).

4. Discussion

Anthropogenic noise is known to alter both trophic and non-trophic interactions (Braga Goncalves et al., 2021; Herbert-Read et al., 2017; Mickle & Higgs, 2018) but how these effects interact to influence the social dimension of foraging through the modulation of multiple-predator effects (MPEs) remains undetermined. To address this question, we derived the functional response (FR) of solitary and pairs of the invasive topmouth gudgeon (*Pseudorasbora parva*) feeding on the water flea *Daphnia pulex* in the absence or presence of motorboat sounds. Noise significantly reduced solitary fish's FR at low prey densities while the pairs of fish displayed similar FR between the two noise conditions, highlighting the importance of social context in the response to noise. The FR obtained with two fish tended to be in the low range of those predicted from individual-level FR and based on additive effects only, suggesting a slight negative MPE (i.e., conspecific presence tends to decrease *per capita* predation rate). Interestingly, noise did not strengthen the MPE as the difference between observed and predicted group-level FR was not greater with noise.

We did not find any effect of motorboat noise on water flea mobility. This is consistent with previous findings (Sabet et al., 2019) and suggests that the alterations in FR we found were related to fish behaviour only. However, because water fleas were purchased regularly and used 24 hours after arrival, they did not experience a 21-36 days pre-exposure period to noise as the fish did. Additional investigation is needed to exclude a potential effect of chronic motorboat noise on the behaviour of water fleas, which could influence FR parameter estimates but should not change our conclusions about the role of conspecific presence on *P. parva*'s individual response to noise (see below). FR shape and magnitude can be influenced by many environmental factors including temperature, habitat complexity or light regimes (Alexander et al., 2012; South et al., 2017). As commonly found in previous experiments made with shelter-free experimental arenas (Cuthbert et al., 2019; Dick et al., 2013; Hanache et al., 2020), the best FR model in our study was always the decelerating type II whose shape is captured by attack rate that determines the initial slope and handling time that fixes the asymptote.

When conspecific interactions were not permitted (i.e., with a companion fish), handling time did not significantly differ between the two noise conditions, leading to similar FR asymptotes, whereas attack rate

was significantly reduced by boat noise making the FR less steep compared to that obtained under ambient noise. This decrease in attack rate could have resulted from the shorter swimming distance also observed with noise during the FR trials. *Pseudorasbora parva* is indeed considered as a cruise searcher (Priyadarshana et al., 2006) so higher mobility provides more opportunities to encounter and catch mobile prey, and *vice versa*. When approaching saturation at high prey densities, prey items are so numerous and reachable (because present everywhere) that predator mobility has little influence on prey capture. This could explain why the negative effect of noise on predation rate through reduced mobility is less perceptible at high prey densities (i.e., right of the FR curve). We also found increased attack rate associated with increased mobility in another invasive fish, the round goby *Neogobius melanostomus* (unpublished data). In the European minnow *Phoxinus phoxinus*, a native counterpart of *P. parva*, the noise-induced decrease in attack rate was associated with reduced searching area (fish swam more but closer to the companion fish, Hanache et al., 2020). This illustrates how linking FR parameter estimates with behavioural metrics, which is not a common approach, can help better explain alterations in feeding rates.

Prior to the FR experiments, *P. parva* experienced a playback track of boating activity for more than 20 days to account for a potential habituation effect, namely when the response to noise weakens with repeated exposure. This is quite common (Bejder et al., 2009; Nedelec et al., 2016; Neo et al., 2018; Rojas et al., 2021) and can happen when the organisms learn that a stimulus is not associated with any threat (i.e., associative learning). In previous FR investigations made on solitary fish, we found that individuals can resume normal values of attack rate (Hanache et al., 2020) or handling time (Rojas et al., 2021) when pre-exposed to noise. Here, we cannot rule out a weakening of the response to noise that could be stronger after first exposure, what we did not assess. It might be that our pre-exposure period was not long enough for associative learning to occur in *P. parva*.

We did not formally test for the presence of auditory damage and hearing loss after the pre-exposure period. Although the relationship between hearing loss and specific behavioural deficits remains to be elucidated (Smith and Monroe, 2016), we carefully checked the community aquariums daily and did not observe mortality or any behaviour that might be expected in case of discomfort, pain or physical damage like abnormal swimming, reduced foraging or aversion for the sound source. If the response to noise of solitary fish resulted from physical damages, then there would be no reason for it to be weakened by conspecific presence. The fact that pre-exposed solitary fish behaved differently both in terms of mobility and feeding under noise suggests that they were still able to perceive the acoustic signals.

When the two *P. parva* were free to interact and foraged concurrently, we found no difference neither in FR nor in swimming distance between the two noise conditions. It was as if in the presence of a conspecific, individual fish did not pay attention - or at least did not respond - to noise. Further experiments are needed to test whether conspecific presence also weakens individual response to stimuli associated with real threats, like predation risk, which could be disadvantageous. From a more methodological perspective, our results tell us about the usefulness of providing a companion fish to the focal fish to promote normal behaviour in fish used to live in groups. Although pilot experiments on another fish indicated that it increased predation rate compared to the focal fish alone (unpublished results), the present study reveals that it does not fully reproduce conspecific presence, probably because direct interactions are not possible.

In the absence of boat noise, the observed group-level FR was in the low range of the predicted group-level FRs inferred from individual predation rates, suggesting antagonism and a negative effect of mutual interference on individual foraging performance. This effect (i.e., the difference between predicted and observed FRs) was stronger when comparing the attack rates, so at low densities. Conspecific presence did not change individual swimming distance and we did not compare the area covered between one and two fish, but the most likely explanation is that the time and attention devoted to the conspecific were not allocated to foraging. Many studies on MPEs have indeed found risk-reducing effects on predation rates

(Cuthbert et al., 2020; Sih et al., 1998), which could be the “null hypothesis”, simply because predators spend time in interactions instead of foraging.

Contrary to our expectation, noise did not promote MPEs as the difference between predicted and observed FRs was not greater than with ambient noise, and even smaller when considering low densities (i.e., the difference between attack rates). This is consistent with the observation that conspecific presence weakened the negative effect of noise on attack rate found with single individuals. Additional investigations are needed to rule out negative effects of noise on other biological traits, but our study suggests that foraging is not compromised.

There have been increasing calls to get away from laboratory experiments because of potential deviations in natural behaviours (Popper and Hawkins, 2019, but see Pieniasek et al., 2020). We acknowledge that extrapolation of lab results to natural populations requires extreme caution and to this respect our study demonstrates how a slight increase in ecological complexity through the presence of a conspecific can influence the results. Hypothesis testing under the FR framework requires highly controlled experimental conditions that are difficult to meet in the field. But in return, this allows to detect fine-tuned relationships, for instance between mobility and functional response parameters, which raise new predictions for further *in situ* validation. Another limitation of tank-based experiments lies in the three acoustic biases that contribute to signal distortion: low frequency attenuation, resonant frequencies and sound reverberation (Akamatsu et al., 2002). We therefore acknowledge that our playbacks did not fully reproduce the original recordings. However, because boat sounds are long and broadband signals compared to complex biological sounds, we assume that even distorted, our playbacks have somewhere mimicked what fish could experience in their natural environment.

We reported sound levels in units of sound pressure while *P. parva* also detects the particle motion component of a sound, which is expected to predominate in lab tanks. We don't have the dedicated sensor needed to measure the kinetic energy (KE) of particle motion that cannot be calculated from the potential energy (PE) of sound pressure in our conditions (Nedelec et al., 2016). However, the lab investigation by Olivier et al. (2023) demonstrated that when source level increases or decreases by N dB, both PE and KE will increase or decrease by N dB. Relying solely on pressure should therefore not qualitatively change our conclusions.

Pseudorasbora parva is known to produce involuntary short broadband pulses while sucking in food items (“suction” feeding) that could serve as auditory cues for the presence of food (Scholz & Ladich, 2006). We don't know if such sounds were emitted during our experiments but even if it was the case, they were unlikely to play a role relative to visual or olfactory cues given the size of our aquariums. If the function of these sounds in food intake is proven, then an interesting perspective would be to test whether they can be masked by elevated noise level thereby disrupting foraging when fish are more distant.

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Conflict of Interest

The authors declare that they have no conflicts of interest.

Data availability

The data that support the findings of this study are open available in Zenodo (<https://doi.org/10.5281/zenodo.7234923>)

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Two individuals of the invasive topmouth gudgeon *Pseudorasbora parva* feeding on water fleas under motorboat noise
Vincent Médoc