



Adding insult to injury: anthropogenic noise intensifies predation risk by an invasive freshwater fish species

Marina Fernandez-Declerck · Emilie Rojas · Prosnier Loïc ·
Teulier Loïc · Dechaume-Moncharmont François-Xavier ·
Médoc Vincent

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Abstract The ecological impact of invasive species is likely to be modulated by human-induced alterations in habitats, which represents another driver of biodiversity loss. We tested the effect of soundscape degradation on predation by the round goby *Neogobius melanostomus*, one of Europe’s “worst invasive species”. For this, we compared the relationship between *per capita* predation rate and prey density (*i.e.*, the functional response) in the presence or absence of motorboat sounds. Unexpectedly, fish displayed a stronger functional response with additional noise, which could be explained by a higher mobility promoting encounters with prey. Our results suggest that anthropogenic noise is likely to exacerbate the impact of invasive species.

Keywords Functional response · Trophic impact · Biological invasion · Noise pollution · Round goby

Introduction

Predation by invasive species is an important threat to biodiversity, estimated as causing a 21% decline in species richness in aquatic habitats (Mollot et al. 2017; Reid et al. 2019). For certain invasive species, higher tolerance to environmental stressors such as hypoxia (Lagos et al. 2017; Dickey et al. 2021), increased temperature (Christensen et al. 2021) and salinity (Karsiotis et al. 2012; Behrens et al. 2017), might promote their ecological impact, allowing them to settle easily in new environments and to maintain strong top-down control on lower trophic levels.

The worldwide increase in boat traffic is a major driver of the spread of invasive species (Hulme 2021), but it also contributes to the degradation of natural habitats on many levels. In particular, motorised boats significantly alter underwater soundscapes (Reid et al. 2019). Anthropogenic (*i.e.*, man-made) noise is indeed one of the most pervasive symptoms of human activities (Buxton et al. 2017). It can induce changes in animal behaviour, physiology and sometimes anatomy, and mask important acoustic cues involved in reproduction, social interactions, foraging or predator avoidance (Kunc and Schmidt 2019). Reduced foraging performance is a common response to anthropogenic noise (Cox et al. 2018), with many

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M. Fernandez-Declerck · E. Rojas · P. Loïc ·
M. Vincent (✉)
Equipe Neuro-Ethologie Sensorielle, Centre de Recherche
en Neurosciences de Lyon, INSERM UMRS 1028, CNRS
UMR 5292, Université Claude Bernard Lyon 1, Université
Jean Monnet - St Etienne, 42023 Saint-Étienne, France
e-mail: vincent.medoc@univ-st-etienne.fr

M. Fernandez-Declerck · T. Loïc · D.-M. François-Xavier
Univ Lyon, Université Claude Bernard Lyon 1, CNRS,
ENTPE, UMR 5023 LEHNA, 69622 Villeurbanne, France

examples both from the lab and field (Sabet et al. 2015; Magnhagen et al. 2017). The consequences of reduced foraging can propagate through nested ecological interactions to ultimately alter community composition and dynamics (Francis et al. 2009).

While the number of invasive species is predicted to increase (Anton 2021) in an underwater world that becomes more and more noisy (Duarte et al. 2021), surprisingly, their tolerance to anthropogenic noise has received scant attention. This is symptomatic of the general picture that there are fewer studies examining the effects of noise pollution on freshwater fishes and invertebrates than on marine organisms (Mickle and Higgs 2018). Tolerance to noise might help invasive species to spread in anthropized environments while maintaining strong trophic and competitive pressures on native species, especially if the performance of the latter are reduced by noise.

In the present study, we investigated whether predation rate by the round goby (*Neogobius melanostomus*) was influenced by anthropogenic noise and particularly motorboat sounds. Although this species uses acoustic cues as part of its reproductive repertoire (males defend a nest and emit calls to attract females, Rollo et al. 2007) it does not possess a swim bladder or obvious hearing specializations and therefore relies on particle motion and not pressure to detect sounds (Belanger and Higgs 2005; Belanger et al. 2010). It hears mainly below 800 Hz, a frequency range where motorboat noise typically has high energy. Regarded as one of the most impactful invasive species, the round goby has spread from the Ponto-caspian region to the North American Great Lakes and throughout Western Europe where it outcompetes native fishes and impoverishes invertebrate communities (Kornis et al. 2012; Henseler et al. 2021; van Deurs et al. 2021). As opportunistic predators, round gobies prey on large epifaunal invertebrates that are available at high abundances, which causes a decrease in taxonomic diversity, trait-based diversity and average body size (Henseler et al. 2021), with potential consequences on ecosystem processes. Native fishes experience competition for food, spawning sites and are pushed to sub-optimal habitats. They can also experience increased apparent competition when fish-eating predators benefit from a dietary shift toward round gobies (Reyjol et al. 2010).

We derived the functional response of the round goby feeding on live dipteran prey with or without

motorboat sounds. The functional response (FR) defines the relationship between resource availability (i.e. prey density) and *per-capita* predation rate (Holling 1959; DeLong 2021). Because FR shape and magnitude are indicative of how the predator can control or destabilize its prey population (Murdoch and Oaten 1975; Kalinkat et al. 2013), it became a pivotal tool in ecology to quantify predation strength and parametrize dynamic models, and more recently in invasion biology to predict the trophic impact of invasive species (Dick et al. 2014). Predation tests were filmed to measure fish swimming distance and link alteration in FR with alteration in mobility. In separate tests, we measured the mobility of the dipteran larvae under the same acoustic regimes to be sure that alterations in FR were due to fish response to noise and not to prey behaviour. For instance, more active prey with noise could elicit higher predation by the fish. No change in functional response nor mobility between the two noise conditions would suggest tolerance to noise.

Materials and methods

Fish collection

In April 2021, 60 round gobies (mean body mass \pm sd = 1.7 ± 0.6 g) were captured by electrofishing in the Saône river at Cendrecourt (47°50'38"N, 05°55'34"E, Haute-Saône, France), an area of active range expansion in France. There is no motorboat activity on this upstream part of the river. This invasive goby population can thus be considered naive regarding motorboat noise. The fish were housed in the rearing facilities of the ENES lab (Equipe de Neuro-Ethologie Sensorielle) in a room thermoregulated at $18 \text{ }^\circ\text{C} \pm 1 \text{ }^\circ\text{C}$ with 12:12 light:dark cycles. They were randomly allocated to two 110-L stock aquariums (30 fish *per* tank) filled with dechlorinated and salted (1.5 g L^{-1}) water and equipped with a 2-cm layer of natural sand (Aquasand Nature, Zolux), PVC tubes to provide shelters, air stones, and an external filter (Tetra EX 600). During a 3-week acclimatization period, they were fed three times a week with 0.11 g of frozen chironomid larvae (Petra-Aqua, Prague-West, Czech Republic) *per* fish and starved

for 24 h prior to experimentation to standardize motivation. Water quality and oxygen content were checked daily.

Fish functional response and behaviour

Measures of functional response (FR) followed the procedure described by Rojas et al. (2021). Briefly, one single fish was introduced in a 50-L aquarium (length \times width \times height: 60 \times 25 \times 35 cm) containing a 2-cm layer of natural sand (Aquasand Nature, Zolux), 15-mm rubber panels covering both ends to control for acoustic reverberation, and a waterproof speaker (Electro-Voice UW30, 0.1–10 kHz) inserted in the middle of one of the two panels (side changed between tests). After a 30-min acclimatization period where the fish experienced the soundscape of their rearing aquarium (ambient noise condition, see 2.3), live chironomid larvae were introduced using a 250-ml glass beaker, and the fish was allowed to feed for 15 min under either ambient noise only (ambient noise condition hereafter) or ambient noise supplemented with motorboat sounds (boat noise condition hereafter). The fish was then removed with a hand net, weighted and the live prey remaining were counted. Each fish was only tested once and was randomly assigned to one trial defined by a noise condition (ambient noise or boat noise) and an initial prey density. The experimental plan was based on seven initial prey densities ($N_0=4, 8, 16, 32, 64, 128, 256$) with four replicates each, corresponding to a total of 56 trials with 56 different fish. We finally did 54 predation trials instead of 56 (missing trials: $N_0=256$ with ambient noise and $N_0=128$ with boat noise) as six of the 60 sampled fish died during transport from the field or acclimatization period in the laboratory prior to tests. For each noise condition, we added four replicates of the highest density without fish to confirm that prey removal was only due to fish predation and that no prey died in the experimental aquarium due to the noise conditions. To reduce the duration of the whole experiment (4 days with the 54 trials distributed in a quasi-systematic way to balance the effect of time), we used four identical 50-L aquariums concurrently, each equipped as explained earlier and placed inside acoustic insulation boxes (81 \times 67,5 \times 73 cm). Fish behaviour was recorded using two cameras (HD-TVI ABUS TVVR33418),

one facing the aquarium and one above. Fish mobility was estimated as the total swimming distance (*i.e.*, cumulative distance covered over the tested period) using the Mousotron software (12.1 version, Blacksun software).

Playback tracks

Using the Audacity software (Audacity Team 2021), we created two 45-min audio tracks starting with a 30-min acclimatization period of ambient noise and continuing with a 15-min feeding period of either ambient noise alone for the control condition or ambient noise supplemented with eleven motorboat sounds distributed over three successive 3-min noise sequences (Table 1) for the boat noise condition.

Ambient noise corresponded to the soundscape of the 110-L rearing aquariums in which the fish spent three weeks before the FR experiments. Root-mean-square sound pressure level (RMS SPL) was approximately 110 dB re 1 μ Pa and included noise from the filtering system and general background noise of the breeding room. Such value is representative of the level of fast-flowing waters (Wysocki et al. 2007). We chose as control noise condition the soundscape that the fish experienced during the 3-week acclimatization period at the lab, and that we considered as the baseline level. An alternative

Table 1 Composition of the 15-min playback track broadcasting ambient noise supplemented with motorboat sounds during the functional response tests. SNR values correspond the signal-to-noise ratios that quantify how boat sounds emerge from ambient noise (in dB)

| Noise sequence | Boat ID | Sound duration (s) | Start position | SNR (dB) |
|----------------|---------|--------------------|----------------|----------|
| 1 | 1 | 70 | 00'00 | 14 |
| 1 | 2 | 36 | 01'10 | 23 |
| 1 | 3 | 47 | 01'46 | 20 |
| 1 | 4 | 28 | 02'33 | 19 |
| 2 | 5 | 38 | 06'00 | 22 |
| 2 | 6 | 110 | 06'38 | 20 |
| 2 | 7 | 33 | 08'28 | 12 |
| 3 | 8 | 67 | 12'00 | 16 |
| 3 | 9 | 20 | 12'20 | 21 |
| 3 | 10 | 60 | 13'27 | 21 |
| 3 | 11 | 34 | 14'01 | 22 |

control could be their natural soundscape. However, a playback of natural soundscape in the rearing aquariums would be superimposed to the noise emissions from the electric devices and the breeding room, resulting in higher levels and something that would not represent what the fish experience in the river. Motorboat sounds have been recorded in September 2018 by V. Médoc in the Grangent lake (45°45'07.54"N, 4°25'56.47"E, Loire, France) at one meter depth and corresponded to small recreational boats with outboard engines passing at various distances. Small tanks present three main acoustic biases that distort sound signals: low frequency attenuation, resonant frequencies and sound reverberation (Akamatsu et al. 2002; Novak et al. 2018). To make the playback as close as possible to the original signal, we used rubber panels as mentioned earlier and modulated some frequency contents of the input signal using the Audacity equalizer. We applied linear fading at both ends to make boat sounds emerge from ambient noise. We adjusted their intensity so as to obtain naturally-occurring signal-to-noise-ratio (SNR) values ranging from 12 to 22 dB (Fig. 1) with:

$$SNR = 20 \log_{10} \left(\frac{RMS_{Boatsound}}{RMS_{Ambientnoise}} \right)$$

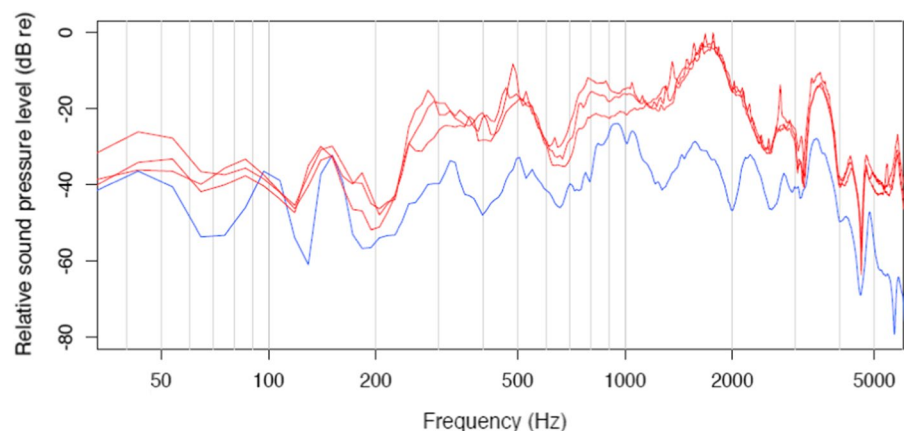
The audio tracks were played back as WAV files using an audio player (VLC media player 1.1.8), an amplifier (Dynavox CS-PA 1MK) and the UW30 speaker. All recordings were made with an Aquarian Audio H2A-HLR hydrophone (frequency

response from 10 Hz to 100 kHz) connected to a Zoom H4next (Mogar Music, France) handy recorder. The spectral density was created with the R software using the *seewave* (Sueur et al. 2008) and *tuneR* (Ligges et al. 2018) packages.

Prey behaviour

We used the same experimental aquarium and procedure as for the FR trials, except the cameras that have been replaced by an underwater GoPro (San Mateo, USA) Hero4 located 5 cm below the surface in the middle of the aquarium to increase resolution for the video analysis. A group of 16 live chironomid larvae was introduced into the aquarium and exposed to the 15-min playback tracks of either ambient noise or boat noise. We selected one of the seven densities used during the FR experiment and decided that 16 was a good trade-off, assuming that larval behaviour does not change with group size. For both noise conditions, we performed ten replicates and analysed the behaviour of two randomly chosen larvae among the group of 16, representing 40 individuals in total. Using the BORIS software (Friard and Gamba 2016), we recorded the time spent moving during two periods: from 6'00 to 9'01 and from 12'00 to 15'04 (repeated measures), corresponding to the second and third sequences of motorboat sounds for the boat noise condition (see 2.3) and to ambient noise for the control. It was not possible to accurately monitor behaviour during the first noise sequence because some larvae were still sinking slowly after their release at the water surface.

Fig. 1 Spectral density of the playback tracks measured in the experimental tank used for the functional response trials. The three red lines correspond to the three sequences of boat sounds from the boat noise condition and the blue line to the ambient noise condition



Statistics

We used the R software (4.1.3 version, R Core Team 2022) with a significance level of 0.05 for all the statistics. FR analysis was done using the *Frair* package (Pritchard et al. 2017). We used the *frair_fit* function to model by maximum likelihood estimation the three main prey-dependant FR models describing a linear (type I), saturating (Rogers's type II) or sigmoidal (Hassel's type III) relationship between prey density and predation rate. The best model was identified based on the second-order Akaike information criterion (AIC) and was always of type II where the *per-capita* predation rate (F) follows the equation:

$$F = \frac{aR}{1 + aRh} \quad (1)$$

where a is the attack rate, R the prey density and h the handling time. This equation describes a diminishing return curve: predation rate increases monotonously with prey density and tapers off to an asymptote at high prey density. To account for the decline in prey density (consumed prey were not replaced to not disturb the fish), we used a modified version of Eq. 1 through the Random Predator Equation (Bolker 2008; DeLong 2021) where the number of prey eaten (N_e) follows:

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

where N_0 is the initial prey density and T the total experimental time. As chironomid larvae are benthic, we standardized prey density to the number of prey *per* square metre as recommended by Uiterwaal et al. (2018). Attack rate, which corresponds to the initial slope of the FR curve, was thus reported as m^2 *per* hour *per* predator. Handling time can be read as the inverse of the asymptotic predation rate (Uiterwaal et al. 2018) and was reported as hour *per* prey. Bias corrected and accelerated 95% intervals (BCa) were generated and plotted on the FR curve using the *frairboot* and *drawpoly* functions respectively. We used the delta method implemented by the *frair-compare* function to compare the estimates of a and h between the two noise conditions, with the null hypothesis that differences in attack rate (Da) and handling time (Dh) do not differ from zero (Pritchard et al. 2017). A complementary approach based on non-parametric bootstraps gave us the same results (see supp. mat.).

Fish swimming distance was log-transformed [$\log(\text{distance} + 0.5)$] to normalize data for the analysis. Non-transformed data were used in the plot for readability. We used a generalized linear model with the *glm()* R function. The effects of noise condition, prey density, fish body mass and their interactions were assessed using AIC model selection (Galipaud et al. 2014) with the *MuMIn* package (Bartoń 2022).

Concerning larvae behaviour, we used generalized linear mixed-effect (GLME) models to take into account the repeated measures on the same individuals and the nested design in which two individuals were observed *per* trial. Individual identity nested in replicate number was used as a random variable. Noise condition, sequence number (second or third noise sequence), and their interaction were used as fixed variables. The proportion of time moving P was modelled using beta regression (Smithson and Verkuilen 2006) with the transformation $P' = ((n - 1)P + 0.5)/n$ in order to comply with the beta regression assumption stating that the data are within the interval [0;1] (Laubu et al. 2017). The analysis was done using the *glmmTMB* package (Brooks et al. 2017). Model selection was based on a backward procedure using likelihood-ratio tests.

Results

For both noise conditions, we did not observe chironomid mortality in the fishless replicates suggesting that chironomid removal was due to fish predation during the FR tests. There was no difference in fish body mass between noise conditions ($F_{1,52} = 0.78, p = 0.38$) and prey densities ($F_{1,52} = 0.015, p = 0.90$), or the interaction between noise conditions and prey densities ($F_{1,50} = 1.07, p = 0.30$). Attack rates were $a = 0.351$ prey *per* square metre, 95%CI = [0.143;1.08] for the ambient condition, and $a = 1.134$ prey *per* square metre, 95%CI = [0.566;2.27] for the boat noise condition. These two rates were significantly different (delta method : $p = 3 \times 10^{-5}$). Handling times were $h = 0.020$ hour *per* prey, 95%CI = [0.01;0.04] for the ambient condition, and $h = 0.012$ hour *per* prey, 95%CI = [0.009;0.015] for the boat condition. These two values were significantly different (delta method : $p = 0.0012$). As a result, FR was higher under boat noise compared to ambient noise,

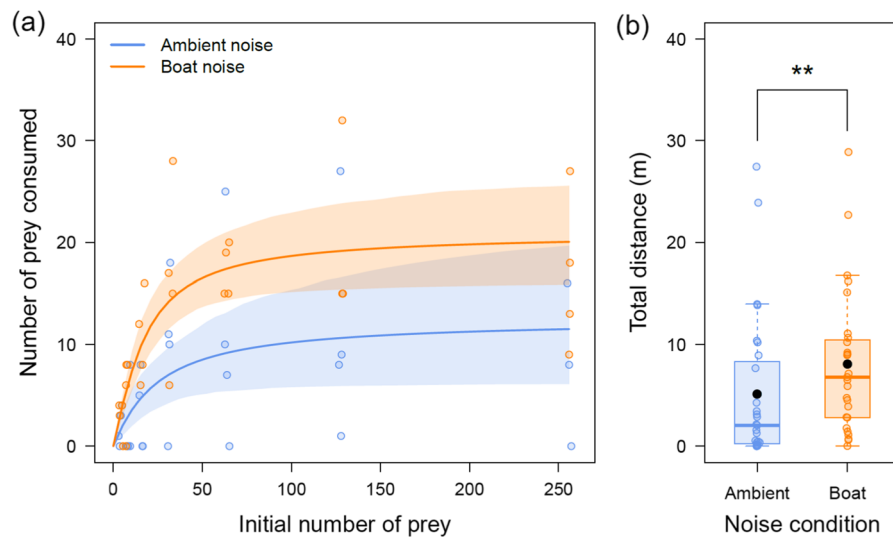


Fig. 2 **A** Functional response of round goby feeding on live chironomid larvae under boat noise (orange, top curve) or ambient noise (blue, bottom curve) condition. Each dot represents the number of prey consumed by a single fish for a given prey density. Curves show the predicted responses with their 95% confidence interval as shaded areas. **B** Total swimming distance of the fish under ambient noise (blue) or boat noise

(orange). The thick horizontal line depicts the median, and the solid dot the mean. The box depicts the interquartile range, and the whiskers are bound to the most extreme data point within 1.5 times the interquartile range. Data points outside this range are outliers. “**” means $p < 0.01$. On both plots, raw data points have been slightly horizontally jittered to avoid overlapping and increase readability

with both a steeper initial slope and a higher asymptote (Fig. 2A).

Concerning fish swimming distance, the best model based on the AICc values was the one that only includes noise condition and there was no other best model as the ΔAICc value of the second model exceeded the threshold value of two (Table 2). Swimming distance was longer under boat noise (Cohen’s $d = 0.71$, $95\%CI = [0.15; 1.28]$, $\chi^2_1 = 6.69$, $p = 0.0097$, Fig. 2B). Taking into account fish body mass, prey density, or any interactions between explanatory variables did not significantly improve the goodness of fit of the model.

The proportion of time spent active by chironomid larvae was affected neither by the interaction between noise condition and sound sequence ($\chi^2_1 = 0.288$, $p = 0.59$) nor by the sound sequence ($\chi^2_1 = 3.11$, $p = 0.077$, Fig. 3). More importantly, noise condition (ambient or boat noise) had no effect on prey activity ($\chi^2_1 = 0.327$, $p = 0.57$).

Discussion

First exposure to anthropogenic noise typically decreases foraging behaviours (Cox et al. 2018) and for some species this response weakens with prolonged exposure suggesting habituation (Pritchard et al. 2017; Rojas et al. 2021), as animals learn it is not associated with direct threat. Through the use of functional response (FR), we found for the first time that motorboat noise suggestively increases predation by an invasive fish, irrespectively of prey density. Noise also made round gobies more mobile, but had no effect on prey behaviour, suggesting that increased predation was solely attributable to fish behaviour. We cannot rule out that noise-disturbed larvae send out some sort of chemical cues like kairomones that might trigger fish mobility. However, this is unlikely given that, in general, non-predatory invertebrates as well as zooplankton usually behave as receivers while fish and predatory invertebrates act as senders (Burks and Lodge 2002). For instance, fish kairomones have been shown to increase digging in the chironomid larvae *Chironomus riparius* (Hölker and Stief 2005) but we did not observe such response in the face of noise.

Table 2 Results of the multimodel inference analysis performed on fish swimming distance and comparing all possible combinations of the three explanatory variables: noise condi-

tion (C), fish body mass (M), prey density (D), and their two-way (C:M, C:D, M:D) or three-way (C:M:D) interaction terms

| Intercept | C | M | D | C:M | C:D | M:D | C:M:D | AdjR ² | df | logLik | AIC _C | ΔAIC _C | Weight |
|-----------|---|--------|--------|-----|-----|-------|-------|-------------------|-------|---------|------------------|-------------------|--------|
| 0.936 | + | | | | | | | 0.121 | 3.000 | -84.033 | 174.546 | 0.000 | 0.390 |
| 1.165 | + | -0.139 | | | | | | 0.126 | 4.000 | -83.881 | 176.578 | 2.032 | 0.141 |
| 1.004 | + | | -0.001 | | | | | 0.126 | 4.000 | -83.885 | 176.586 | 2.040 | 0.141 |
| 1.136 | + | | -0.003 | | + | | | 0.142 | 5.000 | -83.405 | 178.060 | 3.515 | 0.067 |
| 1.239 | + | -0.142 | -0.001 | | | | | 0.132 | 5.000 | -83.726 | 178.701 | 4.156 | 0.049 |
| 1.352 | | | | | | | | 0.000 | 2.000 | -87.376 | 178.988 | 4.442 | 0.042 |
| 1.178 | + | -0.147 | | + | | | | 0.126 | 5.000 | -83.880 | 179.011 | 4.465 | 0.042 |
| 1.661 | + | -0.376 | -0.006 | | | 0.003 | | 0.152 | 6.000 | -83.100 | 179.987 | 5.441 | 0.026 |
| 1.451 | + | -0.181 | -0.003 | | + | | | 0.151 | 6.000 | -83.146 | 180.078 | 5.533 | 0.025 |
| 1.412 | | | -0.001 | | | | | 0.004 | 3.000 | -87.280 | 181.040 | 6.495 | 0.011 |
| 1.448 | | -0.055 | | | | | | 0.001 | 3.000 | -87.355 | 181.189 | 6.644 | 0.014 |
| 1.287 | + | -0.170 | -0.001 | + | | | | 0.132 | 6.000 | -83.719 | 181.225 | 6.680 | 0.014 |
| 1.768 | + | -0.371 | -0.007 | | + | 0.002 | | 0.165 | 7.000 | -82.714 | 181.864 | 7.318 | 0.010 |
| 1.597 | + | -0.339 | -0.006 | + | | 0.003 | | 0.153 | 7.000 | -83.081 | 182.596 | 8.051 | 0.007 |
| 1.513 | + | -0.217 | -0.003 | + | + | | | 0.151 | 7.000 | -83.135 | 182.704 | 8.158 | 0.007 |
| 1.512 | | -0.057 | -0.001 | | | | | 0.005 | 4.000 | -87.257 | 183.330 | 8.784 | 0.005 |
| 2.024 | | -0.354 | -0.007 | | | 0.004 | | 0.037 | 5.000 | -86.392 | 184.035 | 9.489 | 0.003 |
| 1.728 | + | -0.348 | -0.007 | + | + | 0.003 | | 0.165 | 8.000 | -82.707 | 184.615 | 10.069 | 0.003 |
| 1.578 | + | -0.257 | -0.004 | + | + | 0.001 | + | 0.169 | 9.000 | -82.606 | 187.302 | 12.756 | 0.001 |

Each line corresponds to a model. For each model, we reported intercept of the regression, adjusted R² (adj.R²), degree of freedom (df), Log likelihood (LogLik) values, Akaike information criteria values with a correction for small sample sizes (AIC_C), change in AIC_C (ΔAIC_C) from the best model, and model weight. The regression parameter is only given for the corresponding continuous variable (M, D) when this variable is present in the model. The presence of the categorical variable (T being either “boat noise” or “ambient noise”) in the model is indicated by a “+” symbol

Attack rate describes predator’s efficiency at capturing prey, namely the space (here the surface) that a predator searches *per* unit of time (Holling 1959). It fixes the initial slope of the FR curve: the higher the attack rate, the steeper the slope. Round gobies were more mobile with noise, which increased the searched area and provided opportunities to encounter and catch prey (Gerritsen and Strickler 1977), thus explaining the increase in attack rate. In the meta-analysis by Cox et al. (2018), anthropogenic noise was found to increase fish movements in general, which could be part of an escape response as found under predation risk. Fish could also move more to avoid the source of noise or to look for the presence of conspecifics. However, under the assumption of a stress response, we would expect reduced feeding motivation and not increased predation as we observed. Further investigation is needed to explain why round gobies are more mobile with noise, for

instance allowing for conspecific interactions, providing shelters, or mixing behavioural metrics with physiological makers of stress like cortisol (Wysocki et al. 2006).

Ideally, handling time is associated with prey processing and describes the average time spent on a caught prey item (Holling 1959). The reverse of handling time gives an estimation of maximum feeding rate, which fixes the asymptote of the curve. Handling time was significantly lower with noise, suggesting that fish did better in terms of prey processing than under control conditions. This result seems contradictory to the principle of optimal foraging. It might be that experimental duration was long enough so that handling time also included other activities than prey processing (Li et al. 2018). Such activities, like resting, could be modulated and in our case decreased by noise.

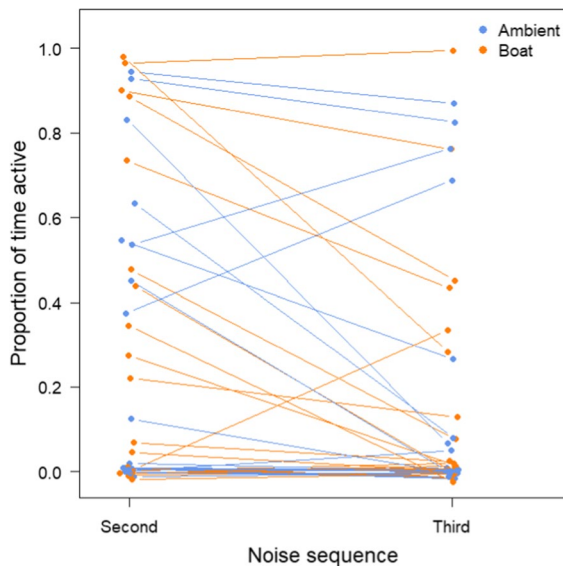


Fig. 3 Reaction norm of 40 chironomid larvae (10 replicates *per* noise condition and two larvae *per* replicate) recorded under either ambient noise (blue lines) or boat noise (orange lines) condition during two three-minute noise sequences. Points are raw data and have been slightly horizontally and vertically jittered to avoid overlapping and increase readability

Supporting our findings that round gobies were not disturbed by boat noise when feeding, Higgs & Humphrey, (2020) reported that noise from recreational boats does not impair the calling behaviour of round goby. Using the same approach, we recently found that the FR of another invasive fish, the pumpkinseed sunfish *Lepomis gibbosus*, was not altered by chronic exposure to boat noise (Rojas et al. 2021). As it has been documented with other environmental stressors like temperature, salinity, hypoxia or food (Elis and MacIsaac 2009; Zerebecki and Sorte 2011; Lagos et al. 2017), tolerance to anthropogenic noise might be another feature of successful invaders. Our results also provide an alternative explanation to the decrease in presence but not in foraging events in response to boat noise reported by Pieniazek et al., (2020). It might be that increased mobility makes some gobies leave the area while those remaining forage more.

Increase in both FR parameters indicates stronger top-down control that might drive the prey to exclusion, especially because high attack rates (i.e. steep initial slopes) can generate unstable boom-burst population dynamics (Murdoch and Oaten 1975). Our study provides additional evidence that anthropogenic

noise can modulate the strength of predator—prey interactions, with potential to reinforce the trophic impact of an invasive species. However, before scaling up these results to communities and generalizations, some limitations have to be discussed.

We reported sound levels in units of sound pressure while round gobies rely on particle motion to detect sounds (Belanger and Higgs 2005). According to Nedelec et al. (2016), we are in the conditions where the kinetic energy (KE) of particle motion has to be measured with a dedicated sensor and cannot be calculated from the potential energy (PE) of sound pressure. We don't have such sensor but in the recent paper by Olivier et al. (2023) where they described the sound field of a tank using a hydrophone and a particle motion sensor concurrently, they demonstrated that acoustic impedance (PE/KE in dB) for a given frequency was constant (i.e., independent from source level). In other words, when source level increases or decreases by N dB, both PE and KE will increase or decrease by N dB. They conclude that relying solely on pressure can be used to detect trends, suggesting that the noise-induced increase in FR we found is still relevant although we did not measure particle motion.

There have been increasing calls to get away from tank-based acoustic studies that oversimplify reality and present acoustic biases as discussed above (Popper and Hawkins 2019). However, there are also studies demonstrating that field and lab results can be consistent see Pieniazek et al. (2020). In our opinion, tank-based studies are relevant to raise new predictions for further *in-situ* validation and identify potential causalities like the relationship between mobility and FR parameters of the present study.

Additional investigations exploring context dependencies in the response to noise are also needed. Functional response is known to be influenced by habitat complexity (Alexander et al. 2012), conspecific presence (Médoc et al. 2015), or natural enemies (Iltis et al. 2018). Individual response to noise might also weaken with repeated exposure in case of habituation (Rojas et al. 2021) and round gobies could resume normal behaviour on the long term. Comparing gobies from noiseless areas with areas where they experienced generations of boat noise would help address this question. As explained in the playback tracks section, we

chose as control noise condition for the FR experiment the background noise that the fish experienced during the 3-week acclimatization period in the rearing aquariums, and that we considered as the baseline level. It would be interesting to also derive the FR under a river soundscape. For some reason that escapes us, most of the round gobies we collected were small sized and it would be interesting to repeat the same experiment with large-sized individuals.

Our sampling location was in an area of active range expansion and it has been shown that round gobies from invasion fronts are bolder, disperse more and have higher metabolic rate compared to individuals from longer-established populations (Myles-Gonzalez et al. 2015; Behrens et al. 2020). An interesting perspective would be to investigate the response to anthropogenic noise between personality types and along the invasion gradient.

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Author contribution MFD, LT, FXDM and VM designed the study. MFD and ER performed the experiments and collected the data. MFD, LP, FXDM and VM analysed the data. MFD and VM drafted the manuscript, and all authors provided critical revisions. All authors approved the final version of the manuscript.

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Data availability All datasets and source code as well as the playback track are available as electronic supplementary materials on public repository: Fernandez Declerck, Rojas, Prosnier, Teulier, Dechaume-Moncharmont, Médoc (2022) Datasets and R source code of manuscript “Adding insult to injury: anthropogenic noise intensifies predation risk by an invasive freshwater fish species” by Fernandez Declerck et al. Zenodo <https://zenodo.org/record/6563528>. <https://doi.org/10.5281/zenodo.6563528>

Declarations

Conflict of interest We declare we have no competing interests.

Ethical approval Round goby capture and transport were approved by the Direction Départementale des Territoires de la Loire (DDT 42). All the procedures were conducted in accord-

ance with appropriate European (Directive 2010/63/EU) and French national guidelines, permits, and regulations regarding animal care and experimental use (Approval no C42-218-0901, Direction Départementale de la Protection des Populations de la Loire, Préfecture du Rhône).

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