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# Multi-scale responses of freshwater communities to anthropogenic noise with a focus on invasive species

Emilie Rojas

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**Multi-scale responses of freshwater communities to anthropogenic noise with a focus on invasive species**

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*« Quand on veut, on peut »*

Merci maman, cette phrase n'a jamais eu  
autant de sens qu'aujourd'hui.

*« Somos los mejores porque somos Rojas »*

Papy, gracias por tu apoyo y tu amor.

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*Sœur, meilleure amie et conseillère de vie.*

*También dedico mi tesis a mis abuelitas, dos ejemplos de fuerza.*



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# Scientific realizations

## Article published

Rojas E, Desjonquères C, Agostini S, Fiorini S, Decencière B, Danger M, Felten V, Médoc V (2023) Chronic anthropogenic noise alters the dynamics of cladoceran species (submitted as a chapter in the AN22 Book publish by *Springer Nature* in December 2022)

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Rojas E, Thévenin S, Montes G, Boyer N & Médoc V (2021) From distraction to habituation: Ecological and behavioural responses of invasive fish to anthropogenic noise. *Freshwater Biology* 66: 1606-1618. DOI: 10.1111/fwb.13778

## Articles in preparation

Fernandez Declerck M, Rojas Emilie<sup>1</sup>, Prosnier L, Teulier L, Dechaume-Moncharmont FX, Médoc V (2023). Adding insult to injury: anthropogenic noise intensifies predation risk by an invasive freshwater fish species (*Biological Invasions*)

Rojas E, Prosnier L, Pradeau A, Boyer N, Médoc V (2023), Anthropogenic noise does not strengthen multiple predator effects in a freshwater invasive fish (submitted to *Journal of Fish Biology*)

## Oral communications

- 20th January 2022: Alt516 Symposium, Saint-Etienne, FR

Rojas E, Thévenin S, Montes G, Boyer N & Médoc V. From distraction to habituation: Ecological and behavioural responses of invasive fish to anthropogenic noise.

- 5th August 2021: Animal Behavior Society, Virtual meeting

Rojas E, Gouret M, Agostini S, Lacroix G, Fonseca P, Médoc V (2021) Do individual responses to anthropogenic noise spread throughout the community scale?

- 14th June 2019: SFECA meeting, Lille, FR

Rojas E, Thévenin S, Montes G, Boyer N & Médoc V. Characterization of an invasive freshwater species responses to anthropogenic noise.

## Poster session:

- 10<sup>th</sup> – 15<sup>th</sup> July 2022: Aquatic Noise on aquatic Life 2022 (AN22, Poster session with speed talk, **Berlin**, Germany).



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# Introduction

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# I. From sound to noise

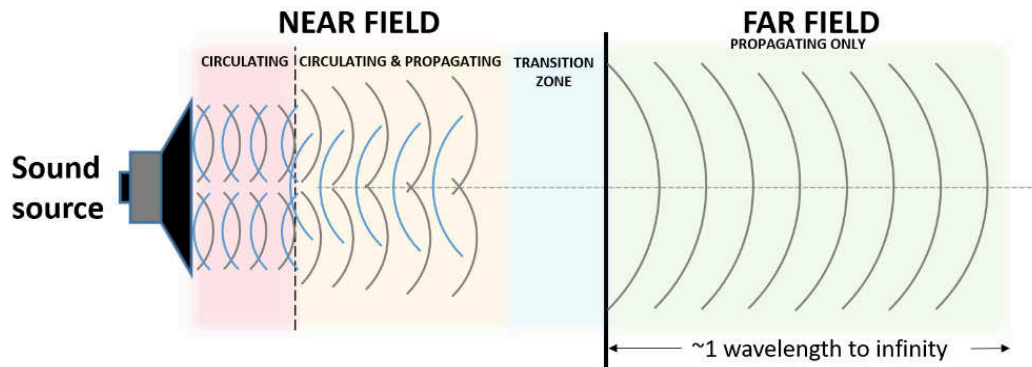
## 1. What is A sound?

Sound is a mechanical vibration and wave generated by the movement of a structure or object that propagated in a solid, fluid or gas medium (Urlick, 1975). This propagation is a disturbance where particles of the medium move back and forth around their initial position (called “particle motion”) and transmit the oscillatory motion to their neighbors without moving with the propagation wave. Sound is also characterized by an alternation of pressure difference, called sound pressure, which causes localized areas of compression (increased pressure) and rarefaction (decreased pressure) (Popper & Hawkins, 2019). Particle motion gives information on the direction of propagation of the wave as well as the magnitude of sound energy, while sound pressure is omnidirectional and gives information about the magnitude of sound energy.

The total energy contained in a sound wave consists of the energies associated with acoustic pressure and acoustic particle velocity (PE and KE respectively) (Popper et al., 2019; Popper & Hawkins, 2019). PE arises from the compression and expansion of the fluid while KE arises from the particle motion. Particle motion may be expressed in terms of the particle displacement (SI unit: meter), or its time derivatives: particle velocity (m/s) or particle acceleration (m/s<sup>2</sup>). Particle motion, like sound pressure, is a function of time (t). (Popper et al., 2019; Popper & Hawkins, 2018).

Closer to the sound source, known as the acoustic "near field", there is no stable relationship between pressure and velocity and measurements with a single microphone can be difficult and unreproducible. The sound energy circulates back and forth with the vibrating surface of the source, never escaping or propagating away (Fig.1). As we move out away from the source, some of the sound field continues to circulate, and some propagates away from the object (far field) (Siemens, 2020). The acoustic far field begins approximately at a distance of 1 wavelength away from the sound source and extends outward to infinity (Fig.1). As wavelength is a function of frequency, the start of the far field is also a function of frequency. The far field is defined as the region where the sound pressure and acoustic particle velocity are in phase, and where the sound pressure level decreases by 6 dB for each doubling of the distance from the source (Siemens, 2020). Near-field measurements require the use of

multiple microphones to accurately capture the energy carried by the circulating and propagating waves. While far field, pressure and velocity are in phase and sound intensity can easily be measured with conventional hydrophones.



**Figure 1.** Propagation of the sound in the near field and the far field (Extracted from [community.sw.siemens.com](http://community.sw.siemens.com))

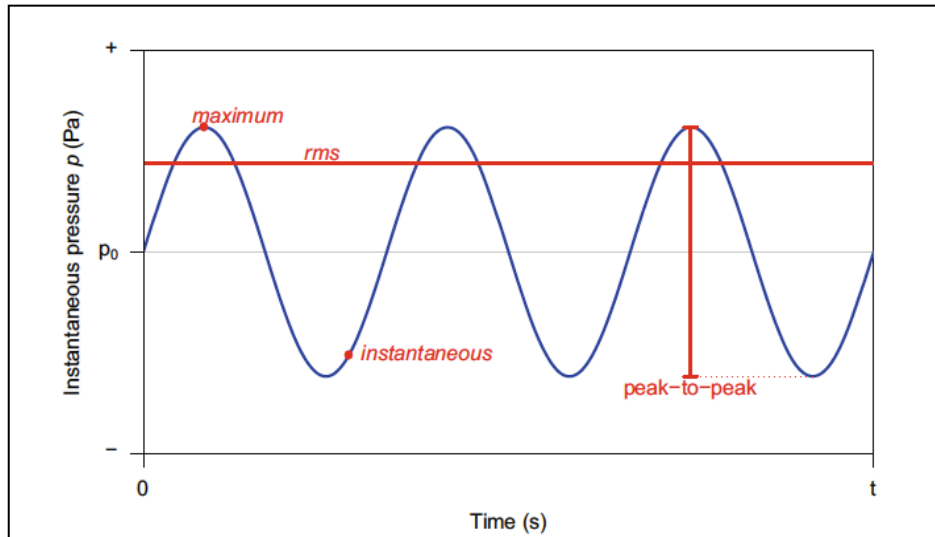
Sound pressure usually is a sinusoidal wave where the difference between the minimum and maximum value of the peak represents the amplitude of the sound. Amplitude is related to the amount of sound energy; high amplitude sounds will carry large amount of energy and inversely for low amplitude sounds. It is measured using a logarithmic scale called decibels (dB). According to J .Sueur (2018), it can be measured in four different ways (Fig.2):

- Instantaneous amplitude ( $a$ ): amplitude measured at time  $t$ ,
- Maximum amplitude ( $A$ ): the maximum of the absolute value of the amplitude
- Peak-to-peak amplitude (pk-pk): the range of amplitude between the minimum and maximum values, this method is used to study very short sound such as impulsive sound, usually less than one second, with an abrupt onset and rapid decay (explosion, drop forge impacts).
- Root-mean-square amplitude (RMS): the root-mean-square or quadratic mean is the square root of the mean of the squares. RMS is commonly used as it provides an estimation of the amplitude average. The sound wave is first squared, then the mean of the squared values is computed, and finally the square root of this mean is computed:

$$\text{rms} = \sqrt{\frac{1}{n} \times \sum_{i=1}^n x_i^2}$$

. RMS is commonly used to measure the relative amplitude of

continuous sounds such as motorboat noise, the type of anthropogenic noise we focused on for this thesis.



**Figure 2.** The four main amplitude measures of a sound: instantaneous amplitude, maximum amplitude, peak-to-peak amplitude, and average amplitude (root-mean-square, RMS). The blue sine wave represents the propagation of an underwater sound wave. Figure extracted from ‘Sound Analysis and Synthesis with R’ book (J.Sueur, 2018).

A ‘period’ is the duration of a complete sinusoidal cycle, and ‘frequency’ is the inverse of the period expressed in Hertz (Hz, the number of cycles per second) (Putland et al., 2019). Therefore, sound pressure is illustrated by a frequency spectrum where amplitude is plotted against frequency.

## 2. The sources of sound

Raymond M. Schafer introduced the concept of soundscape (1977) as all the sounds from a particular environment reaching the human ear. Sound ecology is the study of the relationship between living organisms and their sonic environment, emanating from the landscape and including biophony, geophony, and anthropophony.

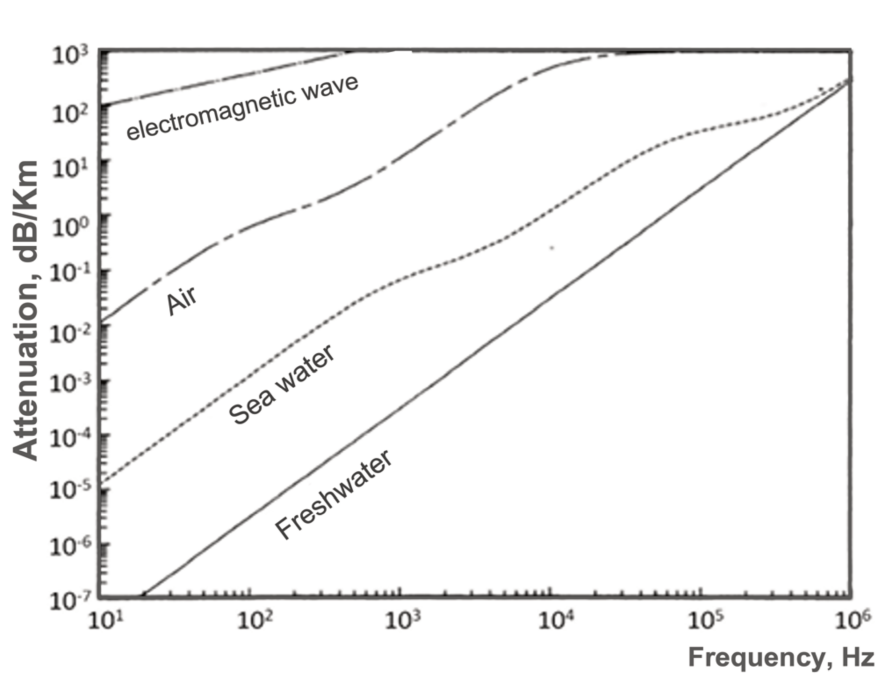
Biophony is defined by the bioacoustician Bernie Krause as all the sounds produced by the living beings of an ecosystem (except for humans, whose sound is qualified as

‘anthropophony’). A large part of biological sounds can be, impulsive (clicks, clacking, pulses) or long (songs, whistles) for instance and can covering a variety of frequency ranges that are specific to each species from tonal to large-bandwidth sounds.

‘Geophony’ refers to the abiotic sounds coming from the geologic events (e.g., eruptions, landslides, etc.) or climatic events (e.g., rain, wind, etc.), or from water movements (torrents flowing, ice cracking, current, waves). Geophony strongly dominates terrestrial and aquatic ambient soundscape emitting sounds ranging from 1 to 100 kHz (Tasker et al., 2010). Wind or large water movements can cause high sound pressure levels.

Anthropophony is generated by a multitude of human activities associated with both commercial and private vehicles, including road traffic (motorcycles, automobiles, buses), waterway traffic (boats, ferries, commercial ships), and non-military aerial traffic (commercial jets, helicopters) (Shannon et al., 2016). Other anthropogenic noise categories are also investigated from industrial activities (construction, machinery, pile driving) or military recreation (gun fire, explosion, sonar) (Shannon et al., 2016).

Man-made sound has prominent frequencies within those naturally occurring windows (Barber et al., 2010; McDonald et al., 2006) and differ from geophony and biophony in acoustics features such as constancy or impulsiveness (Hildebrand, 2009; Normandeau Associates, Inc., 2012; Popper & Hastings, 2009). Indeed, the low-frequency band (10 to 500 Hz) in air and water environments is threatened by anthropogenic sounds (car, train, ship). Sound propagates five times faster in water than in the air ( $1500 \text{ m s}^{-1}$  in water versus  $343 \text{ m s}^{-1}$  in the air), aquatic species are therefore very vulnerable to anthropogenic noise. In general, low frequencies sounds propagate efficiently over long distance while high frequencies are more quickly attenuated over few kilometers (Fig.3). In water sound, according to the type of water (salt- or freshwater) the attenuation differed with a frequency energy loss higher in saltwater than freshwater. Indeed, at 500 Hz (relevant frequencies for the hearing range for most fish) sound suffers only 1 dB of attenuation in 100 kilometers of propagation in seawater and 1 dB in 10,000 kilometers of propagation in freshwater (P. H. Rogers & Cox, 1988).



**Figure 3.** Attenuation of sound in freshwater, seawater and air compared to the attenuation of electromagnetic waves in water (Figure taken from Roger and Cox, 1988)

### 3. Noise pollution

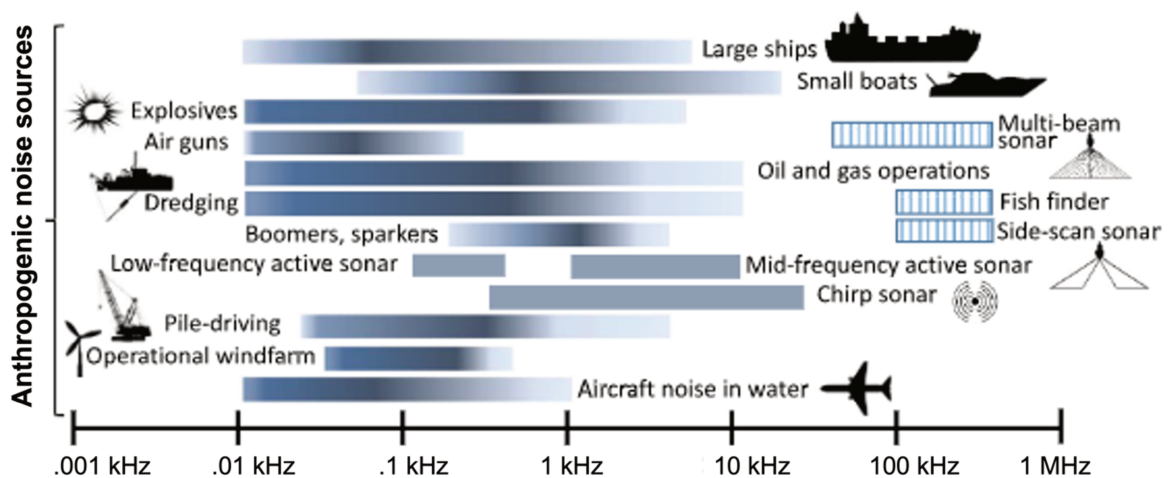
When a sound is perceived as unpleasant or disruptive, when it overlaps with the detection of a signal of interest, then it is considered as unwanted sound or **noise** and convey no information unlike natural sounds. Noise can be classified into two broad classes: impulsive or acute noise and continuous or chronic noise (Popper & Hawkins, 2019). Acute noises are short sounds (typically less than a second, e.g., seismic airguns, pile driving), that can happen as single, or repeated instances. They include fast changes in amplitude and happen over short periods as they are usually the result of a project. At the opposite, chronic noise are longer sounds, with a somewhat constant sound pressure level during a given period (A. D. Hawkins et al., 2015) such as ship noise.

Anthropogenic noise represents a pervasive pollution for terrestrial and aquatic environments (Popper & Hawkins, 2019; Shannon et al., 2016). The industrial development has led to the explosion of noise emissions due to increased human demographics, urbanization, commercial transports, and resource extraction (Fig.4) (Hildebrand, 2009; Shannon et al., 2016). The most spatially extensive source of anthropogenic noise pollution is considerably transportation network . Noise is known to increase terrestrial and aquatic ambient sound



levels (Popper et al, 2019), however, terrestrial environment receive more attention than aquatic ones.

Yet, aquatic systems are threatened by noise sources, that can be classified in five categories according to Popper et al, 2019: (1) Seismic airguns used for sub-sea gas and oil reserves exploration, that are impulsive noise with high intensity emitting in low frequencies range ; (2) Pile driving that are short and impulsive noise (around 180 to 200 dB re 1  $\mu\text{Pa}^2 \text{s}^{-1}$ ) due to bridges, harbor, wind farms and other offshore constructions (Dahl et al., 2015). Pile driving induces vibrations in the water sediments and affect all the animals in the vicinity (Dahl et al., 2015); (3) Industrial activities, especially in lake with dredging activities (used for extract sand and gravel, maintain shipping lanes) that produced high level of noise (Thomsen et al., 2016; Wenger et al., 2017) and generate substrate vibration in the sediments; (4) Operating offshore wind turbines which generated a particle motion accompanying substrate transmissions (Sigray & Andersson, 2012); (5) Motorboat noise which represent a significant proportion of aquatic noise pollution (specifically in freshwater system), due to the diversity of engines (large ships, fishing, pleasure boats), cavitation at propeller blade tips is a particular important source of noise emitting across all frequencies (Ross & Kuperman, 1989). Considering research on aquatic noise pollution, motorboat noise impact is increasingly investigated in marine system since recent decades (Chahouri et al., 2022; Miller et al., 2022; Weilgart, 2018), where the ambient noise was found to be increased by more than 15 dB since 1950 with the number, speed, and horsepower of commercial ships (McDonald et al., 2006).



**Figure 4.** Sources of noise in the underwater soundscape (Duarte et al., 2021)

## II. Noisy waters

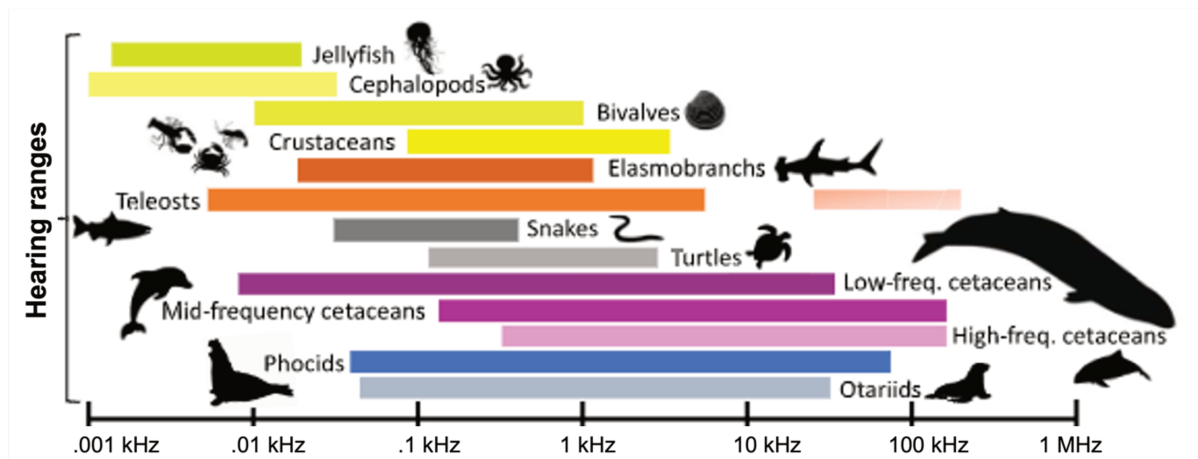
### 1. The importance of underwater cues

Sound provides aquatic animals with information about their environment very quickly and over long distances. Sound perception is crucial for certain animals compared to vision, touch, taste, and smell because it cannot be obstructed by a dark or turbid environment (Fischer & Frommen, 2013). Aquatic animals are able determine the direction of sound source origin, which can help them to locate predators and move away from them or to detect potential prey and move towards them .

The use of sound is context-dependent and species-specific, for example, for territorial defense or aggression towards conspecifics, the domino damselfish (*Dascyllus albisella*) produces distinctive popping sounds while aggressively interacting with other males (Mann & Lobel, 1995). In courtship interactions the calls can convey information about the quality of the male producing the sound (Amorim et al., 2015). For example, in painted gobies *Pomatoschistus pictus*, females preferentially chose males that emit long mating calls (Amorim et al., 2013). Sounds also allow to maintain school or shoal cohesion. For instance, bigeyes, *Pempheris adspersa*, cluster together when emitting calls and increase group cohesion when exposed to ambient reef sound at high sound pressure levels (van Oosterom et al., 2016). Pelagic crustacean larvae have also been found to use acoustic cues to orient themselves to colonize sites at different life stages (Montgomery et al., 2006).

### 2. Sound perception by fish and invertebrates

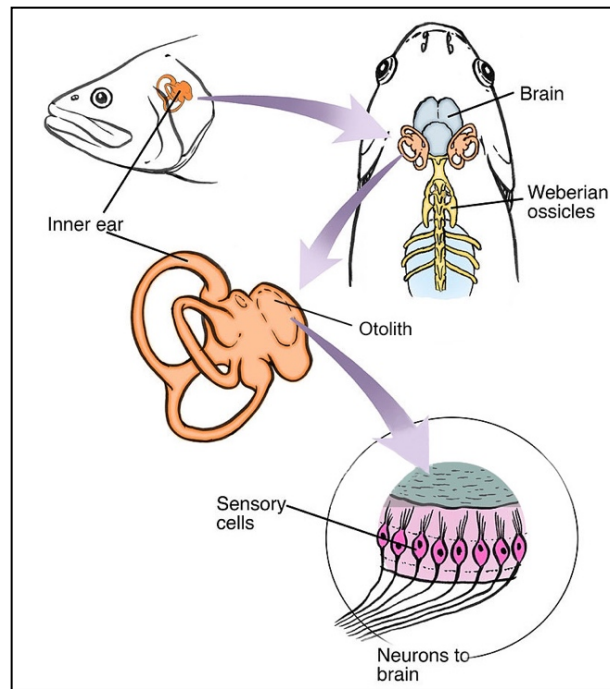
All fish and invertebrates can detect sounds and use them to learn about their environment (Popper et al, 2019). Sounds play an important role in the life-history of many species. A sound can be detected through particle motion by all fish and invertebrates or through sound pressure by some specialist fish (Kunc & Schmidt, 2019). Concerning sound pressure, all fish detect sounds from 50 Hz to 500 Hz (Popper et al, 2019), and a small number of species known as “specialist” can detect sound up to 3-4000 Hz (Fig.5).



**Figure 5.** Animal hearing range (Duarte et al., 2021)

All fish have an inner ear composed of three semicircular canals, with three otolith organs composed of a calcareous matter making the inner ear denser than the rest of the fish. The semicircular system is used for equilibrium orientation in three-dimensional space, while the otolith system is used for hearing and linear acceleration detection (Putland et al., 2019). In simple terms, the otolith system is composed of cilia cells (sensory cells or mechanosensory hair cells) that will deform with particle motion and induce the release of an excitatory neurotransmitter that is interpreted as an acoustic signal by the fish's brain (Putland et al., 2019) (Fig.6).

The movement of the otolith follows the direction of the sound and allows the fish to locate the source (Sand & Enger, 1973). In addition, fish can detect particle motion using cilia cells positioned for most fishes along the lateral line. Indeed, lateral line is a highly specialized mechanoreceptor that it is involved in the feeding, defensive, schooling, reproductive and migration behavior and allows them to orient in darkness (Kasumyan, 2003). Fishes without a lateral line also have cilia cells that serve as mechanoreceptors that translate the movement of particles into the sensory system. Specialist fishes can detect sound pressure using their gas-filled cavities, also known as “swim bladder”, connected directly to or near the inner ear. The swim bladder can compress and change volume in response to fluctuating sound pressure, and translates sound pressure into particle movement (Sand & Hawkins, 1973) in the inner ear. In ostariophysan fishes, the swim bladder is connected to the ear by a mechanical linkage of the Weberian ossicle (Weber, 1820), which enhances hearing ability to high frequencies.



**Figure 6.** The Weberian apparatus of ‘hearing specialist’ fish species

(© 2021 Off the Scale magazine)

Invertebrates possess receptor systems (hairs on the body) used for equilibrium function and directional sensitivity that detect particle motion (Breithaupt & Tautz, 1990). They also possess chordotonal organs associated with the joints of flexible appendages of the body that are connected to the central nervous system. These organs can respond to low-frequency sounds or, in the case of some crabs, to vibrations transmitted from the substrate through the exoskeleton (Popper et al., 2001; Salmon, 1971).

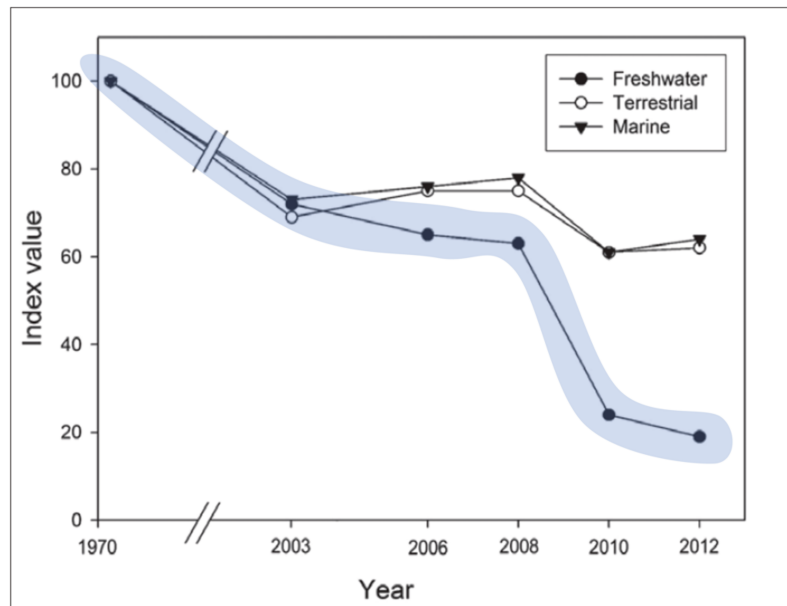
Crustacean species are the most documented to date, particularly hermit crab, crayfish, and lobsters (Budelmann, 1992; Popper et al., 2001). For example, Breithaupt & Tautz (1990) identified the intensity threshold at which cuticular receptors in decapod crustacean cease to respond. They showed that below 150 Hz (low frequencies) the animals showed the greatest sensitivity through their various sensory hairs (receptors that cover most of the exocuticle). Crustaceans also have statolith organs composed of calcareous statocyst, attached to sensory hair cells, dense structures like the sensory hair cells in vertebrate ears (Popper et al., 2001; Popper & Hastings, 2009). These structures are sensitive to particle motion at frequencies between 100 and 3000 Hz (Lovell et al., 2005). Some studies have showed that particle motion can encompass the entire body of crustaceans and force them to move at the same

phase and amplitude, resulting in the stimulation of the statolith organs (Kaifu et al., 2011; Packard et al., 1990). Therefore, detecting sounds and vibrations is possible even for invertebrates.

### **3. Anthropogenic noise as a pervasive pollutant in freshwaters**

Despite the overall breadth of considered impacts, most research was conducted on terrestrial and marine mammals (Chahouri et al., 2022; Jerem & Mathews, 2021) whereas amphibians, fish and invertebrates received limited attention (Jerem & Mathews, 2021; Popper & Hawkins, 2018; Sordello et al., 2020). Yet, man-made noise was recognized as altering multiple aspects of function, demography, and physiology of freshwater animals (de Jong et al., 2020; Di Franco et al., 2020; Draštik & Kubečka, 2005; Mickle & Higgs, 2018; Sabet, Wesdorp, et al., 2016; Simpson et al., 2015).

Freshwater habitats (rivers, lakes, reservoirs, ponds, connecting channels, estuaries) are also affected by increasing urbanization and commercial shipping (Mickle & Higgs, 2018), but are underrepresented in the literature on noise pollution when considering the biodiversity, they host. Yet, freshwater species are exposed to an exceptional range of man-made noise because aquatic (e.g., boating or shipping, construction) and terrestrial (e.g., road traffic, train, plane) noise penetrate freshwater environments (Holt & Johnston, 2015; Mickle & Higgs, 2018). It is a global hotspot system of biological richness, and it accounts for approximately 10% of the planet's species richness with over 30% of vertebrates (Balian et al., 2008; Reid et al., 2019; Strayer & Dudgeon, 2010). Freshwater biodiversity includes organisms that are permanently in the water or for part of their life cycle (Gozlan et al., 2019), and fish represent over half of all of the vertebrate species on the planet (Thomson & Shaffer, 2010). The Worldwide Fund for Nature (WWF) through its Living Planet Index (LPI) revealed a faster decline in freshwater biodiversity between 1970 to 2012 compared to marine and terrestrial ecosystems (Reid et al., 2019) (Figure 7). According to Grooten & Almond (2018), freshwater vertebrate populations have declined at more than twice the rate of terrestrial or oceanic vertebrates.



**Figure 7.** Variation of the living planet index (WWF) quantifying the decline in vertebrate populations over time. For each group (i.e., freshwater - black circle, marine - black triangle, and terrestrial - white circle), the index is calculated on a vertebrate pool. The index is relative to the year 1970 (reference year) for which the value is set at 100%. Adapted from Reid et al. (2019).

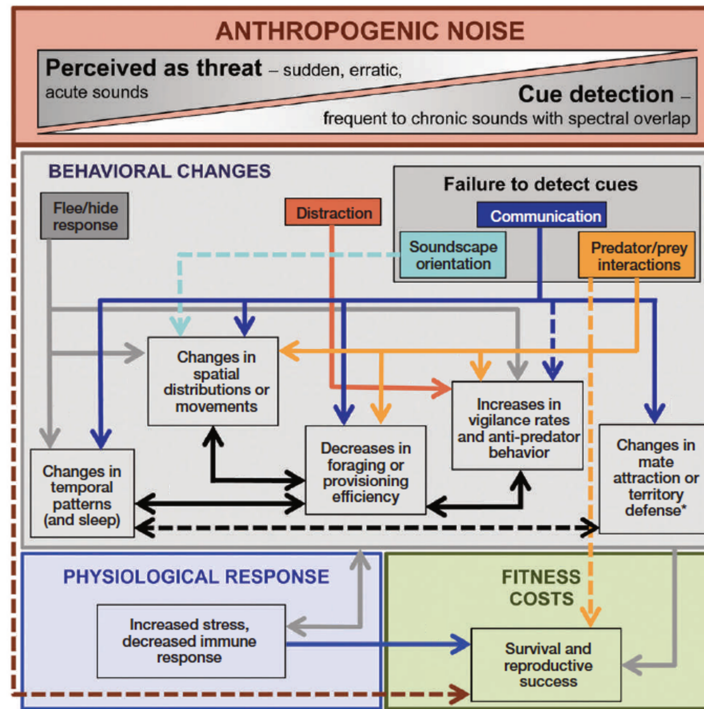
Another consequence of anthropogenic activities and especially due to ship traffic is the introduction of invasive species (Manchester & Bullock, 2000; Savini et al., 2010). Indeed, species take advantage of the construction of canals or dams to disperse or to be transported through the ballast of ships (Johnson et al., 2008; Mavruk & Avsar, 2008; Savini et al., 2010). Invasive species are thought to possess certain biological traits facilitating their invasion success and high tolerance to environmental changes. Therefore, for the purposes of characterizing noise effects in freshwater environments, **it is relevant to integrate the responses of invasive in addition to that of native species whose comparison could help us to help to improve freshwater conservation.**

### III. Anthropogenic noise consequences

#### 1. Noise can affect organisms in many ways

The effect of anthropogenic noise on wildlife has been investigated extensively (Fig.8) across multiple taxa (Francis & Barber, 2013) and shown to vary depending upon context, sex, age,

life history (Kunc & Schmidt, 2019). Research especially targets some species such as birds and marine mammals (Sordello et al., 2020), but recent studies also showed interest on invertebrate response (e.g., response of the mussel *Mytilus edulis*, and the hermit crab, *Pagururs bernhardus*, to sediment vibration, Roberts et al. (2016)).



**Figure 8.** Conceptual framework for understanding how noise stimuli are perceived as a threat or interferes with cue detection and elicit behavioral responses that have direct consequences for fitness or via a physiological stress response. Dashed arrows signify a link that Francis et al., 2013 predicted as important but which no current evidence exists. The asterisk denotes that which could result from a change in behavior or a failure to change behavior in response to noise. Solid lines indicate effects already found in the literature (Adapted from Francis et al., 2013)

Hearing abilities are crucial for aquatic species for communication, predation interaction, reproduction, territory defense (Amorim et al., 2015; Mensinger et al., 2016; Putland et al., 2019). However, noise was found to alter permanently or temporarily hearing abilities, especially when organism is close to the source of the noise (Francis & Barber, 2013). Temporary threshold shift (TTS) occurs when the hair cells of the inner ear are fatigued, yielding an increase in auditory threshold (Putland et al., 2019). Codarin et al. (2009) showed that boat noise exposure (136 dB 1 re  $\mu$ Pa) reduces auditory sensitivity relative to thresholds

in ambient noise of the damselfish *Chromis chromis* and red-mouthed goby *Gobius cruentatus*. Additionally, it was found that boat noise (140 dB re 1  $\mu$ Pa) reduced also auditory sensitivity in the blacktail shiner *Cyprinella venusta* especially at relevant frequencies for this species (300 and 400 Hz; Crovo et al., 2015). In worst scenarios, high intensity of noise, such as exposure to airgun, can induce complete hearing loss for long periods. For example, the silver bream (*Chrysophrys auratus*), exposed to an airgun of 222.6 dB re 1  $\mu$ Pa, did not show evidence of repair up to 58 days post exposure (McCauley et al., 2003). Hearing loss can have serious negatives implications for fish because it reduces their ability to communicate or assess their environment (e.g., detect prey or predators).

Physiological studies were also performed to assess the stress response of species using the measurements of the stress hormones like cortisol. Cortisol represents a good measure as it is related to several physiological processes such as growth, sexual maturation, reproduction, immunity, and survival (Weilgart, 2018). Cortisol measurements were made mainly on fish species and revealed that exposure to ship noise can result in increased levels even with short exposure (Wysocki et al., 2006). For instance, in juvenile giant kelpfish, exposure to intermittent boat noise (around 140 dB<sub>rms</sub> re 1  $\mu$ Pa, noise events occurred in succession lasting 10 sec followed by a 15 sec break) increase cortisol concentration (Nichols et al., 2015). It was found that unpredictable noise (with changes in frequency and levels) induced higher physiological stress than continuous noise (Nichols et al., 2015; Wysocki et al., 2006). Indeed, exposure of 10 min to a frequency sweep of vessel traffic (150 dB re 1 $\mu$ Pa) significantly increased the amount of the European sea bass (*Dicentrarchus labrax*) and the gilthead sea bream (*Sparus aurata*) movement compared to controls accompanied with changes in glucose and lactate concentrations indicating a higher metabolic activity (Buscaino et al., 2010). Other metrics are also used as sensitive indicators of fish stress such as heartbeat, oxygen consumption or clearance rate. For example, an exposure to different man-made noises (trolling motor, 9.9 horsepower combustion engine for 60s) induced higher heartbeat in the Largemouth bass (*Micropterus salmoides*; Graham & Cooke, 2008). Studies performed on marine crustaceans showed that ship noise exposure (around 150 dB<sub>rms</sub> re 1 $\mu$ Pa) increase oxygen consumption (Wale et al., 2013).

Behavioural responses to noise have also been widely investigated for several decades and show that these responses vary between organisms (Mickle & Higgs, 2018; Shannon et al., 2016; Sordello et al., 2020). Indeed, most studies showed impacts on temporal patterns, spatial distribution, foraging, mate attraction and territorial defense (Francis & Barber, 2013).



Depending on the context, the response to the stimuli can induce a panel of different responses. For example, the *Neolamprologus pulcher* fish showed a reduction in anti-predator defense under noise if there were no eggs in the nest but no change if eggs were present (Bruintjes & Radford, 2013). Change in activity level related to avoidance behaviour are also commonly observed. Jacobsen et al. (2014) showed that the perch (*Perca fluviatilis*) and the roach (*Rutilus rutilus*) increased swimming activity under first boat noise exposure. Changes in mobility can be disadvantageous for the species because it makes them more vulnerable to predation (Simpson et al., 2015) or may deflect individuals from their migration route and have negative consequences on habitat selection and settlement (Popper & Hawkins, 2019).

Anthropogenic noise is also known to mask biologically relevant sounds used for communication, interpretation of their environment, or spatial orientation (Francis & Barber, 2013). Chan et al., (2010) pioneered the ‘distracted prey hypothesis’ where animals focus their attention on the noise and have difficulties in perceiving their environment correctly. They showed that even Caribbean hermit crabs, *Coenobita clypeatus*, were distracted by motorboat noise making them more vulnerable to predation. Additionally, the zebrafish, *Danio rerio*, showed an increase in handling error and a delayed response to food when noise gets louder (Sabet et al., 2016) and the damselfly larvae, *Ischnura elegans*, reduced their predation when exposed to motorboat noise for the first time (Villalobos-Jiménez et al., 2017). Therefore, masking effects induce strong negative effects on foraging efficiency. When placing these effects on foraging success at an ecological scale, it becomes clear that noise could have direct consequence for animal survival and reproductive success. However, the few studies that considered this problem, only included repeated short exposure to noise (Jacobsen et al., 2014; Neo et al., 2018) and **there is a lack of long-term experiments.**

## 2. Individual response can weaken with repeated exposure

Fish are able to associate a particular environment (location, time, noise) with a type of response (physiological or behavioural) to a repeated stimulus, besides, there are few experimental studies that investigate how responses may change over time (Wale et al., 2013). Response may be attenuated due to high exposure, if animals continue to respond to a stimulus they will become chronically stressed while if they return to their baseline cortisol level, their behaviour and health will be the same as unstressed animals (Cyr & Romero, 2009). Johansson et al. (2016), compared the effect of noise on cortisol level between

instantaneous response to noise and after 11 days of exposure in the Eurasian perch (*Perca fluviatilis*). They found an increase in cortisol with first exposure but not after the long period suggesting a habituation effect. A process also found in the Nile tilapia, *Oreochromis niloticus*, exposed to 120-days of boat or urban playbacks, showing an increase in respiratory movements and ventilation (opercular beats and pectoral beats) during the first 30 days followed by a decrease during the remaining 90 days of exposure (Kusku, 2020).

A weaker response to noise can result from two processes, a learning memory process (Bloch et al., 2019) or a resistance to muscular fatigue. Learning would result in associating that noise does not represent a threat and result in a diminution of an animal response to the same stimuli over time (Bejder et al., 2009) what is considered as an habituation process. One field-study was performed in a juvenile coral reef fish (*Dascyllus trimaculatus*) and showed habituation after three weeks of repeated exposure of motorboat noise which is long-term exposure for juvenile fish (Nedelec et al., 2016). Concerning resistance to fatigue, there is no evidence that noise could induce it, but in the literature, fatigue resistance is already known in sonic fish exposed to a repeated stimulus (Winn & Marshall, 1963).

There are only a few studies on repeated noise exposure, but they suggest that habituation to noise is possible, especially with the increase of anthropogenic activities inducing multiple exposures during a species lifetime. Assessing their long-term response would allow us to know how widespread these many documented individual responses are on a broader ecological integration scale.

### **3. Individual responses to noise can propagate to communities**

A substantial part of the literature on the effects of noise pollution focuses on individual responses, but noise can also affect ecological interactions such as predation or competition. Alterations in ecological interactions can cause shift in species abundance and therefore induce change in communities (abundances, compositions). The question here is whether noise is able to alter communities from individual responses. A positive or negative effect on predator behavior could have consequences on prey dynamics and indirect impact on lower trophic levels, further resulting in changes in community structure and species diversity (Chase, 2001; Chesson, 1983), in a process that we call trophic cascading effect (Ripple et al., 2016).

Terrestrial communities received more attention and some studies have shown that noise can generate indirect cascading effects within a community. For example, in the study by Francis et al. (2009), exposure to noise from scattered natural-gas extraction infrastructure on woodlands reduces the nesting species richness whereas it indirectly facilitates reproductive success of individuals nesting in noisy areas as a result of the disruption of predator-prey interactions. In another terrestrial trophic cascade, Barton et al. (2018) showed that urban sound and rock music reduces lady bird predation on soybean aphids leading to higher soybean plant density after 14 days, demonstrating the direct and indirect effects of anthropogenic noise in invertebrates.

However, research on freshwater noise pollution is still underrepresented and especially on community effects for which, to our knowledge, there are no equivalent studies. According to Sordello et al. (2020) research about the effect of noise pollution on aquatic species mainly focuses on fish behavior (n=159 studies) compared to effect on the ecosystem (n=32 studies) which received very little interest. This raises the question of whether individual response to underwater noise pollution can propagate to a larger ecological integration scale as some studied have claimed (Kunc & Schmidt, 2019).

## **IV. Aims of the thesis**

Through this thesis, we aimed at improving our knowledge on the ecological response of freshwater communities to anthropogenic noise, particularly to motorboat noise. To achieve this objective, we decided to (i) focus on trophic interactions, (ii) conduct experiments at different biological integration levels and spatiotemporal scales and (iii) account for the response of invasive species.

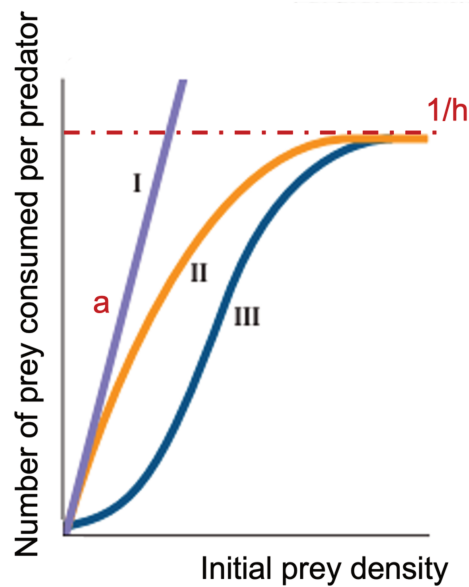
This thesis is organized in three chapters written in scientific paper format (either accepted, submitted, or in preparation), preceded by a synthesis summarizing the main results. The last chapter is a general discussion confronting the results followed by emerging perspectives from my thesis.

## 1. Trophic interactions as an indicator of ecological integrity

Trophic ecology looks at communities through the prism of consumer-resource links. Organisms are distributed across trophic levels with basal species (primary producers), intermediate-level species (herbivores, mesopredators) and top predators that dominate the food chain. Trophic links being the main drivers of matter and energy transfers, they help understand how an ecosystem function relying on Lavoisier's law of conservation matter (nothing is lost, nothing is created, everything is transformed). Energy from feeding allows to regulate individual survival, growth, and fecundity with upscaling effects on population demography (Elser et al., 1987). The strength of trophic interactions quantifies the extent to which a consumer exploits its resource population. Any environmental stressor likely to modulate interaction strength can have important ecological impacts. For these reasons, we decided to focus on trophic links with the aim to better understand the ecological impacts of noise pollution.

The aim of the thesis was to characterize the direct effects of anthropogenic noise on trophic links and the indirect consequences through top-down cascading effects. Trophic ecology offers a range of conceptual and methodological tools to study consumer-resource interactions. The functional response (FR) is one of these tools, which quantifies the consumption rate of a predator as a function of prey density at a given time (Holling, 1959a) (Fig.9). According to Holling (1959a), the FR characterizes feeding behavior and classifies it into three different types: (1) type I where the consumption rate increases linearly with prey density such as in filter feeder organisms (Jeschke et al., 2004); (2) the type II described by a decelerating rise of predation rate with increasing prey density until reaching a plateau (saturation), this type is commonly found in fish predators (Bollache et al., 2008; R. L. Smith, 1997); (3) the type III characterized by an asymptotical sigmoidal curve where predation rate first increases at low prey density and then decreases as prey density increases. Such 'S-shaped' curve can be due to a change in foraging effort with prey concentration commonly found in zooplankton species (Kiørboe et al., 2018) (Fig.9).

The FR tool allows to estimate two key parameters of predation: the **attack rate** (initial slope of the curve) and the **handling time** (inverse of the asymptote). These parameters allow the comparison between populations based on differences in handling time and attack rate (Fig.9).



**Figure 9.** Theoretical functional responses of types I, II, III (Holling 1959) describing the relationship between predator consumption rate and prey density. These functional responses are shown in terms of (a) the number of prey consumed per predator and (b) the proportion of prey consumed per predator. (Adaptation of figure 15.21 of the economy of nature sixth edition).

The FR is used in a broad range of ecological studies such as the effect of climate change, salinization, or biological invasion (Dick et al., 2017; Suárez et al., 2017; Tsoukali et al., 2016). This method has recently been used to assess the effect of anthropogenic noise on terrestrial insect and fish prey-predator relationships. Villalobos-Jiménez et al., (2017) reported decreased magnitude in the FR (lower asymptote due to higher handling time) of larval damselflies (*Ischnura elegans*) towards water fleas under noisy conditions and, more recently, a preliminary study of this thesis showed that motorboat noise decrease attack rate in European minnows (*Phoxinus phoxinus*) foraging on *Chaoborus* sp. larvae, resulting in a less steep initial slope (Hanache et al., 2020).

In Chapters 1 and 2, we empirically characterized and quantified the effects of anthropogenic noise on different aquatic species and their interactions using the FR approach coupled to behavioral measurements to explain the alterations in predation.

More specifically, in **Chapter 1**, we characterized the consequences of a direct exposure to noise (short and long exposure) on predator-prey interactions by assessing the individual FR

of the invasive pumpkinseed sunfish (*Lepomis gibbosus*) and the round goby (*Neogobius melanostomus*) during foraging activity.

Then, in **Chapter 2**, we added social interactions (non-trophic) to assess responses more similar to conditions in the wild. Indeed, the response of an individual can be context-dependent, and the presence of a conspecific or of an enemy can induce changes in foraging strategies. A preliminary study at the origin of this thesis was performed on the effect of motorboat noise exposure on the European minnows (*Phoxinus phoxinus*) feeding on dipteran larvae phantom midge (*Chaoborus* sp.). Boat noise did not induce change in handling time but decreased attack rate and increased social interactions between the predator and a companion fish compared to control condition (Hanache et al., 2020). Noise seems to be able to directly affect different types of interaction, that could lead with long-term exposure to important consequences on the dynamics and stability of ecological communities (Kéfi et al., 2012). Therefore, we characterized pairwise interactions (e.g., competition or aggression) among topmouth gudgeon (*Pseudorasbora parva*) conspecifics sharing the same prey under long-term of noise exposure.

During the FR trials, we recorded fish behaviour through the swimming distance, the distance to the sound source (avoidance) and the distance to visual or physical conspecific to find the behavioural origins of alterations in feeding performance and identify symptoms of a stress response. We supposed that under noise, stress could be manifest through altered swimming distance (either increased or decreased depending on the species) (Voellmy et al., 2014), avoidance of the sound source (De Robertis & Handegard, 2013) and more social interactions (Voellmy et al., 2014). Attack rate is linked to mobility as an increase or a decrease in search area would influence predator-prey encounters. Decreased mobility is therefore expected to decreased attack rate. Under the distraction prey hypothesis, handling time is expected to increase if fish take more time to process their prey, leading to reduced maximum feeding rate and thus a lower FR (see Villalobos-Jiménez et al., 2017). Regarding the three behaviour we recorded, we expected no change related to the reallocation of fish's finite attention to noise.

## **2. From behaviour to communities: upscaling the effects of noise**

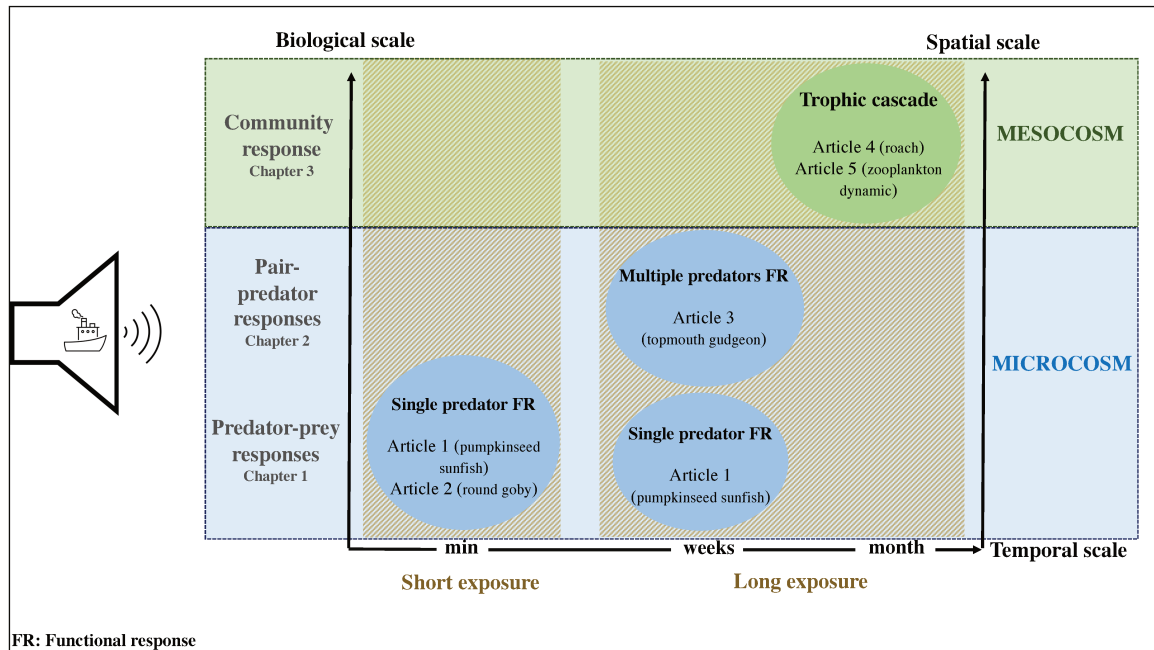
Chapters 1 and 2 will give a good overview of the ecological consequences of noise obtained under controlled environment. Indeed, laboratory designs (microcosms) allow a precise

control of the external factors that could influence the experiment and allow a better observation and assessment of the behavior. In fact, it was found that laboratory observations can be extrapolated to those obtained in the field. For example, the black bullhead (*Ameiurus melas*) exposed to both boat noise and white noise foraged less and startled more in laboratory and wild fishes with differing hearing capabilities exposed to boat noise and a quiet control showed behaviors consistent with the laboratory study (Pieniasek et al., 2020). However, this comparison only depends on the instantaneous responses and don't consider long-term effects. In other scientific domains such as toxicology, contradictory results are often found between laboratory studies and outdoor mesocosms (Mikó et al., 2015). It may thus be questionable whether the extrapolation of results from laboratory studies can inform global ecological problems to long-term noise exposure. Therefore, it is interesting to scale up our laboratory findings to understand community-level responses to freshwater noise pollution.

**In Chapter 3**, we worked on community dynamics at a larger spatial scale but under the same temporal scale (short- and long-term responses), using mesocosms. They are artificial systems designed for controlled experiment and present an alternative to in situ sampling approaches for investigating the effects of potential stressors on aquatic communities (Odum, 1984; Petersen & Englund, 2005). Mesocosms are large structures (the unit of measurement starts at the cubic meter of water) where several species forming a controlled community can interact. The conditions differ from those in the laboratory because some variables cannot be controlled over time such as temperature, sunlight, oxygen content, or the abundance of certain species. Mesocosms are widely used in ecology to study the effect of specific stressors on small communities (Grantham et al., 2012; Lamberti & Steinman, 1993; Ledger et al., 2006; Pearson & Connolly, 2000) and represent ideal structures for the study of noise.

We performed two experiments with mesocosms, the first one tested whether predators' response to noise may propagate downward a three-level trophic chain resulting in structural changes at lower trophic levels. The second experiment was dedicated to the responses of planktonic communities dominated by invertebrate predators in order to better characterize the effect of noise within planktonic communities.

In this thesis we decided to use a multidimension approach (Fig.10) by combining three different dimensions: spatial, temporal, and biological. The first two chapters focused on the effects of short and long-term exposure (temporal scale) on individual responses (biological scale) in aquariums (spatial scale).



**Figure 10.** Overview of the different biological, spatial, and temporal scales studied in this manuscript.

### 3. Freshwater communities are impacted by invasive species

Most of freshwaters are dominated by invasive species so to better extrapolate individual responses to noise, we decided to conduct part of our investigations with invasive species. Some anthropogenic stressors are now known to be highly tolerated by invasive species, compared to native, helping for their invasions. For example, in environments threatened by deoxygenation, the invasive Ponto-Caspian round goby (*Neogobius melanostomus*) showed higher feeding rate than its native analogue the bullhead (*Cottus gobio*) (J. W. E. Dickey et al., 2021). Other stressors were also found to be better tolerated by invasive species, as an elevation of temperature in invasive marine fouling community (Sorte et al., 2010). The introduction of invasive species can have damaging effects on aquatic system of human interest because they can overlap the trophic niches of native species which can lead the restructuration of freshwater food webs (Vander Zanden et al., 1999) and even to the exclusion of native species (Goldschmidt et al., 1993).

Studies on the effects of anthropogenic noise on invasive species have been typically limited to behavioural responses (Graham & Cooke, 2008; Hasan et al., 2018; Pieniasek et al., 2020;



Scholik & Yan, 2002) or, in some case on acoustic communication (Higgs & Humphrey, 2020). Overall, the response of invasive species to noise pollution remains largely overlooked. Thus, we decided to dedicate a large part of the thesis to the direct effect of noise on invasive species. Based on the previous studies and under the tolerance hypothesis, we expected invasive species to display similar responses between control and noise conditions.





# Chapter 1: Investigating how noise can modulate trophic interaction strength using the functional response tool

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Round goby in aquarium



## I. Synthesis

In this chapter, we focused on the effect of noise on foraging responses using the functional response (FR) approach combined to behavioral measurements (mobility, avoidance of noise, social interaction).

We decided to use the FR to characterize the response of two invasive species, pumpkinseed sunfish (*Lepomis gibbosus*) and the round goby (*Neogobius melanostomus*) captured from natural environment to short- and long-term motorboat noise exposure. Considering the strong abilities of invasive species to adapt quickly to environmental changes, we expected similar responses with both noise conditions due to a tolerance effect. We expected repeated exposure to weaken the response to noise suggesting habituation.

Pilot experiments guided us to use a companion fish (visual presence of a congener that cannot interact with predation) to decrease the stress related to a total isolation during tests. We assessed the FR under the ambient noise of their breeding aquarium or under broadcasting of motorboat noise recordings. To help the interpretation of our results if noise was found to influence predation, we measured three behavioral variables: swimming distance, distance to the loudspeaker, distance to the companion fish as proxy of mobility, noise avoidance and social interaction. The experiments involved purchased live prey (larval phantom midge, *Chaoborus flavicans* and the chironomid larvae, *Chironomus plumosus*) that occur in the natural environment of the invasive species to mimic realistic condition.

With the help of Simon Thevenin (master's degree intern) and Gabriella Montes (bachelor's degree intern) we assessed short- (43 min) and long-term (3 weeks) effect of motorboat noise of the invasive pumpkinseed sunfish. For short-term exposure, we observed a decrease in the maximum feeding rate ( $1/h$ ) due to an increase of handling time ( $h$ ). A consistent result with the distracted prey hypothesis (Chan et al., 2010) where noise disrupts cognitive abilities in capturing prey. In the long-term experiment, we pre-exposed fish for three weeks to ambient noise or motorboat noise prior to FR experiments. We obtained similar FR under both noise condition and no significant change in behavior suggesting habituation to noise (Bejder et al., 2009). We also assessed the effect of noise on the anti-predatory defense of the phantom midge prey used to improve the interpretation of the fish response. We observed that short-term exposure to boat noise increased larvae movement (body rotation) compared to ambient

noise, but this was unlikely to influence trophic interaction strength relative to fish behaviour. This study showed that repeated exposure to noise weakens pumpkinseed sunfish response and result in habituation to noise.

In the second experiment we collaborated with two researchers specialized in behavioural ecology and eco-physiology, François-Xavier Dechaume-Moncharmont and Loïc Teulier (Claude-Bernard Lyon 1) respectively, and Marina Fernandez (master's degree intern). We tested the short-term response of one of the most invasive species of Europe the round goby, in the presence or absence of motorboat noise (20 min). Surprisingly, fish showed a higher FR (increased attack rate and maximum feeding rate) under boat noise accompanied by increase in their swimming activity likely favoring encounters with prey. This result suggests that anthropogenic noise is able to exacerbate the impact of an invasive species. However, the decrease in handling time ( $h$ ) was tricky to explain as it usually depends on morphological constraints and it's paradoxical for an organism to do better than in normal conditions. It might be that handling time in our experiment also included other activities (i.e., resting) than prey processing (Li et al., 2018), for which the time dedicated was decreased by noise.

Conclusions of both experiments highlighted two important insights. First short- and long-term responses can be totally different. If one considers only the short-term responses to noise, we will overestimate the negative effect of noise on pumpkinseed sunfish whereas long exposure can lead to habituation. Second, noise is also able to increase predation performance (round goby response), demonstrating the difficulties in generalizing a standard response. Therefore, our results show that conclusion based on individual responses or short-term exposure cannot be scaled up to communities.

## **II. Article 1: From distraction to habituation: ecological and behavioural responses of invasive fish to anthropogenic noise**

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## 1. Abstract

1. Tolerance to human-induced environmental stressors is known to contribute to the spread and success of invasive species but their response to anthropogenic noise has still to be explored. Anthropogenic noise might modulate the trophic impact of invasive species and their competitiveness against native species.

2. We used an ecological approach through the derivation of the functional response (FR) to test whether the strength of the trophic interaction between the invasive Pumpkinseed sunfish and Chaoborus larvae was influenced by motorboat noise, with or without pre-exposure.

3. Boat noise decreased maximum feeding rate in the fish that never experienced boat noise before, resulting in a lower functional response compared to the ambient noise condition. We hypothesized that fish were distracted and reallocated a part of their finite attention to this new acoustic stimulus at the expense of prey processing.

4. The distraction effect weakened with repeated exposure suggesting a habituation process. Although we cannot exclude persistent adjustments in behaviour, we did not find evidence for altered predation.

5. Pumpkinseed sunfish did not exhibit clear symptoms of a behavioural stress response. Chaoborus movements were more numerous under boat noise, but this was unlikely to influence trophic interaction strength relative to fish behaviour. Local species might experience increased trophic competition if they are disturbed and do not habituate contrary to invasive species.

**KEY WORDS:** Anthropogenic noise, habituation, biological invasions, trophic interaction strength, distraction

## 2. Introduction

Freshwater communities worldwide include many exotic invasive species whose spread is facilitated by the increase in shipping for commercial and recreational purposes (Levine & D'Antonio, 2003; Perrings et al., 2005; Reid et al., 2019). Tolerance to human-induced environmental changes like thermal stress (Zerebecki & Sorte, 2011), hypoxia (Lagos et al., 2017), and increased salinity (Ellis & Macisaac, 2009), contributes to the success of invasive species. Among the various threats to freshwater communities (Dudgeon et al., 2006), the degradation of soundscapes concomitant with commercial and recreational activities is considered an emerging threat likely to continue according to Reid et al. (2019). Recently, increased levels of noise resulting from boat traffic were found to have no effect on the natural calling behaviour of round goby (*Neogobius melanostomus*), a highly invasive fish (Higgs & Humphrey, 2020). However, from a broader perspective, the response of invasive species to anthropogenic noise has not received sufficient interest so far to test whether tolerance to noise is a general pattern.

Predation by invasive species was estimated to be associated with a 21% decrease in species richness in aquatic habitats by (Mollet et al., 2017). This trophic impact is likely to be modulated by anthropogenic noise that can mask the acoustic cues used for predator (Kern & Radford, 2016) or prey (Siemers & Schaub, 2011) recognition, or be interpreted as a threat and induce a shift from feeding to stress responses with typical behavioural and physiological symptoms (Cox et al., 2018; Wysocki et al., 2006). Under the distraction hypothesis, predators can take longer to process their food and make foraging errors (Purser & Radford, 2011) while prey can increase (Rabin et al., 2006; Voellmy et al., 2014) or decrease (Chan et al., 2010; Simpson et al., 2015) their vigilance. In some species, the response to noise was found to weaken after repeated exposure (Gallego-Abenza et al., 2020; Johansson et al., 2016; Magnhagen et al., 2017; Mooney et al., 2016; Nedelec et al., 2016), suggesting they can habituate to noise. Tolerance and habituation to anthropogenic noise in invasive species might make them more competitive than their native analogues, thereby promoting their trophic impact.

In the present study, we tested whether the feeding performance of the invasive pumpkinseed sunfish *Lepomis gibbosus* was altered by repeated exposure to motorboat noise. We also recorded fish behaviour through the swimming distance, the distance to the sound

source and the distance to conspecific, to find the behavioural origins of alterations in feeding performance and identify symptoms of a stress response. Pumpkinseed sunfish is a North American centrarchid that has established self-sustaining populations in at least 28 countries across Europe and Asia Minor (Copp et al., 2017; Copp & Fox, 2007). It can exhibit fast lifestyles (i.e. rapid growth and maturation, strong investment in gonads) with age at maturity ranging from 1 to 2.8 years and total length at maturity from 60 to 95 mm in populations from north-western Europe (Cucherousset & Olden, 2011). Mesocosm experiments demonstrated that native fish coexisting with pumpkinseed show alterations in their trophic niches and growth rates (Copp et al., 2017). In the field, the presence of *L. gibbosus* has been linked to declines in macroinvertebrate abundances (García-Berthou & Moreno-Amich, 2000), while aggressive behaviours towards native fish and crayfish have been recorded (Almeida et al., 2014). Pumpkinseed sunfish tolerate hypoxia (Farwell et al., 2007), thermal stress (Rooke et al., 2017), and salinity (Venâncio et al., 2019), but, although they are capable of perceiving and emitting sounds (Ballantyne & PW, 1978; Wysocki et al., 2006; Wysocki & Ladich, 2005), their susceptibility to anthropogenic noise remains unknown.

Feeding performance was assessed through the derivation of the functional response: the relationship between resource use and resource density (Holling, 1959a; Solomon, 1949), whose shape and magnitude provide information on trophic interaction strength and predator foraging behaviour. Functional response magnitude corresponds to the maximum feeding rate and was found to correlate positively with the documented field impacts of some predatory invertebrates (Dick et al., 2013). It allows the estimation of the handling time  $h$ : the average time spent on a caught prey item, which is usually allocated to subduing and ingestion, as the predator is at saturation (Holling, 1959a). Functional response (FR) shape informs us about predator–prey stability: decelerating FRs (type II) are expected to promote unstable boom–bust population dynamics and therefore to be more destabilising than sigmoidal FRs (type III), which offer low-density refugia for prey (Gentleman & Neuheimer, 2008; Juliano, 2001; Kalinkat et al., 2013; Murdoch & Oaten, 1975). The FR curve's initial slope allows the estimation of the attack rate  $a$ , which is the instantaneous rate of searching for prey and defines the consumption rate at low prey densities (the higher the attack rate, the steeper the initial slope).

Although widely used in community ecology, predation theory, and, more recently, invasion biology (Dick et al., 2014), the FR approach has been, to our knowledge, used only twice in the field of noise pollution. Villalobos-Jiménez et al. (2017) reported decreased

magnitude in the FR of larval damselflies (*Ischnura elegans*) towards water fleas under noisy conditions and, more recently, motorboat noise was found to decrease attack rate in European minnows (*Phoxinus phoxinus*) foraging on *Chaoborus* sp. larvae, resulting in a less steep initial slope (Hanache et al., 2020). We expected to find type II (i.e. decelerating) FRs, the FR type usually displayed by fish in shelter-free experimental arenas (Alexander et al., 2014, 2015; Hanache et al., 2020; Lavery et al., 2017). Under noise, stress could manifest itself through behaviour with altered swimming distance (either increased or decreased depending on the species, Voellmy et al., 2014), avoidance of the sound source (De Robertis & Handegard, 2013) and more social interactions (Voellmy et al., 2014). Any reduction in mobility and search area would decrease predator–prey encounters and therefore attack rate, resulting in a less steep FR (see Hanache et al., 2020). Under the distraction hypothesis, handling time should increase if fish take more time to process their prey, leading to reduced maximum feeding rate and thus a lower FR (see Villalobos-Jiménez et al., 2017). Regarding the three behaviors we recorded, we expected no particular change related to the reallocation of fish's finite attention to noise. In case of tolerance to noise, we expected no alteration in behaviour and FR with the pumpkinseed sunfish that experienced repeated exposure to motorboat noise.

### **3. Methods**

#### 1. Animal collection

In March 2019, 160 pumpkinseed sunfish (body length =  $8.47 \pm 0.64$  cm) were collected with electrofishing from the leisure base lake of Saint-Pierre-de-Boeuf (45°22'54.48"N, 4°45'73.07"E, Loire, France), which is connected to the Rhône river and where only non-motorised boats are permitted. We did not distinguish between males and females, and we had no egg-carrying females.

#### 2. Conditioning to noise

##### 2.1 Setup

Fish were transported in aerated fish containers to a breeding room of the ENES laboratory thermoregulated at 17°C with a 12:12 light:dark regime and randomly allocated to four 110-L Aquariums (40 fish each) filled with dechlorinated tap water and containing a 2-cm layer of Loire sand (Aquasand Nature, Zolux déco), artificial plants, an air stone connected to an external air pump and the output of an external filtering system (Tetra EX 600). An underwater speaker (Electro-Voice UW30, 0.1–10 kHz) was inserted in the middle of a black foam rubber panel (15-mm thick) covering one of the two ends of the aquarium (Figure S1a). During 25–32 days, which corresponds to a prolonged exposure period following Johansson et al. (2016), half of the fish (2 aquariums) were conditioned to motorboat noise while the other half experienced the ambient noise of their aquarium, with the speaker turned on and broadcasting silence (see section 2.2.2). Fish were fed daily with commercial fish pellets instead of real prey to remove potential search images that they might have developed and that might beget variability in the results.

To standardise hunger, fish were starved for 24 hr prior to FR experiments, starved fish (five fish per aquarium per day) being isolated from the others using a plastic canvas fixed at the opposite side of the speaker. Live *Chaoborus* sp. larvae (Diptera, Chaoboridae) purchased from a commercial supplier ([www.aquap.lante.fr](http://www.aquap.lante.fr)) and stored in a fridge at 8°C were used as prey. *Chaoborus* larvae can be found in the diet of pumpkinseed (Wolfram-Wais et al., 1999) and they have been used in previous FR experiments (Hanache et al., 2020; Médoc et al., 2013, 2015), which promotes comparison of results.

## 2.2. Audio tracks

Audio tracks were generated, and the sounds modified using Audacity® Software 2.2.1. All recordings were made with an Aquarian Audio H2A-HLR hydrophone (frequency response from 10 to 100 kHz) connected to a ZOOM H4next Handy recorder. For fish conditioned to ambient noise, a 1 hr audio track of silence was looped continuously so that fish experienced the soundscape of their community aquarium. For fish conditioned to motorboat noise, we used 15 original recordings made in September 2018 by V. Médoc in the Grangent lake (45°45'07.54"N, 4°25'56.47"E, Loire, France) at 1-m depth and corresponding to small recreational boats with outboard engines passing at various distances. From these 15 original files, we created 75 boat sounds (5 per original signal) by changing the amplitude and applying a linear fading on both ends to make them emerge from silence. The relative

importance in decibel (dB) of these sounds over the ambient noise of the aquarium was quantified using the signal-to-noise ratio (SNR) function of the seewave R package (Sueur et al., 2008):

$$SNR = 20\log_{10}(RMS_{boat\ noise} / RMS_{ambient\ noise})$$

where RMS corresponds to the root-mean-square sound pressure of either the re-recordings of the boat sounds in the aquarium with all the devices turned off (except the speaker), or the recording of ambient noise with all the devices turned on. On average, ambient noise level in the aquariums used for conditioning was 95 dB RMS sound pressure level with all the devices turned on and the SNR values of the various boat sounds ranged from 4.81 to 27 dB (Table S1), corresponding to what can be found in the lake of a small leisure base (V. Médoc, personal observations).

Finally, the 75 different boat sounds were duplicated, and the resulting 150 sounds were randomly allocated to nine consecutive audio tracks of 1 hr of silence, with varying intensities between tracks (from six to 25 boats per hour, Table S1) to mimic the daily activity of a small leisure base. Boat sounds were randomly positioned along the 1-hr tracks and in case of overlap, we spaced the consecutive sounds of a few seconds. Each day of the conditioning period, fish were exposed to motorboat noise from 9 a.m. to 6 p.m. and silence was broadcasted the rest of time. Tracks were played back as stereo WAV files using, for both aquariums of the same conditioning, a ZOOM recorder, an amplifier (Dynavox CS-PA 1MK), and two UW30 speakers (one per aquarium).

### 3. Functional response experiments

Briefly, 96 predation tests were undertaken as we tested six prey densities with four replicates of each, run for the two pre-exposure conditions (ambient and boat noise) and two noise conditions during foraging (ambient and boat noise again). We added two replicates per noise condition at the highest prey density without fish to be sure that *Chaoborus* mortality was due to fish predation. The whole investigation therefore included 100 trials distributed in a quasi-systematic way over 10 consecutive days (10 experiments per day) to balance the effect of time. Further details are given below.

### 3.1. Setup

Experiments took place in a room thermoregulated at 17°C. One single pumpkinseed starved for 24 hr was placed in a glass aquarium (60 cm long × 30 cm wide × 32 cm high) filled with 50 L of filtered and aerated dechlorinated tap water (28-cm water height) and containing a 2-cm layer of Loire sand (Aquasand Nature, Zolux déco, Figure S1b,c). An underwater speaker (Electro-Voice UW30, 0.1–10 kHz) broadcasting either ambient noise or ambient noise supplemented with boat noise was inserted in the middle of a black foam rubber panel (15-mm thick) covering the left end of the aquarium, such that the center of the speaker was 11 cm below the water surface. At the opposite (right) end, we placed another rubber panel 8 cm from the wall with a hydrophone behind (Aquarian Audio H2A-HLR Hydrophone, frequency response from 10 to 100 kHz) connected to a ZOOM H4next Handy recorder to control the sound signal during the experiments. To promote normal behaviour in pumpkinseed which are gregarious (Blanckenhorn, 1992), we placed a plastic tube (11.5 cm diameter) allowing visual communication only in the middle of the aquarium with a companion fish inside, used only for this purpose and coming from the same community aquarium as the focal fish (i.e. same conditioning treatment). To isolate the experiments from external sounds, we placed the aquarium inside an acoustic box (silent box, 89 cm long × 78.5 cm wide × 75 cm high) with acoustic foam covering the inner surface, a diffuse light source centered on the aquarium 34.5 cm above the water surface (185 lux light intensity at the water surface, Light Meter for Apple devices), one camera (HD-TVI ABUS TVVR33418) facing the aquarium, and another one above to record behaviour. The experimental setup (aquarium + silent box) was duplicated to run two experiments concurrently.

### 3.2. Experimental design

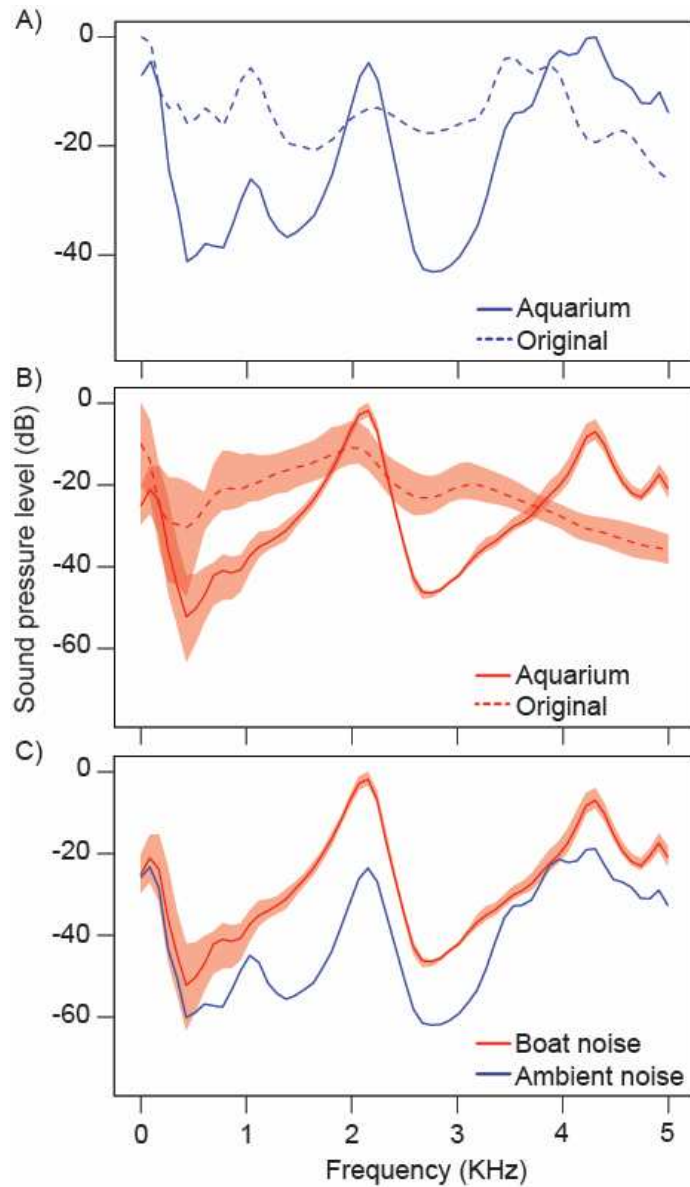
After a 30-min acclimatization period of ambient noise, experiments started with the introduction of *Chaoborus* larvae at a single time using a 250-ml glass beaker trying to cover the whole aquarium to homogenize prey distribution. Based on our previous investigations (Hanache et al., 2020) we fixed the duration of the experiment at 43 min and tested six initial prey densities:  $N_0 = 8, 16, 32, 64, 128$  and  $256$ , with four replicates per density ( $n = 4$ ). These densities were expected to saturate the predator (high densities) and promote discrimination between types II and III FRs (low densities), while the duration was not sufficient to reach predator satiation. At the end of each experiment, the fish were gently removed with a hand

net, measured for fork length and returned to their respective community aquarium to keep fish density constant. We clipped a small part of the tail fin to avoid reuse. Because we had not enough companion fish to use them once, some of them (randomly chosen) were used in two consecutive feeding trials before returning to their aquarium. Remaining live Chaoborus larvae were counted and removed, and water was changed every two experiments to remove the chemical signals that fish might have released. At the end of the whole investigation, and because *L. gibbosus* is invasive in France, all the fish were sacrificed using MS-222.

### 3.3. Audio tracks

For fish foraging under ambient noise, we used a track of 73 min of ambient noise to encompass the 30-min acclimatization period and the 43-min foraging period. Ambient noise was recorded in the middle of one of the four community aquariums used for conditioning and calibrated to have the same RMS sound pressure when re-recorded in the middle of the two aquariums used for FR experiments. For fish foraging under motorboat noise, we added 24 boat sounds to the 43-min foraging period of the ambient noise track. They were randomly chosen from the 75 boat sounds (see above) and distributed over six consecutive noise sequences (from two to six consecutive boat sounds per sequence, without overlap) separated by a few minutes of ambient noise. Each boat sound was re-recorded and calibrated to fall in the same range of SNR values than for the conditioning (Table 1 and see Figure 1 to compare the spectral properties of the two noise treatments). Tracks were played back using, for each experimental setup, an audio player (VLC media player 1.1.8), an amplifier (Dynavox CS-PA1MK), and a UW30 speaker. As we used two experimental setups to reduce the time needed to do all the FR experiments, we alternated the noise conditions (ambient or boat noise) between the two setups to balance the experimental setup effect.





**Figure 1:** Spectral density of the audio signals used for the functional response experiments in the frequency range up to 5 KHz where most of the freshwater fish detect sounds. Original signals (discontinuous lines) are compared to their re-recordings in the experimental aquarium (solid lines) for the ambient noise (A) and boat noise (B) conditions. Both noise conditions are also compared to each other (C). Shaded areas delimit the min and max values from the six noise sequences over which the boat sounds were distributed (see main text)

**Table 1:** Composition of the 73-min playback track broadcasting ambient noise supplemented with boat noise during the functional response experiments (see text for further detail).

Noise sequence <sup>1</sup>	Start position	Boat IDs (duration in sec)	SNRs (dB) <sup>2</sup>
1	34'15''	21(33); 48(20); 15(36); 65(28); 56(34); 28(35)	13.2; 18.4; 15.5; 23.4; 23.7; 21.1
2	42'30''	5(70); 17(47); 29(35); 40(38)	20.5; 24.3; 21.3; 17.4
3	49'50''	66(110); 1(70)	24.4; 25.4
4	56'38''	44(67); 46(20); 24(33); 53(60)	18.1; 21.1; 4.6; 20.2
5	62'26''	7(14); 41(67); 69(110)	18.9; 23.7; 18.5
6	70'36''	61(28); 33(60); 71(101)	15.9; 24.3; 20.1

<sup>1</sup>Boat sounds were distributed over six consecutive noise sequences of approximately three minutes.

<sup>2</sup>Signal-to-Noise Ratio quantifying the difference in dB between a boat sound and ambient noise when re-recorded in the experimental aquarium.

### 3.4. Behavioural responses

Fish behaviour was recorded for 3 min during each of the six successive noise sequences, and on the same time intervals for individuals experiencing ambient noise. We measured the swimming distance by visual tracking using Mousotron 12.1 (Blacksun Software), a video player (VLC media player 1.1.8) and the above camera. Social interactions and noise avoidance (RMS sound pressure decreased with distance to the speaker, results not shown) were assessed every 15 s (12 values per 3 min of recording) by measuring the distances to the companion fish (head-to-head) and to the speaker, respectively, with the front camera and the PixelStick application (for Apple devices). These behavioural responses determine how the

fish use their space and can therefore be related to attack rate, which fixes FR curve's initial slope.

*Chaoborus* behaviour was recorded using the experimental setup of the FR experiments (with the plastic tube of the companion fish removed) but in a separated investigation because the resolution of the cameras was not high enough to detect the larvae. We introduced one single larva in the middle of the aquarium and played back the 43-min foraging period of either the ambient noise track or the boat noise track ( $n = 30$  replicates per noise condition). Through the door of the silent box open, we continuously observed the larva on the same 3-min recording periods as for fish (see above) and encoded two types of movements in the BORIS software (7.4.14, Friard & Gamba, 2016): single body rotations and sequential body rotations, the latter resulting in larger displacements and can be viewed as an escape response (Burrows & Dorosenko, 2014).

### 3.5. Statistical analyses

We used the R software (version 3.5.1, R Core Team, 2018) with a significance level of 0.05 for all the statistics. We performed a one-way ANOVA followed by Tukey HSD test to detect heterogeneity in fish size between the four experimental groups (2 conditionings  $\times$  2 treatments) as the normality and homoscedasticity assumptions were met (Wilk–Shapiro and Bartlett tests, all  $p > 0.05$ ).

Functional response analysis was done with the *frair* package (Pritchard et al., 2017). The three types of FR (linear type I, Rogers' type II, Hassel's type III) were modelled by maximum likelihood estimation (Bolker, 2008) with the *frair\_fit* function and the fits were compared using the second-order Akaike information criterion (AIC). This allowed us to exclude the type I FR whose AIC value was always the highest ( $\Delta AIC > 2$  with the types II and III). To then decide between the type II and type III FR models whose AIC values were close, we used the *frair\_test* function that fits a polynomial logistic function to the proportion of prey eaten, which is more able than a non-linear curve to detect the subtle difference in curve shape between the two models at low prey densities (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). We then modelled by maximum likelihood estimation (Bolker,

2008) the appropriate model with the *frair\_fit* function. Because the appropriate model was always of type II, we used the Random Predator Equation (Rogers, 1972, *fr\_rogersII* in *frair*) which is a modified version of the Holling's original type II model dedicated to non-replacement experiments. The number of prey eaten ( $N_e$ ) follows the relationship:

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

where  $N_0$  is 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, *lambertW0* function from the *lamW* package).

Because all the FRs were of the same categorical form (type II), it was possible to use the delta method implemented by the *frair\_compare* function to perform pairwise FR comparisons from estimated parameters, with the null hypothesis that the differences in attack rates ( $Da$ ) and handling times ( $Dh$ ) between the two FRs do not differ from zero (Pritchard et al., 2017). In addition to the delta method, we also inspected how the 95% confidence intervals (CIs) overlapped. Multiple estimates of the FR curves and parameters were obtained by non-parametric bootstrapping ( $n = 2,000$ ) with the *frair\_boot* function. As recommended by Pritchard et al. (2017), we used bias corrected and accelerated intervals (BCa) to account for the bias and skew as well as the bounded nature of the estimated parameters ( $a$  and  $h > 0$ ). Because the delta method detects differences at extreme prey densities ( $Da$  for low densities and  $Dh$  for high densities), differences at intermediate densities were addressed by visual comparison of the entire FR curves after plotting empirical estimations of the BCa intervals with the *drawpoly* function.

We employed model averaging and an information-theory approach to analyze fish behaviour. Linear mixed-effect models were used to model each of the three Box-Cox transformed response variables (swimming distance per 3-min recording, average distances to the companion fish and to the speaker obtained from the 12 measures taken during the 3-min recordings) as a function of *Pre-exposure Noise* (*i.e.* the noise condition during the pre-exposure period with ambient noise as control), *FR Noise* (*i.e.* the noise condition during FR derivation with ambient noise as control), *Time* (implemented as the start position of the first boat sound for each noise sequence), *Prey density*, *Fish size* and taking individual fish as random factor. We also included a *Pre-exposure Noise* x *FR Noise* interaction to detect whether the behavioural response to boat noise changed after pre-exposure, and a *Noise* x *Time* interaction as the trend in fish behaviour during the course of the FR experiment was

part of within-individual variation and might have changed under the effect of noise. Predictors being on different scales, they were centred and standardized following the approach of Gelman (2008) to better interpret the relative strength of parameter estimates (*standardize* function from the *arm* package, Gelman et al., 2018). We then used the *dredge* and *get.models* functions of the *MuMIn* package (K. Barton, 2009) to generate respectively the full set of submodels from the global model, ranked based on small sampled-corrected AIC values (AICc), and a confidence set of models with a cut-off of  $10AIC_c$ , a conservative threshold suggested by Bolker et al. (2009). Model averaging was performed on the confidence set with the *model.avg* function of the *AICcmodavg* package. To interpret parameter estimates, we looked at their magnitude and most importantly if their 95% CI included the value of zero, indicating no significant effect.

Concerning *Chaoborus* behaviour, we performed a Wilcoxon – Mann-Whitney test to compare the number of movements between the two noise conditions as data did not meet the normality and homoscedasticity assumptions (Wilk-Shapiro and Bartlett tests, all  $P < 0.01$ )

### 3.6. Ethical notes

Pumpkinseed sunfish capture and transport were approved by the Direction Départementale des Territoires de la Loire (DDT 42). All the procedures were conducted in accordance with appropriate European (Directive 2010/63/EU) and French national guidelines, permits and regulations regarding animal care and experimental use (Approval n°C42-218-0901, Direction Départementale de la Protection des Populations de la Loire, Préfecture du Rhône).

## **4. Results**

All the *Chaoborus* larvae survived in the replicates without fish, suggesting that death or removal during FR experiments resulted from fish predation. There was no significant difference in fish length between the four experimental groups (One-way ANOVA:  $F_{3,92}=2.649, P=0.091$ ).

All the logistical regressions returned significant negative first order terms, indicating that type II was always the appropriate FR model (Table 2).

**Table 2:** First order linear coefficients from logistic regressions fitted to the proportion of *Chaoborus* larvae consumed by the invasive Pumpkinseed sunfish (*Lepomis gibbosus*) with or without boat noise (treatment), and conditioned or not to boat noise. All linear coefficients indicate a type-II functional response.

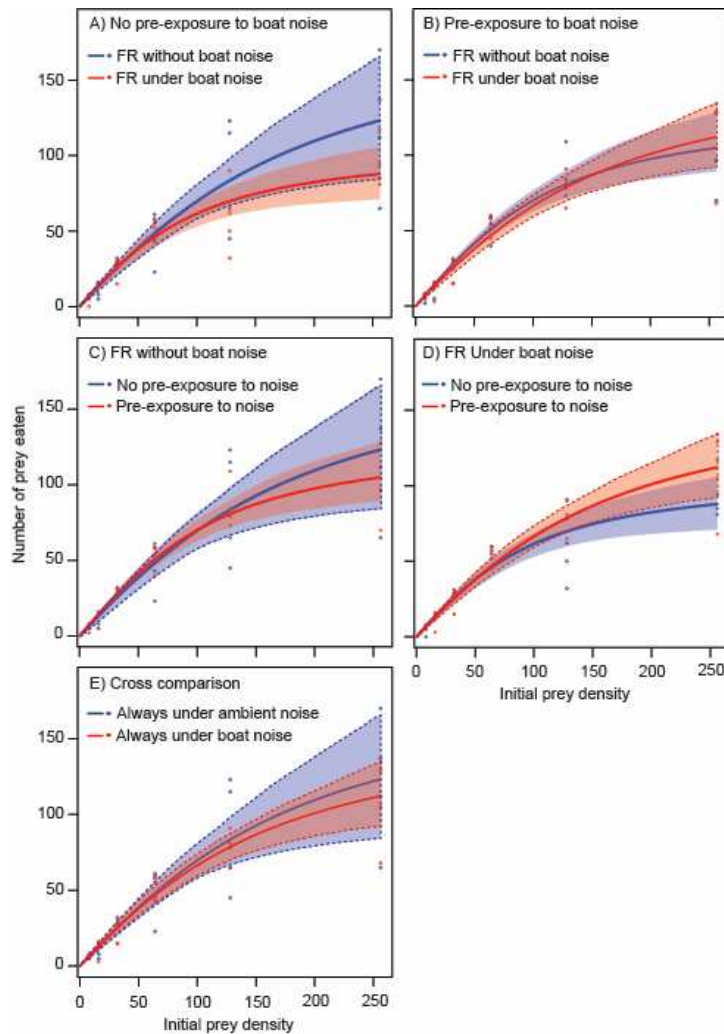
Conditioning	Treatment	Linear coefficient (1 <sup>st</sup> order) [SE]	P value
Ambient noise	Ambient noise	-0.0072 [0.0006]	<0.001
Ambient noise	Boat noise	-0.0077 [0.0005]	<0.001
Boat noise	Ambient noise	-0.0089 [0.0006]	<0.001
Boat noise	Boat noise	-0.0067 [0.0005]	<0.001

The results of the delta method used for pairwise FR comparisons are summarized in Table 3.

**Table 3:** Pairwise functional response (FR) comparisons for the invasive Pumpkinseed sunfish (*Lepomis gibbosus*) feeding on *Chaoborus* sp. larvae with or without boat noise (treatment), and conditioned or not to boat noise.

FR curve 1		FR curve 2		D	Estimate	SE	z	P
Conditioning	Treatment	Conditioning	Treatment					
Ambient	Ambient	Ambient	Boat	Da	-0.44	0.31	-1.419	0.156
				Dh	-0.003	4E-04	-5.953	<0.001
Boat	Ambient	Boat	Boat	Da	1.008	0.308	3.272	0.001
				Dh	0.001	4E-04	2.562	0.01
Ambient	Ambient	Boat	Ambient	Da	-0.937	0.309	-3.037	0.002
				Dh	-0.002	3E-04	-4.191	<0.001
Ambient	Boat	Boat	Boat	Da	0.511	0.309	1.651	0.098
				Dh	0.002	5E-04	4.568	<0.001
Ambient	Ambient	Boat	Boat	Da	0.071	0.249	0.286	0.775
				Dh	-0.0005	4E-04	-1.466	0.143

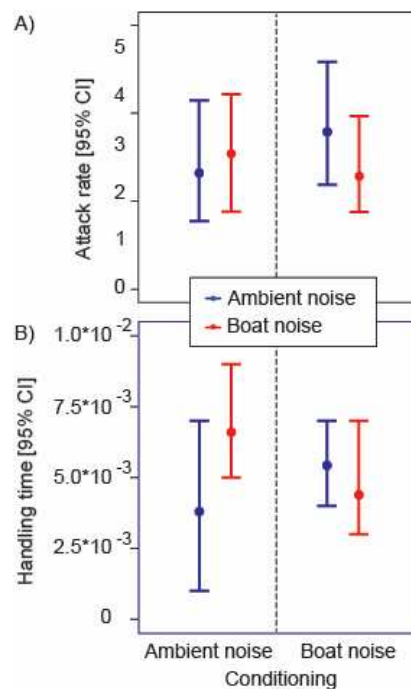
When conditioned to ambient noise, fish showed no difference in attack rate, but handling time was significantly longer under boat noise compared to ambient noise (Table 3), resulting in a lower FR (Fig. 2.A).



**Figure 2.** Number of prey eaten as a function of prey density (functional response: FR) for Pumpkinseed sunfish (*Lepomis gibbosus*) feeding on dipteran larvae (*Chaoborus* sp.). The FR derived under boat noise (red) was compared to that obtained under ambient noise alone (control, blue) in fish that never experienced boat noise before (A) or in pre-exposed fish (B). The FR derived with fish pre-exposed to boat noise (red) was compared to that obtained with fish that never experienced boat noise before (control, blue) when feeding without boat noise (C) or under boat noise (D). Dots are direct observations; curves are the fits of the functional responses and shaded areas represent bootstrapped ( $n = 2,000$ ) 95% confidence intervals. Discontinuous lines show the curves used to compare the FRs between fish having experienced the same noise condition during both conditioning and functional response experiments (E).

With pre-exposure to boat noise, both handling time and attack rate were found lower under boat noise using the delta method (Table 3), but overlap was high between the two FRs (Fig. 2.B). When feeding under ambient noise, fish pre-exposed to boat noise had higher attack rate and handling (Table 3). Although the resulting decrease in FR asymptote was visible, overlap was high between the two FRs (Fig. 2.C). When feeding under boat noise, fish pre-exposed to boat noise showed similar attack rate but lower handling time (Table 3), leading to an upper asymptote (Fig. 2.D). The FR of fish pre-exposed to boat noise and foraging under boat noise was fully nested in that of fish always exposed to ambient noise (Fig. 2.E) and consistently, there was no significant difference in handling time and attack rate (Table 3). Visual inspection of the entire FR curves did not suggest differences at intermediate prey densities that would not have been detected by the delta method (Fig. 2).

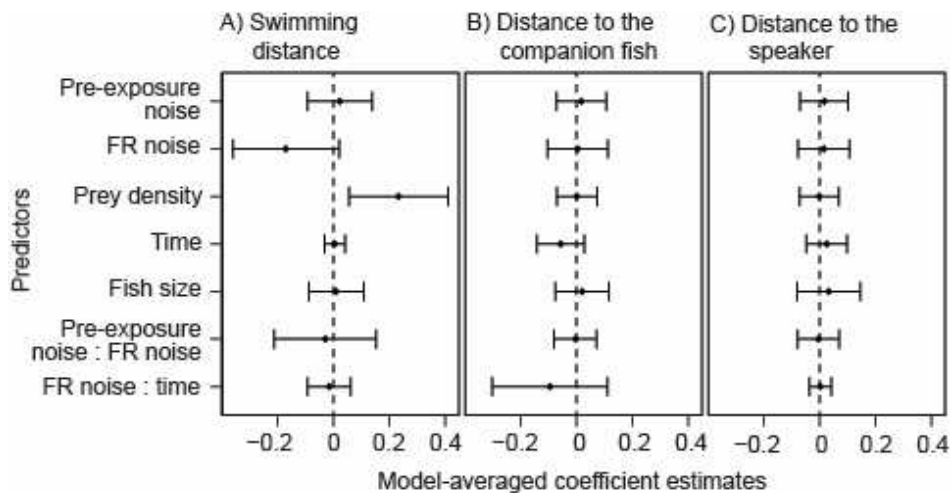
The BCa 95% CIs of the parameter estimates largely overlapped between the noise conditions (Fig. 3) except for the handling time of fish conditioned to ambient noise (Fig. 3.B).



**Figure 3:** Estimates of the functional response parameters: attack rate (A) and handling time (B) for Pumpkinseed sunfish (*Lepomis gibbosus*) feeding on dipteran larvae (*Chaoborus* sp.) under two noise conditions: ambient noise alone (control, in blue) or supplemented with motorboat sounds (in red) and conditioned or not to boat noise. Error bars are bootstrapped ( $n = 2,000$ ) confidence intervals (CI).

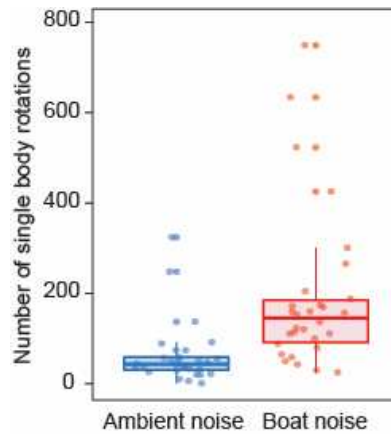


The results of model averaging for fish behaviour are depicted in Fig. 4. We excluded three fish from the analysis ( $n = 93$ ) because the video recording system crashed during the FR experiment. None of the predictors had any significant effect on the distances to the companion fish and to the speaker. The swimming distance was positively affected by initial prey density and tended to decrease with exposure to boat noise during foraging.



**Figure 4:** Model-averaged coefficient estimates and 95% confidence intervals for the predictors included in the confidence set of models explaining the behaviour of the invasive Pumpkinseed sunfish (*Lepomis gibbosus*) when feeding on *Chaoborus* larvae during functional response (FR) experiments. Predictors correspond to the noise condition during the pre-exposure period (*Pre-exposure noise*, with boat noise as treatment and ambient noise as control), the noise condition during FR derivation (*FR noise*, with boat noise as treatment and ambient noise as control), initial prey density (*Prey density*), time, fish size and two interactions. Results are shown for three response variables: the swimming distance (A), the distance to the companion fish (B) and the distance to the speaker (C).

Over the 7,574 *Chaoborus* movements recorded, only 32 were sequential body rotations and they were all observed under boat noise. Single body rotations were significantly more numerous with boat noise than with ambient noise (Wilcoxon – Mann-Whitney test:  $W=761$ ,  $P<0.01$ , Fig. 5).



**Figure 5:** Number of single body rotations displayed by the dipteran larvae *Chaoborus* sp. under two noise conditions: ambient noise alone (control, in blue) or supplemented with motorboat sounds (in red)

## 5. Discussion

Predation by invasive species is a main driver of biodiversity loss in aquatic habitats (Mollot et al., 2017). Human-induced environmental changes are likely to modify the strength of trophic interactions and may therefore substantially modulate the ecological impact of invasive species (see Alexander et al., 2015 for the role of habitat simplification). Using the FR approach to quantify interaction strength, we found a negative effect of motorboat noise on the maximum feeding rate of the invasive pumpkinseed sunfish *Lepomis gibbosus* that had never experienced motorboat noise before.

Interestingly, this decrease in maximum feeding rate was not observed with fish previously exposed to boat noise for several days, suggesting a form of tolerance through habituation. Whatever the experimental conditions, we always found type-II FRs where predation rate increases at a decelerating rate to an upper asymptote, which is consistent with our expectation based on the FR displayed by other fish species foraging on dipteran prey in shelter-free experimental arenas (Boets et al., 2019; Hanache et al., 2020; Laverty et al., 2017). This does not preclude the FR to be of type III with other prey species or in more complex environments where predator's efficiency at low prey densities can be decreased by predator learning, the presence of alternative prey or predator-free areas (Barrios-O'Neill et al., 2015; Croy & Hughes, 1991; Médoc et al., 2018). Adding boat sounds to ambient noise

decreased the maximum feeding rate of the fish that had never experienced boat noise before, resulting in a lower FR. Maximum feeding rate being the reverse of handling time, this means that the fish took longer to process the dipteran larvae. The levels at which we played back the boat sounds (roughly from 100 to 122 dB re 1  $\mu$ Pa SPL) were moderate and naturally-occurring sound pressure levels (Wysocki & Ladich, 2005) and we did not observe any behaviour such as aversion for the sound source (De Robertis & Handegard, 2013) that might be expected in case of pain or physical damage.

Alterations in the morphological and anatomical features involved in prey processing were therefore unlikely, and an alternative explanation might come from the cognitive perspective. Under the distraction hypothesis (Chan et al., 2010), the fish might have reallocated their finite attention to the acoustic cue at the expense of prey processing (Chan & Blumstein, 2011). When prey are scarce (i.e. left of the FR curve), predation rate is not determined by handling time but rather by the activity of searching, estimated by the attack rate and that seemed to be not affected by boat noise. It might also be that overall stimulation by prey and boat sounds together did not exceed what the fish could process, explaining why the distraction effect was less perceptible at low prey densities. Attentional deficits seem to be common under anthropogenic noise, leading to wrong decisions or non-optimal behaviors with potential consequences on fitness. Among aquatic organisms, sticklebacks (*Gasterosteus aculeatus*) show more unsuccessful attacks and discrimination errors between food and non-food items after a brief exposure to white noise compared to a silent control (Purser & Radford, 2011). More recently, motorboat noise was found to disrupt the behavioural response to olfactory alarm cues in the fathead minnow *Pimephales promelas* (Hasan et al., 2018) and shell assessment in the European hermit crab *Pagurus bernhardus* (Tidau & Briffa, 2019).

The FR curves of pumpkinseed sunfish pre-exposed to boat noise largely overlapped between the two noise conditions, resulting from two simultaneous causes: compared to non-pre-exposed fish, they showed a shorter handling time (leading to a higher asymptote) under boat noise but a tendency for a longer handling time (leading to a slightly lower asymptote) under ambient noise. The shorter handling time under boat noise might suggest that repeated exposure to boat noise has weakened the distraction effect. There is increasing evidence that some species can tolerate anthropogenic noise (Holmes et al., 2017; Jacobsen et al., 2014; Johansson et al., 2016; Nedelec et al., 2016; Neo et al., 2018). In Lake Malawi, cichlids from

low-disturbance sites had higher oxygen-consumption rates in response to motorboat noise than cichlids of the same species from highly disturbed sites (Harding et al., 2018).

In our study, the weakening response to boat noise (what we call habituation) might have resulted from learning that the acoustic stimulus did not have any detrimental consequence and not from adaptation through selection over generations as it could be in field investigations. The small increase in handling time of pre-exposed fish foraging under ambient noise might suggest persistent effect of repeated exposure on prey processing. Repeated exposure to noise did not induce any change in swimming distance, distance to the speaker or to the companion but further investigations are needed to rule out physiological alterations or other behavioural adjustments that we might have missed. The absence of stress response could for instance be assessed by the quantification of cortisol release in the water (Wysocki et al., 2006).

The swimming distance of foraging pumpkinseed sunfish tended to be decreased by boat noise, a result to be confirmed with additional experiments in large enclosures or ideally free-ranging fish (Jacobsen et al., 2014). Reduced mobility in response to anthropogenic noise is often interpreted as an anti-predatory response, which could also be triggered by predation risk (Frid & Dill, 2002). Pumpkinseed sunfish did not move away from the sound source and did not come closer to the companion fish in response to boat noise. So, from the three behavioural metrics recorded, we did not find evidence for a significant noise-induced alteration in the spatial pattern of prey searching. This is consistent with the lack of strong variation in the attack rate parameter, leading to FRs with close initial slopes between the noise conditions. By contrast, the native European minnow *Phoxinus phoxinus* exposed to boat noise for the first time displayed behavioural symptoms of a stress response with altered mobility and reduced distance to the companion fish. Accordingly, the initial slope of FR curve was less steep with boat noise than under ambient noise (Hanache et al., 2020).

*Chaoborus* larvae made significantly more body rotations in the presence of boat noise, which is not surprising given that they have particle-velocity sensitive mechanoreceptors (Giguère & Dill, 1979). Although this might influence their vulnerability to predation, making them more conspicuous or harder to handle, the contribution of *Chaoborus* behaviour relative to fish behaviour in the strength of the trophic interaction seems to be little. Non-pre-exposed fish indeed differed in their maximum feeding rate between ambient noise and boat noise, and we would expect the same difference with pre-exposed fish if it resulted only from the noise-

induced movements of the *Chaoborus* larvae. Our findings provide additional support that invertebrates, as well as vertebrates, may be sensitive to noise pollution (Morley et al., 2014; Solé et al., 2016; Villalobos-Jiménez et al., 2017; Wale et al., 2019), a topic that deserves more attention given the ecological processes within which they are embedded (e.g. leaf-litter breakdown, nutrient recycling, see Solan et al. (2016)). *Chaoborus* larvae are ubiquitous predators of crustacean zooplankton and rely on water-borne vibrations to detect their prey (Kirk, 1985; Neill, 1981). Investigating whether the predation pressure caused by *Chaoborus* larvae is affected by noise pollution and whether they habituate to noise are interesting perspectives.

To conclude, our results suggest that invasive pumpkinseed sunfish are still able to feed efficiently under anthropogenic noise as we did not find evidence for any change in the interaction strength towards *Chaoborus* larvae. It might be that the distraction effect observed when fish experienced boat noise for the first time weakened as they got used with this new stimulus and learned that it was not associated with any threat. Considering anthropogenic noise, which has received very little interest compared to increased salinity, hypoxia, or increased temperature in invasion ecology, our study provides additional evidence that high tolerance to environmental stress is one of the attributes of successful invaders. Tolerance to noise could promote the spread of invasive species in disturbed environments and also promote asymmetric competition with native species if they do not cope with noise as well as invasive species do. Laboratory-to- field extrapolation remains tricky (but see Pieniazek et al., 2020): playbacks of recorded sounds in experimental units do not fully reproduce what animals experience in the field and many environmental variables are likely to influence individual responses. However, lab experiments have the merit of providing valuable insights on the behavioural mechanisms that may affect ecological features such as interaction strength. Additional investigations are also needed to test whether tolerance to noise is widespread among invasive species and might help them spread across human-impacted ecosystems.

## **SUPPORTING INFORMATION**

SI are available here: <https://onlinelibrary.wiley.com/doi/abs/10.1111/fwb.13778>

### III. Article 2: Adding insult to injury: anthropogenic noise intensifies predation risk by an invasive freshwater fish species

*This article was submitted in **Biological Invasion** journal*

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## 1. 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

## 2. 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 (J. Dickey et al., 2021; Lagos et al., 2017), increased temperature (Christensen et al., 2021) and salinity (Behrens et al., 2017; Karsiotis et al., 2012), 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, motorized 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 (R. T. 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 & Schmidt, 2019). Reduced foraging performance is a common response to anthropogenic noise (Cox et al. 2018), with many examples both from the lab and field (Magnhagen et al., 2017; Sabet et al.,

2015). 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, Andraso 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 et al., 2010; Belanger & Higgs, 2005). 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, it 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 (Henseler et al., 2021b; Kornis et al., 2012; 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., 2021a), 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 (DeLong, 2021; Holling, 1959b). Because FR shape and magnitude are indicative of how the predator can control or destabilize its prey population (Kalinkat et al., 2013; Murdoch & Oaten, 1975), 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.

### 3. Methods

#### 1. Fish collection

In April 2021, 60 round gobies (mean body mass  $\pm$  sd =  $1.7 \pm 0.6$  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  $18^{\circ}\text{C} \pm 1^{\circ}\text{C}$  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 ( $1.5 \text{ g} \cdot \text{L}^{-1}$ ) 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 acclimatisation period, they were fed three times a week with 0.11g of frozen chironomid larvae (Petra-Aqua, Praque-West, Czech Republic) per fish and starved for 24 hr prior to experimentation to standardise motivation. Water quality and oxygen content were checked daily.

#### 2. 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×width×height: 60×25×35 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 acclimatisation 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 minutes 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 acclimatisation period in the laboratory prior to tests. For each noise condition, we added four replicates of the highest density without fish have been added 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.

Fish behaviour was recorded using two cameras (HD-TVI ABUS TVVR33418), one facing the aquarium and one above. We used four experimental aquariums concurrently placed inside acoustic insulation boxes (81 x 67,5 x 73 cm) 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). 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).

### 3. Playback tracks

Using the Audacity software (Audacity Team 2021), we created two 45-min audio tracks starting with a 30-min acclimatisation 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.

**Table 1.** Composition of the 15-min playback track broadcasting ambient noise supplemented with motorboat sounds during the functional response tests.

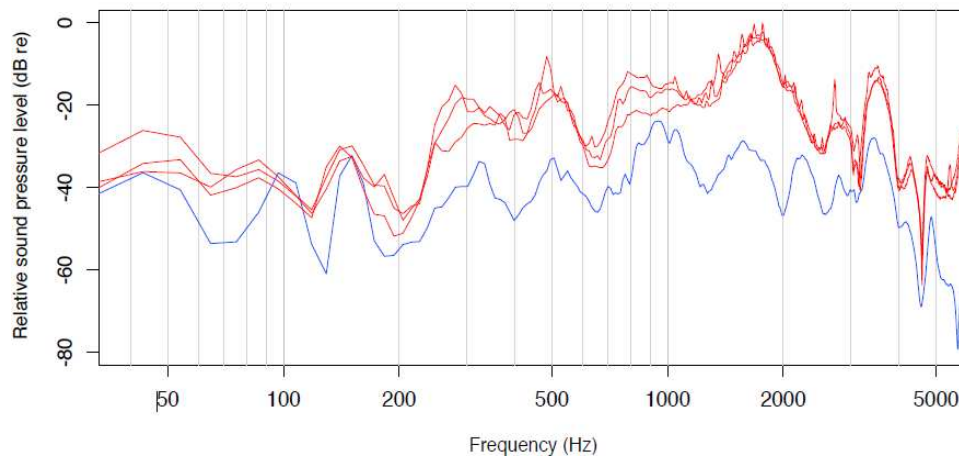
Noise sequence	Boat ID	Sound duration		
		(sec)	Start position	SNR (dB)
1	1	70	00'00	14
1	2	36	01'10	23
1	3	47	01'46	20
1	4	28	02'33	19
2	5	38	06'00	22
2	6	110	06'38	20
2	7	33	08'28	12
3	8	67	12'00	16
3	9	20	12'20	21
3	10	60	13'27	21
3	11	34	14'01	22

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 re 1  $\mu$ 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 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 metre 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:

$$SNR = 20\log_{10}(RMS_{boat\ noise} / RMS_{ambient\ noise})$$

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 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.



**Figure 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.

#### 4. 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 in 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 , 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.

## 5. 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:

$$F = aR / (1 + aRh) \quad (\text{Eq. 1})$$

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:

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

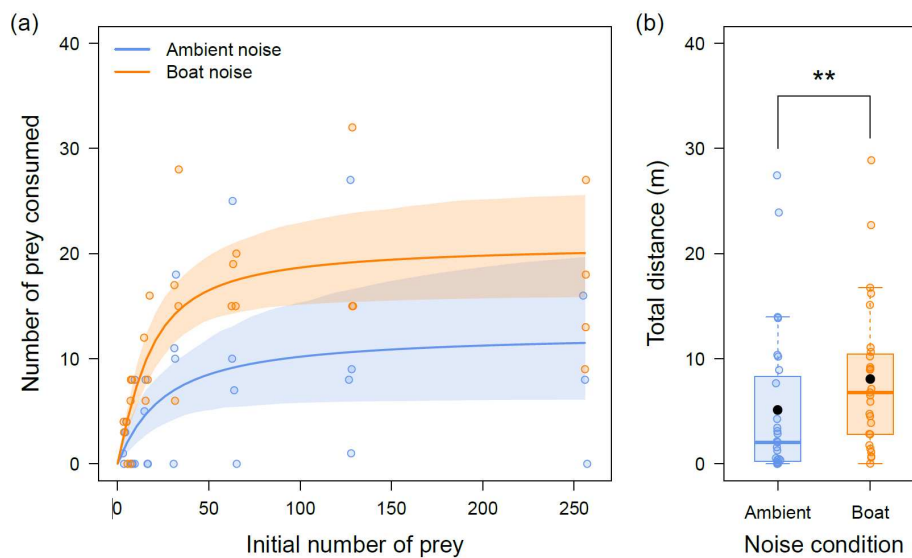
where  $N_0$  is the initial prey density and  $T$  the total experimental time. As chironomid larvae are benthic, we standardized prey density to the number of prey *per* square metre as recommended by Uiterwaal et al. (Uiterwaal et al., 2018). Attack rate, which corresponds to the initial slope of 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 *frair-boot* 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.

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 (K. Barton, 2009). 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 & 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.

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



**Figure 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.

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  $\Delta AICc$  value of the second model exceeded the threshold value of two (Table 2). Swimming distance was

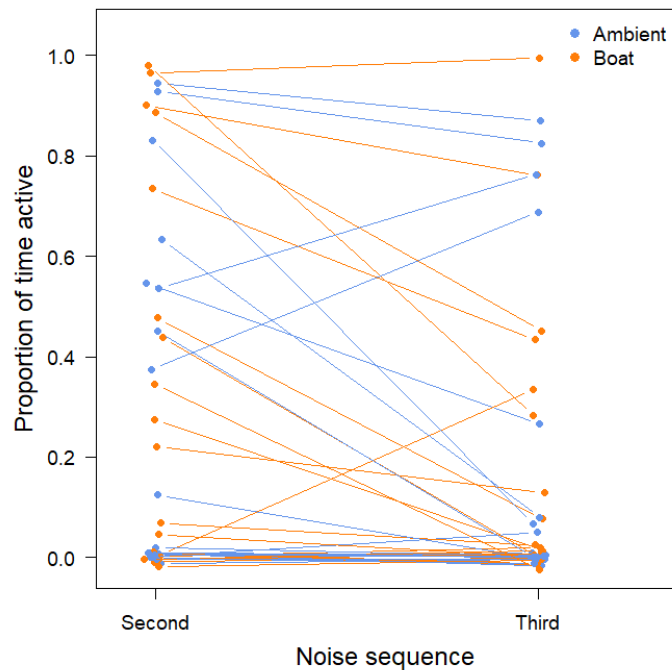
longer under boat noise (Cohen's  $d=0.71$ ,  $95\%CI = [0.15;1.28]$ , ( $x_I^2 = 6.69$ ,  $p = 0.0097$ ), Fig. 2B). Taking into account fish body mass, prey density, or any interactions between explanatory variables did not significantly improve the goodness of fit of the model.

**Table 2.** Results of the multimodel inference analysis performed on fish swimming distance and comparing all possible combinations of the three explanatory variables: noise condition (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. Each line corresponds to a model. For each model, we reported intercept of the regression, adjusted R<sup>2</sup> (adj.R<sup>2</sup>), degree of freedom (df), Log likelihood (LogLik) values, Akaike information criteria values with a correction for small sample sizes (AICc), change in AICc ( $\Delta AICc$ ) 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.

Intercept	C	M	D	C:M	C:D	M:D	C:M:D	adjR <sup>2</sup>	df	logLik	AICc	$\Delta AICc$	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	0,015
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

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





**Figure 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 for two three-minute noise sequences. Points are raw data and have been slightly horizontally and vertically jittered to avoid overlapping and increase readability.

## 5. Discussion

First exposure to anthropogenic noise typically decreases foraging behaviors 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. Using the 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. However, 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.

Attack rate describes predator's efficiency at capturing prey, namely the space (here the surface) that a predator searches *per* unit of time (Holling, 1959a). It fixes the initial slope of the FR curve: the higher the attack rate, the steeper the slope. It fixes functional response's initial curve. Round gobies were more mobile with noise, which increased the searched area and provided opportunities to encounter and catch prey (Gerritsen & 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, 1959a). 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. 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 functional response 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 (Ellis & Macisaac, 2009; Lagos et al., 2017; Zerebecki & Sorte, 2011), 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 Pieniasek et al. (2020). It might be that increased mobility makes some gobies leave the area while those remaining forage more.

Increase in both functional response 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 & 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 Pieniasek 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 escape 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 (Behrens et al., 2020; Myles-Gonzalez et al., 2015). An interesting perspective would be to investigate the response to anthropogenic noise between personality types and along the invasion gradient.

**Ethics.** Round goby capture and transport were approved by the Direction Départementale des Territoires de la Loire (DDT 42). All the procedures were conducted in accordance 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).

**Data accessibility.** All datasets and source code 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/7706393>. DOI: 10.5281/zenodo.6563528

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### **Statements & Declarations**

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We declare we have no competing interests.

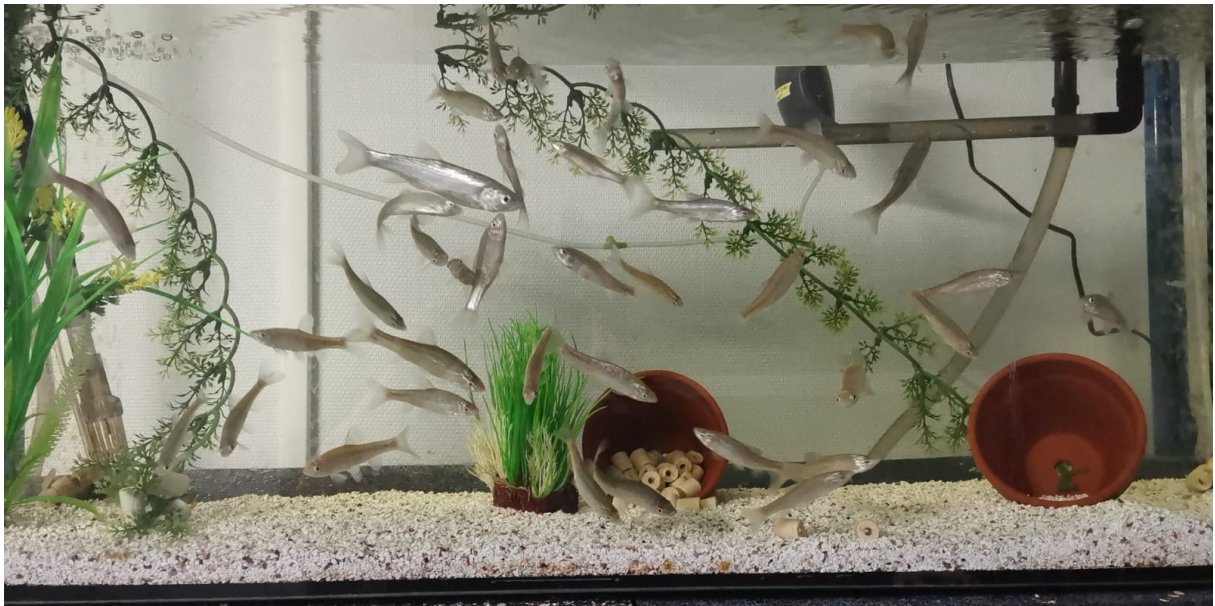
MFD, LT, FXDM and VM designed the study. MFD and ER performed the experiments and collected the data. MFD, LP, FXDM and VM analysed the data. MFD and VM drafted the manuscript, and all authors provided critical revisions. All authors approved the final version of the manuscript.





## Chapter 2: Context-dependencies in the effect of noise

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Topmouth gudgeon in a breeding aquarium





## I. Synthesis

In **Chapter 1** we showed the potential of the FR to detect subtle effects of noise on per capita predation rate. However, in its natural environment, a predator is facing a variety of interactions including trophic or social interactions (conspecific). These multiple interactions may affect the outcome of the predator-prey interaction (Vonesh & Osenberg, 2003). Social interactions may indirectly have implication for predator-prey interactions outcomes (Bolker et al., 2003; Sih et al., 1998; Vonesh & Osenberg, 2003). As noise can stress and mask communication and biological sounds, this can result in alteration of group interaction (Herbert-Read et al., 2017). Individuals sharing the same resources may interfere positively (e.g., cooperation) or negatively (competition, or intraguild predation), leading to what we call multiple predator effects (MPE).

MPE are all non-trophic interactions that can be categorized as: **additive**, where the number of prey killed is proportional to the number of predators; **synergistic**, resulting in prey consumption enhancement (Losey & Denno, 1998; Soluk, 1993) where combined predators kill more prey than predicted by their individual effects; **antagonistic**, resulting in a reduction of prey consumption (Wasserman et al., 2016) where fewer prey are killed than expected given the number of predators (Sentis & Boukal, 2018). Studies of MPE consist in the comparison of observed patterns of prey survival in the presence of multiple predators to expected survival predicted from the independent effect of each single predator (Griffen, 2006; McCoy et al., 2012; Sentis & Boukal, 2018; Soluk, 1993). The functional response was already used in a few studies to quantify emergent MPE (Cuthbert et al., 2020; McCoy et al., 2012; Sentis & Boukal, 2018; Wasserman et al., 2016).

In this **Chapter 2**, we continued to use the functional response combined to behavioral measurements (as in Chapter 1) to assess the potential effect of noise on MPE in the invasive topmouth gudgeon (*Pseudorasbora parva*). We assessed long-term (3 weeks) effects of motorboat noise, we pre-exposed fish for three weeks to motorboat noise in their breeding aquarium prior to FR experiments. We derived single- and multiple-predator FR with two individuals feeding simultaneously under ambient or motorboat noise.

Functional response of single preexposed predator showed a decrease in attack rate at low densities and no effect in the maximum feeding rate under boat noise. Contrary to chapter 1

result, we did not observe habituation. Moreover, we found a decrease in mobility that was consistent with the attack rate: more stationary predators tend to encounter fewer prey, which limits attack rates. Surprisingly, with two predators; the physical presence of a conspecific restored predation: we did not find a difference in FR parameters nor in behavior between ambient and motorboat noise. This suggests that social interactions have the potential to shape predation and mitigate the impact of noise.

To assess MPEs, we predicted the FR of two predators under ambient and boat noise from single-predator FR and compared them to the FRs observed with two fish. We found that under both noise conditions, antagonistic interactions were detected showing that irrespectively of the noise condition, the interaction remained of the same nature. An interesting result, because the visual cue of a companion fish in preexposed single predator test was not enough to predict the physical presence of a conspecific whereas a recent study showed that topmouth gudgeon was more sensitive to visual cues than to chemical cues (Chao Fan & Yanming Zhang, 2020). But it was also shown that the topmouth gudgeon produced sounds non intentionally during feeding. These sounds allow to identify food source (Scholz & Ladich, 2006), therefore, the visual and interactive presence of a conspecific had restored per capita predation potentially due to social stimulation.

## **II. Article 3: Anthropogenic noise does not strengthen multiple predator effects in a freshwater invasive fish**

*This article was submitted in Fish Biology journal*

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## 1. 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 strengthen 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 in the presence or absence of motorboat sounds. 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. The FR of single fish exposed to noise was significantly lower at low prey densities than without noise, which might result from reduced mobility. 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. Observed group-level FRs were slightly lower than 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 topmouth gudgeon.

**Keywords:** Functional response, predator-predator interaction, anthropogenic noise, *Pseudorasbora parva*, *daphnia pulex*

## 2. 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 nowadays considered a pervasive pollutant, inducing behavioural, physiological, and sometimes anatomical alterations in animals (Erbe et al., 2018; Popper & Hastings, 2009; Shannon et al., 2016). It 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. (Bruitjes & 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, 1959a), 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, decelerating (type II) FRs 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 chronic motorboat 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). Although invasive species can dominate freshwater communities in terms of biomass and therefore contribute strongly to the bioenergetics of food webs, their response to anthropogenic noise has received scant attention. Prior to the FR experiments, fish were exposed to boat sounds as the response to noise was found to weaken with repeated exposure in some fish species (Rojas et al., 2021). 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, Dalu, 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). 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.

### 3. Methods

#### 1. Animal collection and husbandry

*Pseudorasbora parva* ( $7.144 \pm 0.4$  cm, no distinction of sex) were collected in November 2019 using net fishing from the Grandes Lèches pond at Saint-Nizier-le-Désert (46°03'27.8"N, 5°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°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<sup>-1</sup>. 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 (Aguasand 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). They were purchased from a commercial



supplier (AQUARIUS, Andrézieux-Bouthéon, Auvergne-Rhône-Alpes, France), stored at 4°C and transferred into a 54-L aquarium 24 hours before being used in the predation tests to habituate them to the temperature of the experimental room.

## 2. Pre-exposure to noise

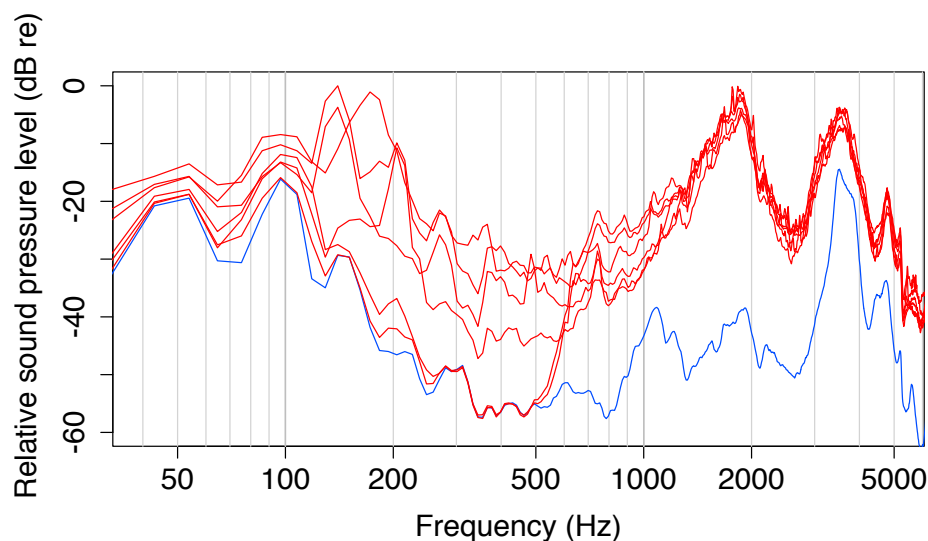
We used the same procedure as in Rojas et al. (2021). Briefly, we tried to mimic the daily activity of a small leisure lake by broadcasting from 9 am to 6 pm 150 sounds from recreational boats (from six to 25 *per* hour), previously generated from 15 original recordings made by V. Médoc in a surrounding lake (45°45'07.54"N, 4°25'56.47"E, Loire, France) at 1-m depth. 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 RMS sound pressure level and the signal-to-noise ratios quantifying the relative importance of boat sounds over ambient noise ranged from 4.81 to 27 dB (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 (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.

## 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 Fig. S1b, c in Rojas et al. 2021). Because *P. parva* belongs to Cyprinidae family which are shoaling fish (Pitcher, 1986, personal observation), 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 (Laverly 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 either ambient noise (control condition) or ambient noise supplemented with 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 sounds *per* sequence) separated by a few minutes of ambient noise (Fig.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).



**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*.

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. 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.

#### 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).

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).

## 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, 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:

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

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 et Boukal (2018) and McCoy et al. (2012), we parametrized 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 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 used AIC model selection using the *MuMIn* package (K. Barton, 2009) and ranked based on small sampled-corrected AIC values ( $AIC_c$ ), and with a  $\Delta AIC_c$  cut-off at 3, a conservative threshold suggested by Bolker (2008).

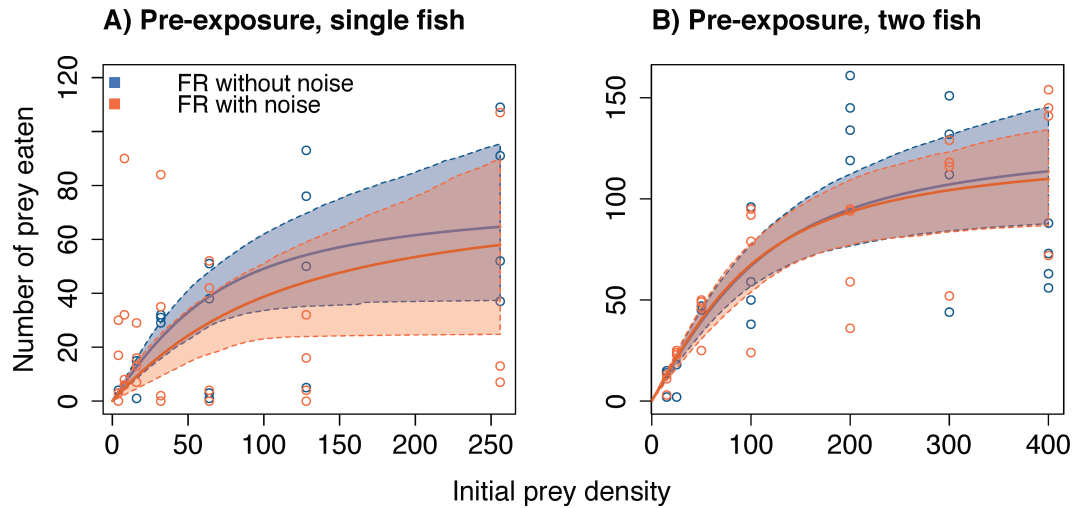
A linear mixed-effects model was also used to explain the cumulative swimming distance of water fleas as a function of noise condition (ambient noise or boat noise) interacting with test duration and taking position in the 4-well box as a random factor.

#### 6. Ethical notes

The capture and transport of *Pseudorasbora 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.

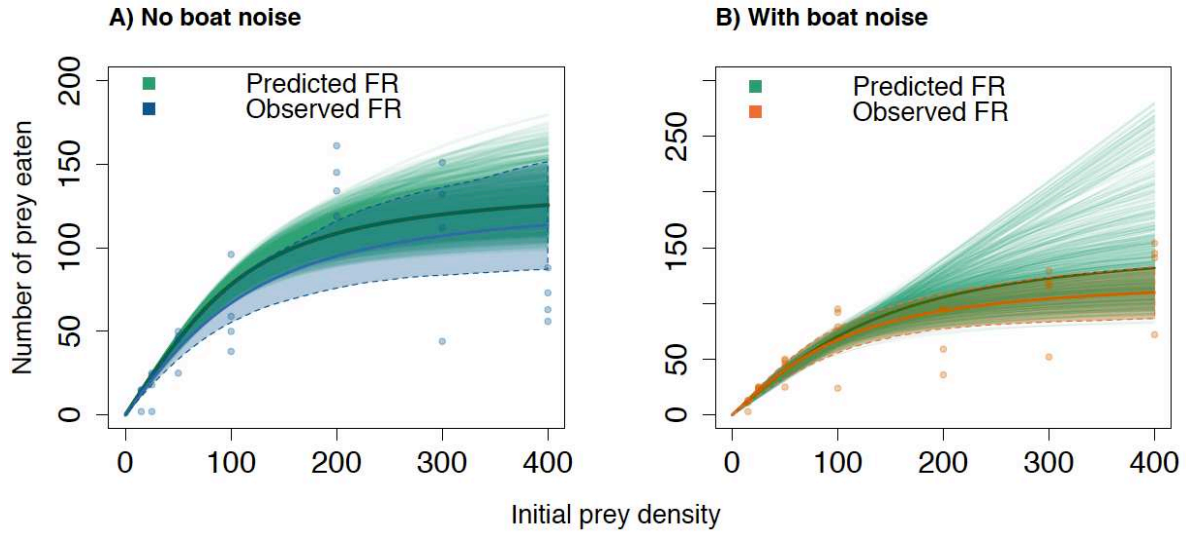
## **4. Results**

*Daphnia* survival was 100% in absence of fish demonstrating that mortality during FR tests was due to the predation by *P. parva* only. Fish body length did not differ between the experimental groups (Wilcox test, for one fish:  $W=351.5$ ,  $p\text{-value} = 0.51$ ; ANOVA for two fish,  $\text{Sum-square} = 0.0112$ ,  $df = 1$ ,  $F\text{-value} = 0.699$ ,  $p\text{-value} = 0.407$ ). Whatever noise condition and predator density, the type-II FR was always the best model (Fig.2). When alone, fish exposed to chronic noise showed a significantly decreased attack rate compared to control but no difference in handling time, resulting in a less steep FR curve with a similar asymptote (Fig.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 (Fig.2B).



**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.

Observed group-level FRs were in the low range of predicted group-level FRs for both noise conditions (Fig.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, Fig. 3). 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, Fig. 3).



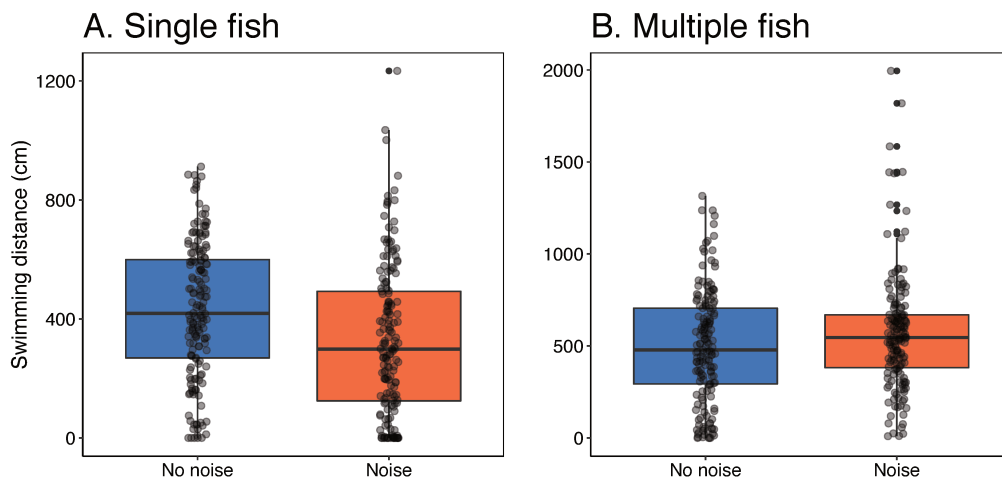
**Figure 3:** Predicted type-II functional responses (green solid lines,  $n=1000$ ) for two invasive topmouth gudgeon (*Pseudorasbora parva*) feeding on *Daphnia pulex* and inferred from the functional responses obtained with single individuals under (A) control ambient noise and (B) motorboat noise. Predicted functional responses 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.

**Table 1:** Results (p values) of the delta method used to compare both functional response 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*. The 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 value of  $Dh$  indicate when the observed FR are below the predicted FR.

	No boat Noise		With boat Noise	
	P-value < 0.05	P-value > 0.05	P-value < 0.05	P-value > 0.05
$Da > 0$	4	126	392	<b>508</b>
<b><math>Da &lt; 0</math></b>	<b>870</b>		100	
<b><math>Dh &gt; 0</math></b>	358	<b>511</b>	<b>566</b>	300
$Dh < 0$	131		134	



The swimming distance travelled by single predator decreased under noise condition ( $estimates = -3.58$ ,  $std.error = 1.62$ ,  $p-value = 0.028$ ; Fig 4), and the distance to the companion fish also decreased over time and especially under noise condition ( $estimates = -0.23$ ,  $std.error = 0.06$ ,  $p-value = 0.0004$ ). No difference was observed regarding the avoidance of fish to noise (distance to the loudspeaker). None of the predictors had any significant effect on the distances to the speaker, between conspecific and on swimming distance in multiple-predators behavior. The cumulative swimming distance of water fleas increased over time ( $X_1^2 = 8.69$  and  $p = 0.003$ ) but did not differ between ambient and boat noise conditions ( $X_1^2 = 0.74$  and  $p = 0.39$ ).



**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).

## 5. 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 to make emerge multiple-predator effects (MPEs) remains undetermined. To address this question, we derived the relationship between *per capita* predation rate and prey density, namely the functional

response (FR), of single or pairs of invasive topmouth gudgeon (*Pseudorasbora parva*) feeding on the water flea *Daphnia pulex* in the absence or presence of motorboat sounds. We also recorded the behaviour of both species and to detect noise-induced MPEs, we compared the FR of two fish (observed group-level FR) to a theoretical FR inferred from the individual-level FR and based on additive effects only (predicted group-level FR), for both noise conditions. Prior to the FR experiments, fish from the boat noise condition experienced repeated exposure to noise to be more ecologically relevant and account for a potential habituation effect (i.e. when the response to noise weakens with repeated exposure, (Bejder et al., 2009)).

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. As expected from previous FR experiments made in simple (i.e. no shelter) experimental arenas (Cuthbert, Dalu, et al., 2019; Dick et al., 2013; Hanache et al., 2020), the best FR model 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), attack rate was significantly reduced by boat noise, making the FR less steep compared to that obtained under ambient noise. Handling times and therefore FR asymptotes did not significantly differ between the two noise conditions. The decrease in attack rate could have resulted from the shorter swimming distance also observed with noise during the FR trials. We already observed such correlation between mobility and attack rate in another invasive fish, the pumpkinseed sunfish *Lepomis gibbosus* (Rojas et al., 2021). *Pseudorasbora parva* is considered as a cruise searcher (Priyadarshana et al., 2006) so higher mobility provides more opportunities to encounter and catch mobile prey. When approaching saturation, the role of predator mobility in prey capture becomes marginal, prey items being numerous and almost everywhere. 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).

Prior to the FR experiments, topmouth gudgeon 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 and can

happen when the organisms learn that a stimulus is not associated with any threat (i.e. associative learning). In previous FR investigations, we found that fish 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 associate learning to occur in *P. parva*.

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 is like if conspecific presence made that 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 species 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, that is to say 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. Topmouth gudgeon 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.



# Chapter 3: From individuals to community: scaling up the effects of noise

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Experiments at the PLANAQUA CEREEP-Ecotron Platform



## I. Synthesis

All the experiments of this chapter were performed at the PLANAQUA CEREEP-Ecotron ÎleDeFrance experimental research platform. We conducted two outdoor mesocosm experiments combined with microcosms experiments to scale up the responses to noise observed in Chapters 1 and 2.

The first study was part of the Master-2 internship of Mélanie Gouret and led to a collaboration with Gérard Lacroix (ENS, Cereep-Ecotron), specialist in trophic ecology and freshwater communities, and Paolo Fonseca (Univ. Lisboa), expert in aquatic acoustics. We tested the long-term effect of motorboat noise on the strength of top-down effects in a three-level trophic cascade, with fish as top consumer (third trophic level), zooplankton as mesoconsumer (consumers of intermediate trophic position) and phytoplankton as primary producers (first level). A pilot experiment was run in 2019, which allowed us to plan the design. The full experiment had to be delayed due to logistical constraints and COVID-19 restrictions.

We crossed two factors with two modalities: (i) the noise treatment (either natural ambient noise of the mesocosm or motorboat noise broadcasting as already used in previous chapters), (ii) the fish treatment (absence or presence of roach) to create 4 treatments: no fish-ambient noise, no-fish-boat noise, fish-ambient noise, and fish-boat noise. We made three replicates per treatment resulting in 12 mesocosms. Mesocosms without top predator (fish) were used as a control of the trophic cascade. The experiment lasted six weeks which can be considered as a long period of exposure (Jacobsen et al., 2014). Over this period, we assessed the dynamics of zoo- and phytoplankton through water samples collected every 2/4 days. We decided to use a native fish species, the roach *Rutilus rutilus* to optimize our chances of seeing the potential cascading effects of noise, as this species is known to be disturbed by noise up to at least five days of exposure (Jacobsen et al., 2014). At the end of the experiment, all fish (exposed either to ambient or boat noise) were removed from the mesocosms and transferred into aquariums in groups of three individuals to assess their foraging activity under both noise conditions. This allowed better understanding of the mechanism underlying community dynamics in the mesocosms by bringing information about fish behavior when naive (mimicking the beginning of the mesocosm experiment and also being the control of microcosm experiment) or after chronic exposure to noise (mimicking the end of the experiment). In aquarium



experiments, fish were exposed to two different preys commonly found in the mesocosms: the cladoceran water flea *Daphnia* sp. and the insect phantom midge larvae *Chaoborus* sp.

The presence of fish induced cascading effects irrespectively of the presence of boat noise in the mesocosms. In other words, the top-down control by roach had the same structural consequences on planktonic communities for both noise conditions. Microcosm experiments showed that fish were distracted by noise when exposed for the first time, with less prey consumed, but they resumed a basal amount of prey eaten after repeated exposure. We also found that roach showed a higher preference for *Daphnia* sp. could be linked to the noise-induced anti-predatory movements of the *Chaoborus* larvae found in Chapter 1, making them harder to capture.

In fishless mesocosms, noise induced slight changes in the zooplanktonic dynamics which were intermediate between control communities and communities from the noisy mesocosms with fish. Indeed, the major effect found in these mesocosms was the changes in cladoceran species composition with less *Daphnia* species under boat noise resulting in the increase of competitive species such as *Bosmina* sp. Our fishless-mesocosm results suggested that noise could directly alter zooplankton communities, an effect probably masked by fish top-down control.

We wanted to explore further the effect of noise on zooplankton by performing a second mesocosm-microcosm experiment with more replicates (eight tanks instead of three) to improve statistical power. I collaborated with Michael Danger and Vincent Felten (Univ. Lorraine), experts in freshwater macro-invertebrates, and Camille Desjonquères (Univ. Grenoble Alpes), a post-doctoral researcher interested in the acoustic signature of ecological processes. In parallel to the main objective of this experience, we tried to assess the response to noise of an invasive amphipod species, *Echinogammarus Berilloni*, involved in leaf-litter breakdown. We performed a design to assess zooplankton dynamics and the foraging activity of *E.berilloni* with the implementation and monitoring of leaf-litter bags. However, gammarids faced a high mortality for reasons that escape us, making this second part of the experiment impossible to exploit.

We monitored zooplanktonic dynamics for six weeks at four different dates and under two noise conditions (ambient or boat noise). We predicted that predation by *Chaoborus* larvae, the main pelagic predator of our community, should be reduced by boat noise favoring cladocerans species and especially *Daphnia* sp. To capture such effect, we identified all the

taxonomic groups present at the beginning and the end of the investigation (performed by an engineering office and ourselves) and counted only our groups of interest (*Chaoborus* larvae and cladocerans) for the other sampling dates. We only found a significant positive effect of noise on the dynamic of cladocerans.

We completed our mesocosm experiment with a derivation of functional response of *Chaoborus* larvae on *Daphnia* in aquarium. We exposed larvae from the ambient and boat noise mesocosms to five densities of *Daphnia* sp. (n=3, 6, 12, 24, 48) for eight hours under ambient and boat noise respectively to match with the noise they experienced in their mesocosm. We also assessed their behavior through the recording of their body rotations (i.e., the anti-predatory response found in Chapter 1). As reported in Chapter 1, *Chaoborus* larvae made more body rotations with noise, but this did not result in any difference in FR between the two noise conditions suggesting that long-exposure to noise led to tolerance to noise. Therefore, we were not able to confirm that the increase in cladocerans was due to a noise-induced reduction in the predation by phantom midge larvae.

## **II. Article 4: From behaviour to complex communities: Resilience to anthropogenic noise in a fish-induced trophic cascade**

*This article was submitted to **Proceeding B** journal.*

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## 1. Abstract

Sound emissions from human activities represent a pervasive environmental stressor. Individual responses in terms of behaviour, physiology or anatomy are well documented but whether they propagate through nested ecological interactions to alter complex communities needs to be better understood. This is even more relevant for freshwater ecosystems that harbour a disproportionate fraction of biodiversity but receive less attention than marine and terrestrial systems. We conducted a mesocosm investigation to study the effect of chronic exposure to motorboat noise on the dynamics of a freshwater community including phytoplankton, zooplankton, and roach as a planktivorous fish. As expected under the trophic cascade hypothesis, roach predation induced structural changes in the planktonic communities. Surprisingly, although roach changed their feeding behaviour in response to noise, the dynamics of the roach-dominated planktonic communities did not differ between noisy and noiseless mesocosms. This suggests that the top-down structuring influence of roach on planktonic communities might be resilient to noise and reveals the difficulties on extrapolating impacts from individual responses to complex communities.

**Key words:** chronic noise pollution, freshwater plankton, predation, mesocosms, *Rutilus rutilus*, cascading effect

## 2. Introduction

The trophic cascade, one of the most influential concepts in ecology, specifies the effects of predators that propagate downward through food webs across multiple trophic levels (Fretwell, 1987; Ripple et al., 2016). Considering a series of nested consumer-resource interactions (i.e., a food chain), top predators have a direct negative effect on mesopredators and indirect positive and negative effects alternatingly on lower trophic levels. Top-down cascade effects can result from changes in predator density (density-mediated trophic cascade) or behaviour (trait-mediated trophic cascade) and much attention has focused on identifying the intrinsic and extrinsic determinants of their strength (Schmitz et al., 2004; Su et al., 2021). In particular, this helped to better understand the structural impact of several

anthropogenic stressors including warming, salinization, chemical pollution or habitat degradation (Cheng & Grosholz, 2016; Duchet et al., 2018; Hebblewhite, 2005).

Noise emissions from transportation, cities, industry, military and recreational activities represent another pervasive anthropogenic stressor . They span all ecosystems even in the most remote places (R. T. Buxton et al., 2017) and have been shown to alter communication, social interactions, use of space, activity patterns, foraging and reproduction in a wide range of taxa (Francis & Barber, 2013; Kight & Swaddle, 2011; Shannon et al., 2016). First evidence of the cascading effects of noise pollution came from the long-term investigations conducted in the natural gas fields of northwest New Mexico. Bird response to gas-well-compressor noise was found species-specific with some key seed dispersers (mountain bluebirds and Woodhouse's scrub-jays) avoiding noisy areas where pollinators like hummingbirds had on the contrary higher reproductive success (Francis et al., 2012). Long-term consequences include alterations in plant communities that persist after removal of the noise source (Phillips et al., 2021). The propensity of anthropogenic noise to indirectly affect species, and typically primary producers, through a series of nested direct interactions has also been suggested experimentally. Barton et al. (2018) exposed a three-level terrestrial food chain to various soundscapes for 14 days in plant growth chambers and found that urban sounds and rock music made lady beetles less effective predators, reducing the strength of top-down control on aphids, whose density increased. More aphids ultimately resulted in reduced soybean biomass.

Although freshwaters harbour a disproportionate fraction of earth's biodiversity (Dudgeon et al., 2006) and suffer a greater decline in species richness compared to terrestrial and marine habitats (Dudgeon, 2019; Maasri et al., 2022), they often receive less attention, and research on the impacts of noise pollution is no exception. For instance, we know that fish responses to noise include changes in behaviour and abundances (Cox et al., 2018; Kunc et al., 2016; Mickle & Higgs, 2018; Slabbekoorn et al., 2010) but whether these effects spread along food webs to alter planktonic communities through cascading effects remains to be investigated. Similarly, the response of freshwater plankton to noise is largely overlooked. Available evidence to date comes from water fleas, *Daphnia* spp., which are widespread pelagic crustaceans (Cladocera) and an important source of food for upper trophic levels (Lampert, 2006; Reynolds, 2011). Surprisingly, knowing that marine invertebrates of similar

size were found to adjust their swimming activity in response to natural or artificial sounds (Tidau & Briffa, 2016), water fleas exposed to band-pass filtered white noise either continuous or intermittent did not show any alteration in swimming speed or depth (Sabet et al., 2015, 2019). However, long-term effects of chronic exposure on their survival and reproductive success have yet to be explored, and overall, we lack knowledge on the dynamics of plankton under anthropogenic noise.

Here we conducted a mesocosm investigation to study the temporal dynamics of a zooplankton – phytoplankton system under the presence or absence of a planktivorous fish, with and without exposure to motorboat noise. We used roach *Rutilus rutilus* as top predator: a widespread Eurasian cyprinid fish whose response to motorboat noise has been documented (Jacobsen et al., 2014). Roach have specialized hearing structures, the Weberian ossicles, that conduct sound from the swim-bladder to the inner ear and provide high sensitivity to sound pressure (Andersson et al., 2007; A. Hawkins & Myrberg, 1983; Popper & Fay, 2011). They can detect sounds between 10 Hz and 5 kHz with a maximum sensitivity of 60 dB re. 1  $\mu$ Pa between 500 and 1000 Hz (Amoser et al., 2004).

Roach have been found to respond to authentic motorboat sounds with fewer feeding attempts, higher latency to enter the open area and longer time spent in the vegetation, and these effects persisted after five days of exposure suggesting the absence of habituation (Magnhagen et al., 2017). After our mesocosm investigation, and in order to get insights into fish growth and behaviour, the roach have been collected, weighted, and measured, and moved to aquaria to assess prey consumption, mobility and group cohesion in the presence or absence of boat noise. Given the lack of knowledge on how freshwater plankton respond to chronic noise exposure, we had no clear prediction on the effect of boat noise on the dynamics of the zooplankton – phytoplankton system without fish. Under the trophic cascade hypothesis, we expected roach presence to reduce the top-down control of phytoplankton by zooplankton. Considering that motorboat noise was found to negatively influence foraging in roach (Magnhagen et al., 2017), we predicted a decrease in the strength of top-down cascading effect. Concerning roach behaviour, we expected behavioural alterations consistent with the weakening of the trophic cascade in the noisy mesocosms.

### 3. Methods

The investigation has been conducted at the PLANAQUA experimental platform of the CEREEP-Ecotron Île-de-France research station (48° 16'10.92 N, 2° 43'50.879 E, Seine et Marne, France) and lasted six weeks (August 31 – October 14, 2020), which corresponds to a prolonged exposure to motorboat noise following Johansson et al. (2016). We assigned three mesocosms to one of four treatments ( $N = 3$  replicates, 12 mesocosms in total): (1) no fish – no noise, (2) no fish – noise, (3) fish – no noise, and (4) fish – noise.

### 1 Preparation of the mesocosms and animal collection

Each mesocosm (3.4 m diameter, 1.1 m depth) was filled with 9,079 L of water from the storage lakes of the field station that naturally host zooplankton and phytoplankton communities. An underwater loudspeaker (Electrovoice UW30) was submerged five cm below the surface in the center of each mesocosm. It was connected to an amplifier (Dynavox CS-PA 1MK) and then to an audio player (Handy's H4n zoom), both placed inside a waterproof electric box next to the mesocosm. To promote the growth of phytoplankton, we added 30 mL of Algoflash® (41.4 µg of phosphorus, nitrogen, and potassium per liter) at the beginning of the investigation (August 20) and 50 additional mL at the middle of the investigation (September 19) after we detected a drop in the amount of chlorophyll in the mesocosms using a multiparameter probe (YSI ExO-2).

From March to April 2020, we used fish traps to gradually collect roach from the storage lakes of the PLANAQUA platform, and we stored them in a pond containing the same planktonic communities as the mesocosms. These fish were the descendants of roach used in previous investigations conducted on the platform. They grew in quiet conditions and had never experienced motorboat noise before. At Day 0, 96 roach of similar size ( $8.54 \pm 2.32$  cm for standard length, SL) were randomly collected from the storage pond using a seine net, measured, and weighted to the nearest 0.01 cm and 1 g, and distributed in groups of 16 between the six mesocosms (fish – no noise and fish – noise treatments) so as to homogenize size distribution and total biomass between the mesocosms. We placed anti-bird nets on top of the mesocosms to avoid avian predation.

### 2. Plankton dynamics

To assess plankton dynamics, we sampled the mesocosms 13 times from Day 0 to Day 42 every two or four days. The temporal variation of phytoplankton was assessed through the quantification of green algae, cyanobacteria, and diatom densities. We sampled eight liters of water per mesocosm using a 2-L sampling bottle (Uwitec) at four different positions. Analyses were made in the laboratory using a BBE FluoroProbe™ spectrofluorometer (BBE Moldaenke GmbH, Schwentinal) on a 125-mL subsample previously kept in the dark for one hour. For detecting potential top-down effects on zooplankton, we choose to focus on mesoplankton organisms (Cladocera, copepodits and adults of Copepods, and *Chaoborus* larvae), which appeared as the most responsive organisms in previous mesocosm experiments realized in comparable conditions (Bertolo et al., 1999). To assess their temporal variation in zooplankton, we sampled 24 liters of water using a 2-L sampling bottle at twelve different positions and depths in each mesocosm. Water was filtered with a 50-µm nylon filter and zooplankton fixed in 15-mL of 90% ethanol. Taxa identification and counting was made on a 3-mL subsample following (Haney & et al, 2013) for cladocerans and copepods (nauplii not counted), and (Winterbourn et al., 1989) for aquatic insects.

### 3 Fish growth and behaviour

The behavioural tests took place in an experimental room of the PLANAQUA platform thermo-regulated at 17°C. We equipped four 110-L aquaria (80 cm length x 35 cm width x 40 cm height) with an underwater loudspeaker (Electrovoice UW30) in the middle of the left end surrounded by acoustic foam (1.5-cm thick) to attenuate vibrations, a neon light, and a camera (HD-TVI ABUS TVVR33418) above, and black plastic boards outside to avoid visual contacts with the experimenters that may provide stress. The speaker was connected to an amplifier (Dynavox CS-PA 1MK) and to an audio player (Handy's H4n zoom). The aquaria were filled with water from the control mesocosms (no fish – no noise treatment) filtered through a 50-µm nylon mesh filter to remove zooplankton.

This experimental design allowed us to run four tests simultaneously with one treatment *per* aquarium depending on the noise condition in the mesocosm and later in the aquarium (“mesocosm – aquarium” noise conditions): (1) no noise – no noise, (2) no noise – noise, (3) noise – no noise and (4). Between two consecutive runs of tests, each aquarium was assigned another treatment to avoid an effect of the aquarium, while water was changed to remove chemical cues.



At the end of the mesocosm investigation (Day 44), roach were removed from the mesocosms using a seine net and measured and weighted to the nearest 0.01 cm and 1 g. We matched these values with the weights and lengths measured at the beginning of the mesocosm investigation to recognize fish and calculate individual growth. Roach were then randomly assigned to groups of three individuals and moved into one of the four experimental aquaria. In total, we formed 28 groups ( $N = 7$  replicates per treatment) with two or three groups per mesocosm. Once in the aquarium, they first experienced ambient noise during an acclimatization period of one hour, and then 40 minutes of either ambient noise or ambient noise supplemented with motorboat sounds, depending on the treatment (see section 2.4 for further detail on the playback tracks). At the middle of the exposure period (i.e. after 20 min), we introduced 50 *Chaoborus* larvae (Diptera) and 50 *Daphnia* sp. (Crustacea: Cladocera), previously collected from the control mesocosms using a 2-L sampling bottle and 50- $\mu\text{m}$  nylon mesh filter. Both invertebrates are common prey of roach, differ in terms of size and mobility, and were found in the mesocosms.

Although *Chaoborus* larvae are natural predators of *Daphnia* (Spitze, 1991), we expected no predation events considering the short duration of the experiment. At the end of the experiment, roach and invertebrates were removed from the aquarium, counted, and returned to the storage pond. The videos were analyzed using Kinovea v. 0.9.4 to get the xy coordinates of each fish each second and during each boat sound (for a total of 691s and corresponding to ambient noise for the other treatment), and then the following parameters were calculated: (1) the cumulative swimming distance (total distance covered by the three individuals) as a proxy of mobility, (2) the distance between the barycenter of each group and the center of the speaker as a proxy of aversion to noise, and (3) the area occupied by the group as a proxy of group cohesion.

Group's barycenter was calculated using individual coordinates as follows:

$$X_{\text{barycenter}} = (X_{\text{fish1}} + X_{\text{fish2}} + X_{\text{fish3}}) / 3$$

$$Y_{\text{barycenter}} = (Y_{\text{fish1}} + Y_{\text{fish2}} + Y_{\text{fish3}}) / 3$$

The distance between the barycenter and the loudspeaker ( $D$  in cm) was calculated as follows:

$$D = \sqrt{((X_{\text{barycenter}} - X_{\text{loudspeaker}})^2 + (Y_{\text{barycenter}} - Y_{\text{loudspeaker}})^2)}$$

Group's area ( $A$  in  $\text{cm}^2$ ) was calculated as follows:

$$A = \sqrt{((P * (P - d_{\text{fish1-fish2}}) * (P - d_{\text{fish1-fish3}}) * (P - d_{\text{fish2-fish3}})))}$$

Where  $d$  corresponds to the distance between two fish in cm and  $P$  to the perimeter of the group in cm with:

$$P = \frac{1}{2} (d_{\text{fish1-fish2}} + d_{\text{fish1-fish3}} + d_{\text{fish2-fish3}})$$

Group barycenter and area were calculated every second during the boat sounds and then averaged.

The behavioural tests took place from 8 am to 6 pm and needed two consecutive days with four mesocosms (two from the fish – no noise treatment and two from the fish – noise treatment) processed on Day 43 and the two others (one *per* treatment) on Day 44. We also conducted four additional tests (two *per* noise condition) without roach to control for *Chaoborus* predation on *Daphnia* and overall invertebrate mortality in the absence of predation.

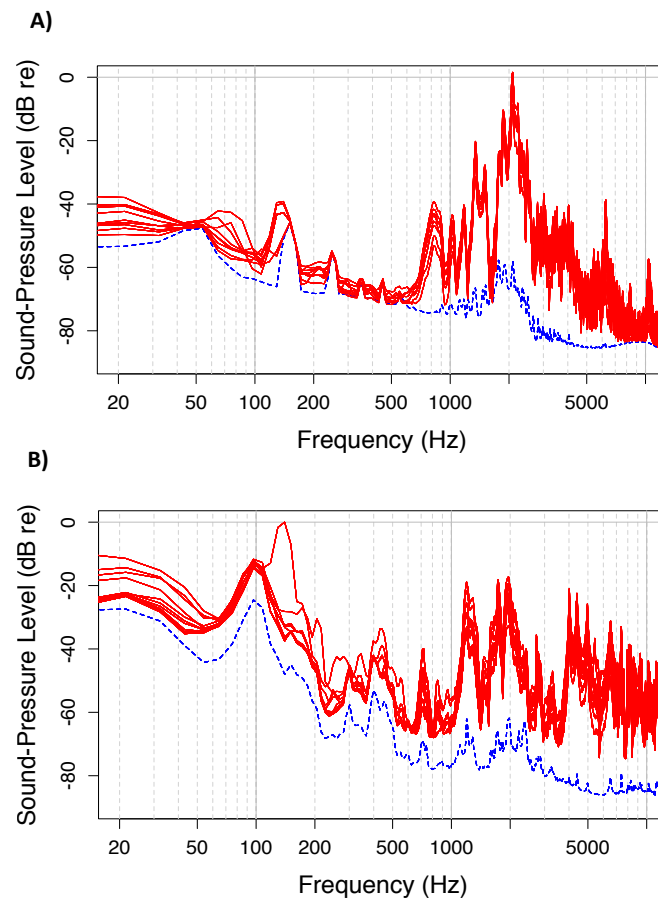
#### 4 Noise treatments

We used Audacity 2.2.1 to generate the audio tracks and an Aquarian Audio H2A-HLR hydrophone (frequency response from 10 to 100 kHz) connected to a ZOOM H4next Handy recorder for all the recordings. The level of background noise did not differ between the mesocosms and ranged from 90 to 95 dB re 1  $\mu$ Pa. In the mesocosms without boat noise, a 1-hr audio track of silence was looped continuously. In the mesocosms with boat noise, we used the audio tracks described in (Rojas et al., 2021) where 150 sounds of small recreational boats have been distributed over the nine consecutive 1-hr audio tracks of silence going from 9 a.m. to 6 p.m. so as to mimic the daily activity of a small leisure boat base (Fig. 1A and Supp. Mat. 1, see Rojas et al. (2021) for more details on the audio tracks and the original recordings). We broadcasted silence the rest of the time. We applied a linear fading on both ends of the boat sounds to make them emerge from background noise and adjusted their levels with Audacity to obtain naturally occurring signal-to-noise ratios (SNR) ranging from 4.81 to 27 dB re 1  $\mu$ Pa. We used the SNR function of the *seewave* R package (Sueur et al., 2008):

$$\text{SNR} = 20 \log_{10}(\text{RMS}_{\text{boat sound}} / \text{RMS}_{\text{background noise}})$$

where RMS is the root-mean-square sound pressure of either the re-recordings of the boat sounds in the mesocosm or the recording of background noise.

In the aquaria without boat noise and to encompass the 1-h acclimatization period and the 40-min exposure period, we used a 100-min audio track of background noise previously recorded in the center of one mesocosm from the no noise – no fish treatment. We adjusted sound level to match that of the mesocosms. In the aquaria with boat noise, we used the 100-min audio track of background noise to which we added twelve boat sounds randomly selected from those broadcasted in the mesocosms. We randomly distributed the sounds over the 40-min exposure period and adjusted their level to match the range of SNR values we had in the mesocosms (approx. 4.81 to 27 dB). In terms of boat traffic, this acoustic regime was representative of the highest activity that roach experienced within a day in the mesocosms (Fig. 1B and Supp. Mat. 1).



**Figure 1:** Sound spectra of the two noise conditions (control: dashed lines, boat noise: one solid lines for each hour from 9 am to 6 pm) broadcasted in A) the mesocosms and B) the aquaria. Spectra were made from 1-hour recordings in the mesocosms and 20-min recordings in the aquaria.

## 5 Data analysis

All the statistics were performed using R (R Core Team, 2021) with a significance level of 0.05. We used the Principal Response Curve (PRC, *prc* function of the *vegan* R package (Oksanen et al., 2013)) to study how the planktonic communities exposed to roach, boat noise, or both, have diverged over time compared to control communities (i.e. from the no fish – no noise treatment). PRC is a special case of redundancy analysis including time-series data particularly suited to the study of community dynamics in mesocosms (Van den Brink & Braak, 1999). It typically results in a diagram with one curve for each treatment, the time on the x-axis, the first major component of the community effects on the left y-axis and the weights of the taxa on the right y-axis. The more the weight deviates from zero the more the corresponding taxon contributes to the deviation from the control. We used Hellinger-transformed taxa (square root of the relative abundance) to reduce the influence of both rare (low abundances and/or many zeros) and abundant taxa (Legendre & Gallagher, 2001). Significance in the PRC was tested using a permutation test (*anova.cca* function of the *vegan* R package) accounting for the non-independence of data due to repeated measurements on the same mesocosm. Significance in the difference between each treatment and the control was assessed with a multiple comparison test (*multiconstrained* function of the *BiodiversityR* R package). Roach' growth rate ( $G$ ) was computed using the formulae:

$$G = (L_{\text{final}} - L_{\text{initial}}) / L_{\text{initial}} * 100$$

where  $L_{\text{final}}$  and  $L_{\text{initial}}$  are the final and initial SL of roach, respectively.

Because growth data met the normality and homoscedasticity assumptions (Shapiro-Wilk and Bartlett tests, all  $p$  values  $> 0.05$ ), we used a linear mixed-effect model (*lme4* R package, (Bates et al., 2015)) with the noise condition as fixed factor and the mesocosm as random factor to test for significance of the difference in growth rate between the treatments.

The effects of noise and pre-exposure to noise on roach predation were assessed in two ways. First, we used a generalized linear mixed-effect model assuming a Poisson distribution to explain the total number of prey eaten as a function of the noise condition in the mesocosm, the noise condition in the aquarium and their interaction as fixed factors, and the mesocosm ID as random factor. Second, we estimated the preference of roach for *Daphnia* over

*Chaoborus* larvae using the Manly's alpha ( $\alpha$ ) preference index (Chesson, 1983; Manly, 1974):

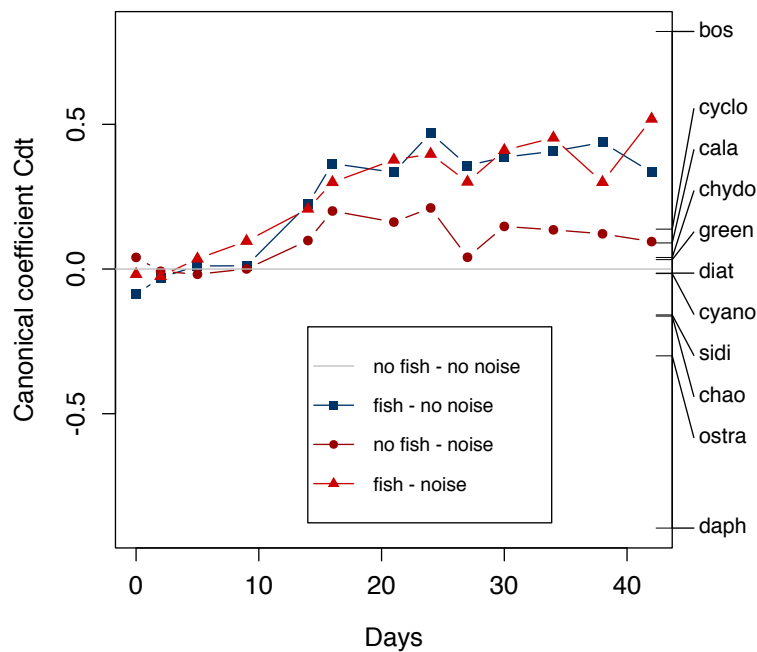
$$\alpha_{daphnia} = \ln(50 - N_{daphnia}) / (\ln(50 - N_{daphnia}) + \ln(50 - N_{chaoborus}))$$

where 50 is the initial number of each prey, and  $N_{daphnia}$  and  $N_{chaoborus}$  the numbers of daphnia and *Chaoborus* larvae eaten. The Manly's alpha accounts for prey depletion during the predation test and ranges from zero when only the alternative prey (here *Chaoborus* larvae) is eaten to one when only the focal prey (here *Daphnia*) is eaten. The value of 0.5 indicates a lack of preference. As recommended by (Manly, 1995), we compared obtained values to the theoretical value of 0.5 using  $t$  tests except for the "no fish – noise" treatment where we used a Wilcoxon test to deal with the non-normality of data.

Roach behaviour was analyzed with model averaging and an information-theory approach. We used linear mixed-effect models to model each of the three response variables (cumulative swimming distance, distance to the speaker and area of the group) as a function of the noise condition in the mesocosm, the noise condition in the aquarium, the time, and taking the mesocosm ID as random factor as several groups came from the same mesocosm. Because the noise condition that roach have experienced in the mesocosm might have changed their response to boat noise in the aquarium and because the effect of time may vary with the noise condition, we also included the interactions between the two noise treatments and between each noise treatment and time in the predictors. All predictors were centered and scaled using the *standardization* function of the *arm* R package. We ranked all the submodels based on small sampled-corrected AIC values ( $AIC_c$ , *dredge* and *get.models* functions of the *MuMIn* Rpackage) and performed model averaging on a confidence set of models using a cut-off of 10  $AIC_c$  (*model.avg* function of the *AICcmodavg* R package). The predictors whose parameter estimate had a 95% confidence interval (CI) that included the value of zero were considered as having no significant effect.

## 4. Results

The pelagic zooplankton communities of the mesocosms included four cladoceran families (Bosminidae, Daphniidae, Sididae and Chydoridae), cyclopoid and calanoid copepods, dipteran larvae of the genus *Chaoborus*, and some ostracods captured in the pelagic zone although being mainly benthic organisms. The diagram of the PRC analysis illustrates how adding roach, boat noise or both make the planktonic communities gradually deviate over time from those of the no fish – no noise treatment (i.e., control) considered as the baseline (Fig. 2).



**Figure 2:** Principal Response Curve (PRC) showing the effects of adding fish (squares), motorboat noise (dots) or both (triangles) on freshwater plankton communities compared to control communities (no fish – no noise, horizontal line, see text for further detail). Species weights are on the left axis (bos: Bosminidae, cyclo: cyclopoid copepods, cala: calanoid copepods, chydo: Chydoridae, green: green algae, diat: diatoms, cyano: cyanobacteria, sidi: Sididae, chao: *Chaoborus* larvae, ostra: ostracods, daph: Daphniidae). See Table 1 for the percentages of variance accounted for and the significance levels.

Adding boat noise made the communities deviate from the control and adding roach induced a larger deviation without variation between the two noise conditions (i.e., similar trajectories, Fig. 2). Table 1A shows that 30% of total variance was attributed to time and 34% to the treatment regime, including its interaction with time. On the basis of the permutation tests, the treatment regime as well as time and their interaction had a significant influence on the community dynamics (Table 1B). The pairwise comparisons revealed that the difference between the two treatments with roach (with or without noise) was the only to be not significant (Table 1C). *Bosminidae* and to a lesser extent *Chydoridae*, both copepod taxa and green algae are indicated with a positive taxon weight in the PRC, suggesting they were expected to increase in abundance with the treatments relative to the control and in proportion to their weight. On the other hand, *Daphniidae* and, to a lesser extent ostracod, *Sididae* and *Chaoborus* larvae exhibited negative species weights and were expected to decrease in abundance with the treatments. The taxa weights of diatoms and cyanobacteria were the smallest and close to zero (Fig. 2).

**Table 1:** Results of the Principal Response Curve (PRC) for the effect of motorboat noise (absence / presence) and fish (absence / presence, for a total of four treatments) on freshwater planktonic communities. A) Proportion of the total variance explained by the constraints: time, treatment, and their interaction, captured by the canonical 1st axis of the PRC. B) Significance of the PRC diagram on the basis on the permutation test for Constrained Correspondence Analysis (CCA, 999 permutations). C) Pairwise comparisons for all the possible treatment combinations following a CCA analysis.

A)

	<b>Inertia</b>	<b>Proportion</b>	<b>Rank</b>
Total	0.236	1	
Conditional (% of the total variance explained by time)	0.071	0.3	12
Constrained (% of the total variance explained by time*treatment)	0.085	0.36	11
Unconstrained (% of the total variance not explained by predictors)	0.08	0.34	11

B)

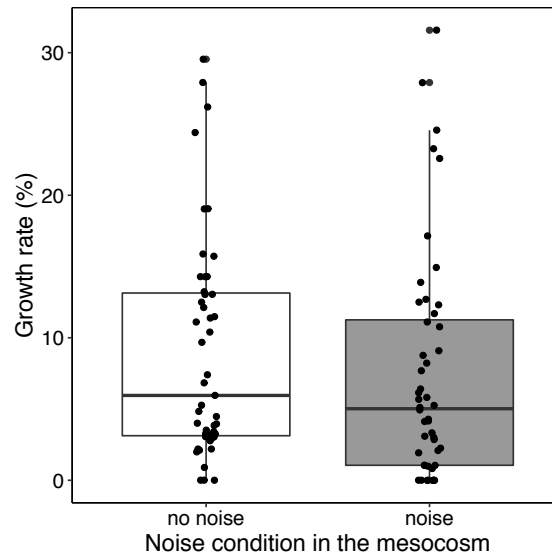
	Df	Variance	F	Pr(>F)
Treatment	3	0.04	19.28	0.001 ***
Time	1	0.06	77.32	0.001 ***
Treatment*Time	3	0.02	8.98	0.001 ***

C)

Pairwise comparison	Df	Sum of Sqs	F	Pr(>F)
no fish - no noise fish - no noise	1	0.054	23.856	0.001 ***
no fish - no noise no fish - noise	1	0.011	4.801	0.003 **
no fish - no noise fish - noise	1	0.059	22.593	0.001 ***
fish - no noise no fish - noise	1	0.022	8.902	0.001 ***
fish - no noise fish - noise	1	0.005	1.624	0.177
no fish - noise fish - noise	1	0.027	9.523	0.001 ***

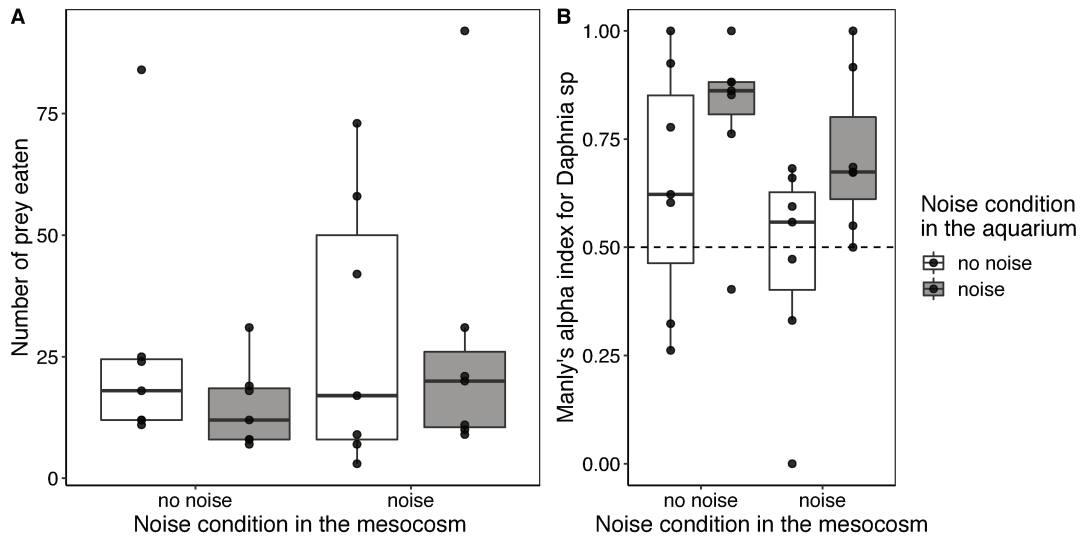
Individual fish growth did not significantly differ between the noise conditions ( $X_1^2 = 1.4813$  and  $p = 0.2236$ , Fig. 3). In the absence of roach, prey survival in the aquaria was 100% for both prey in the absence of boat noise, and 100% for *Chaoborus* larvae and 98% for *Daphnia* in the presence of boat noise.





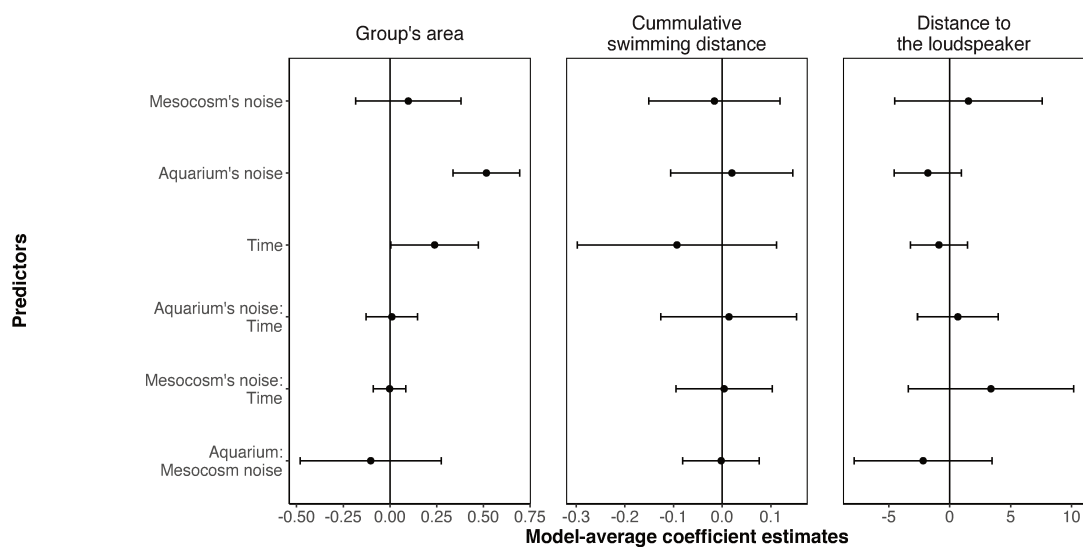
**Figure 3:** Fish growth rates (medians and interquartile ranges) in the mesocosms depending on the noise condition (white box: ambient, grey box: boat noise,  $n = 48$  per condition).

We therefore considered prey mortality during the predation tests to be the result of fish predation only. The effect of noise on the total number of consumed prey depended on the noise condition in the mesocosms, with significantly less prey consumed only for roach coming from the noiseless mesocosms ( $X^2 = 18.36$  and  $p < 0.001$  for the interaction between the two noise conditions, Fig. 4A). Whatever the noise condition in the mesocosm, the Manly's alpha index did not differ from the theoretical value of 0.5 in noiseless aquaria ( $t = 1.36$  and  $p = 0.22$  for ambient noise,  $t = -0.32$  and  $p = 0.76$  for boat noise) but was significantly higher with boat noise ( $V = 27$  and  $p = 0.03$  for ambient noise,  $t = 3.10$  and  $p = 0.02$  for boat noise, Fig. 4B). Concerning the cumulative swimming distance and the distance to the speaker, the 95% CI of the parameter estimate included the value of zero for all the predictors.



**Figure 4:** Results of the predation tests in aquaria with A) the total number of prey eaten *per* group of three fish (n=7 groups per acoustic mesocosm-aquarium treatment) presented to 50 *Daphnia* and 50 *Chaoborus* larvae and B) the Manly's alpha preference index for *Daphnia* over *Chaoborus* larvae (medians and interquartile ranges) as a function of the noise condition previously experienced in the mesocosms and the noise condition in the aquaria (white box: ambient, grey box: boat noise).

Concerning the area occupied by the group, boat noise in the aquarium and time were the only predictors whose parameter estimate 95% CI did not include the value of zero, with significantly positive values (Fig. 5).



**Figure 5:** Model-averaged coefficient estimates and 95% confidence intervals for the predictors included in the confidence set of models explaining the behaviour of roach *Rutilus rutilus* in groups of three individuals when feeding on *Daphnia* and *Chaoborus* larvae during the predation tests in aquaria. We used as response variables A) the area of the group, B) the cumulative swimming distance and C) the distance to the speaker. Predictors correspond to the noise condition in the mesocosms (boat noise or ambient noise as control), the noise condition in the aquaria of the predation tests (boat noise or ambient noise as control), the time, and the two-way interactions between time and the noise condition in the two experimental units and between the noise conditions of the two experimental units.

## 5. Discussion

Exposure to anthropogenic noise is known to elicit physiological or behavioural responses in individual organisms (Cox et al., 2018; Francis & Barber, 2013; Kight & Swaddle, 2011; Shannon et al., 2016; Sordello et al., 2020). But to what extent these alterations spread across ecological interactions to alter community dynamics and ecosystem functions is not clear. We conducted a mesocosm investigation to study the impact of chronic exposure to motorboat noise on the dynamics of a zooplankton – phytoplankton system either alone or dominated by a planktivorous fish. Although we detected alterations in fish feeding and behaviour, the strength of top-down control and its consequences on the structure of the planktonic communities were resilient to motorboat noise. This suggests that individual responses to noise do not necessarily result in ecological effects at the level of communities.

The pelagic mesoplankton communities of our mesocosms were dominated by cladocerans and copepods, two major groups of herbivorous microcrustaceans widespread in freshwater bodies. In smaller proportions, they also included ostracods (coming from the benthic areas of the mesocosms), and predatory larvae of the *Chaoborus* genus, known to feed on small zooplankton (Elser et al., 1987). In fishless mesocosms, daphnid cladocerans gradually became the most abundant taxa. Compared to copepods, cladocerans have higher reproduction rates. Moreover, because daphnids are the largest cladocerans, they suffer smaller predation risk by *Chaoborus* larvae than the other cladocerans (Jäger et al., 2011).

The presence of roach made the planktonic communities gradually deviate from those of the fishless communities with a shift in the dominant taxon of zooplankton from daphnids to bosminids whose abundance greatly increased. Visual-feeding fish like roach tend to prefer large zooplankton (Jarolím et al., 2010) and it might be that selective predation on the two largest taxa: *Chaoborus* larvae and daphnids, has released bosminids from predation and competition. Alteration in the daphnids – bosminids balance is symptomatic of fish presence (J. R. Post & McQueen, 1987).

To a lesser extent, copepods and Chydoridae have also benefited from the roach-induced decrease in daphnids. This might be explained by the greater availability of food resources like green algae, which slightly increased in the presence of roach, but also rotifers that represent another important taxon of freshwater zooplankton. Due to their small size, we did not count the number of rotifers but they are known to increase in the presence of fish because of the removal of large cladocerans (Gilbert, 1988). The slight increase in green algae in the presence of roach is consistent with the trophic cascade hypothesis: fish have a negative direct effect on zooplankton (here daphnids) and indirectly benefit phytoplankton that is released from grazing (Bertolo et al., 1999). Another way roach can influence the planktonic communities is through the modulation of diel migration patterns. Indeed, some taxa migrate to the bottom under chemical cues by predators and become less frequent in the pelagic realm (Cohen & Forward, 2016).

Motorboat noise did not alter the top-down structuring effect of roach on the planktonic communities and particularly the shift from daphnids to bosminids. This suggests that chronic exposure to noise had no effect on the feeding behaviour of roach, which is consistent with the absence of difference in growth rate between the two noise conditions. This is also consistent with the total number of prey eaten recorded during the predation tests, which was significantly reduced by motorboat noise for the roach that never experienced boat noise before but not for those pre-exposed to boat noise in the mesocosms. Weakening of the response to noise after repeated exposure has been reported in other fish species (Nedelec et al., 2016; Neo et al., 2018; Rojas et al., 2021), and might reflect habituation through associative learning: naïve animals first allocate attention to noise at the expense of other activities like feeding, and then resume normal behaviour as they learn that it is not associated with any threat. However, when looking closer to what has been eaten, we found motorboat

noise to elicit selective preference for daphnids over *Chaoborus* larvae even for roach pre-exposed to boat noise in the mesocosm.

This persistent response could find its origin in behaviour. Concerning invertebrates, although we did not record their behaviour, we know from past investigations that motorboat triggers body rotations in *Chaoborus* larvae (Rojas et al., 2021), interpreted as an anti-predatory response (Berendonk & O'Brien, 1996; Burrows & Dorosenko, 2014) that could have driven the choice of roach towards daphnids. Concerning roach behaviour, we found no alteration in mobility and no evidence for any avoidance of the sound source, but the area occupied by the three individuals was larger under motorboat noise. This effect seems to be persistent as it was also observed with the roach pre-exposed to boat noise in the mesocosms. Similarly, playback of pile driving was found to make juveniles of seabass less cohesive (Herbert-Read et al., 2017). Noise could mask the perception of nearest neighbours' movements through the lateral line or impair the ability to process sensory information as a consequence of stress and/or distraction (Herbert-Read et al., 2017). Compared to stress or distraction, masking does not weaken with repeated exposure. This could explain why the reduced group cohesion was also observed in the roach that experienced motorboat noise in the mesocosms. Disruption of group cohesion could ultimately compromise the benefits of grouping associated with the dilution and confusion effects (Krause et al., 2002).

Regarding feeding, we can expect the strength of intra-specific competition to decrease with the distance between individuals. Together with the lesser catchability of moving *Chaoborus* larvae, this could explain why the roach showed selective preference for daphnids under motorboat noise. At the level of communities, a selective preference for daphnids, who were the main grazers, should have strengthened the trophic cascade, which we did not observe. The change in feeding we found in the aquaria may not have been strong enough to be detected in the mesocosms or maybe does not occur in a larger and more complex environment where other prey items are available.

In the fishless mesocosms, adding motorboat noise induced a small but detectable deviation from the control communities. This is interesting but also tricky to interpret since very little is known on the response of freshwater plankton to chronic anthropogenic noise. *Chaoborus* larvae occupied the highest trophic level of the fishless communities and we know that they are sensitive to motorboat sounds with more body rotations (Rojas et al., 2021),

interpreted as an anti-predatory response (Burrows & Dorosenko, 2014). If noise also interferes with prey processing and reduces the capture efficiency of *Chaoborus* larvae, then it could be beneficial to small zooplankton. Noise could also trigger vertical migration to the bottom, as chemical cues from predators do (Cohen & Forward, 2016), making some taxa like ostracods less detectable in the pelagic realm. Additional long-term investigations in mesocosms but also *in situ* are needed to better understand the response of planktonic communities to chronic anthropogenic noise.

Our investigation illustrates how extrapolating the impact of anthropogenic noise from individual responses to complex communities is far from obvious. Although we observed persistent alterations in roach behaviour with less group cohesion and altered feeding preference, these effects did not propagate downward along the food chain through trait-mediated cascading effects. A valuable perspective would be to study the dynamics of roach under chronic anthropogenic noise to test whether the behavioural responses we observed ultimately decrease survival and/or reproductive success (Amorim et al., 2022), and result in density-mediated cascading effects.

#### **ACKNOWLEDGEMENTS**

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#### **ETHIC STATEMENTS**

All the procedures were conducted in accordance 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).

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#### **DATA AVAILABILITY**

The data that support the findings of this study are open available in Zenodo at <https://doi.org/10.5281/zenodo.6760791>.

### III. Article 5: Response of freshwater zooplankton communities to chronic anthropogenic noise

*This article will be a chapter of the next AN2022 book by Springer Nature as part of the Aquatic Noise Life congress of Berlin. It is not finish yet, but it will be submitted in December 2022.*

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## 1. Abstract

Man-made sounds are now recognized a pervasive pollutant and impacts on wildlife have been researched for many years. However, less knowledge is available on certain species and particularly small freshwater invertebrates, although abundant, highly diversified and occupying key positions in food webs. Also, it's not clear whether the responses to noise observed at the level of individuals have consequences on communities. A mesocosm investigation was performed to assess the response of a freshwater planktonic community to chronic motorboat noise. Noise was expected to disturb trophic links within the community and particularly the consumption of cladocerans by dipteran larvae. To test this hypothesis, the functional response *Chaoborus* larvae feeding on *Daphnia* was derived and their behaviour during the foraging process was recorded in aquariums. Although noise did not induce obvious alteration in the community composition, a significant increase in the abundance of cladocerans was found that was not supported by the results of our aquarium investigation, showing no difference in *Chaoborus* functional response or behaviour between the noisy and noiseless conditions. The results of this chapter suggest that the composition of freshwater zooplankton and particularly cladocerans is likely to be altered by chronic noise, with further investigations needed to understand the mechanisms. They also illustrate how scaling up the effects of noise from individual responses to community remains difficult.

**Key words:** Freshwater zooplankton, motorboat noise, functional response, trophic links, daphnids, *Chaoborus* larvae

## 2. Introduction

Threats to freshwaters include habitat degradation, flow modification, overexploitation, invasive species and disease (Dudgeon et al., 2006; Williams-Subiza & Epele, 2021), and result in a decline in biodiversity at rates that exceed what is reported in most terrestrial and marine habitats (McRae et al., 2017). Anthropogenic pressures on freshwaters are not expected to ease given the growing of human needs and also because people seek to reconnect with nature, a need reinforced by the recent crises like the Covid-19 pandemic. Managers of freshwaters socio-ecological systems worry about the rise of recreational motorized activities

and their associated noise emissions (Reid et al., 2019) that can disturb the various populations of users as well as wildlife.

Noise pollution has recently been categorized as an emergent threat to freshwaters (Reid et al., 2019), with motorized boats as the most widespread source of noise. Impacts of noise on fishes are well documented with physiological stress responses and alterations in communication, reproduction, mobility, foraging and predator avoidance (reviewed by Mickle & Higgs, 2018; Popper, 2003; Slabbekoorn et al., 2010). Although invertebrates are highly diverse, widespread and possess statocysts or external sensory hairs that allow them to perceive sounds through particle motion (Popper & Hawkins, 2018), interest in their response to noise pollution came later compared to vertebrate species and 77% of the impact studies on invertebrates are less than ten years (Wale et al., 2021). While cephalopods, large crustaceans (crabs, lobsters, shrimps) and bivalves are among the most common model species studied (Fernández Robledo et al., 2019; C. S. Smith et al., 2018), little is known about small zooplankton despite its pivotal role in the functioning of aquatic food webs, maintaining energy flow between primary producers and higher trophic levels (Turner, 2004; Vargas et al., 2010).

Available evidence on zooplankton shows a diversity of effects. While very loud emissions from seismic surveys have been found to cause mortality in both larval and adult stages of marine zooplankton (McCauley et al., 2017), vessel noise can act as a positive cue for larval settlement in the blue mussel *Mytilus edulis* (Jolivet et al., 2016). Exposure to low (30 Hz) and high (20 KHz) frequencies seems to promote grazing in the marine copepod *Acartia tonsa* (Yiwei & Berggren, 2018). The water flea *Daphnia magna* (Cladocera) shows no alteration in mobility when exposed to either continuous or intermittent 300-1500 Hz band-pass filtered white noise (Sabet et al., 2016). More recently, it was found that larvae of the phantom midge *Chaoborus* (Diptera) made more body rotations in response to motorboat noise (Rojas et al., 2021).

In addition to the imbalance between vertebrates and invertebrates in the very rich literature on the impacts of noise pollution, there is also a discrepancy between the biological integration levels with a lack of research on ecosystems compared to behavioural and physiological outcomes (Sordello et al., 2020). Although few empirical evidence from terrestrial systems illustrate how noise-induced changes in behaviour can propagate through nested ecological interactions (Francis & Barber, 2013; Phillips et al., 2021), scaling up the

effects of noise from individuals to populations and communities without any experimental validation might overestimate impacts.

In this chapter, the effect of chronic motorboat noise on the dynamics of a freshwater zooplankton community was investigated bringing together cladocerans, copepods, ostracods, and dipterans. Noise was expected to alter the structure of the community through changes in abundances and/or changes in the activity of the predators. To test this hypothesis, the response of the community was evaluated in mesocosms over six weeks and, as a second part, it was assessed how the *per capita* predation rate of *Chaoborus* larvae (dipterans) varied with cladoceran density (the functional response) under control and noisy conditions. *Chaoborus* larvae are a relevant dominant predator of large filter-feeder zooplankton (cladoceran species) known to be a main structuring force within the community (Castilho-Noll & Arcifa, 2007; Vanni & Findlay, 1990). *Chaoborus* larvae have been found to make more body rotations in response to motorboat noise (Rojas et al., 2021), which could be associated with reduced foraging. Noise might therefore alter community dynamics through the modulation of the trophic pressure by *Chaoborus* larvae.

### 3. Methods

#### 3.1 Mesocosm experimental design

The mesocosm experiment lasted six-weeks from September to October 2021 and was carried out on the PLANAQUA platform of the CEREEP-Ecotron Ile -de-France research station (48° 16'10.92 N, 2° 43'50.879 E, Seine et Marne, France). Two acoustic conditions (with or without boat noise, see 4.4) were applied in 16 outdoor plastic enclosures (diameter: 1.40 m, depth: 1 m, volume: 1 m<sup>3</sup>, n = 8 replicates *per* condition) positioned in two lines and distributed in a systematic way to balance the effect of spatial distribution between the two conditions. All mesocosms included a 15-cm layer of Loire sand and were filled two months before the experiment with water from the littoral zone of one of the two storage lakes from the PLANAQUA platform, to reach a 70-cm water column. An underwater loudspeaker (Electrovoice UW30, 0.1–10 kHz) was fixed 10 cm below the water surface in the middle of each mesocosm. It was connected to an amplifier (Dynavox CS-PA 1MK), itself connected to an audio player (Handy's H4n zoom), both placed inside a waterproof electric box next to the

mesocosm. One week before starting the experiment, temperature loggers attached to a ballast were positioned in the sunniest part of each mesocosm. Water temperature was 24°C at the beginning of the experiment and decreased with some small fluctuations over time to reach 18 °C at the end of experiment.

## 2. Zooplankton dynamics

At Day 0, +10, +26, and +42, eight liters of water were sampled with a 2-L sampling bottle at four different positions and depths in each mesocosm. Water was filtered with a 50- $\mu$ m mesh size nylon filter to collect zooplankton species which were immediately fixed in 15 mL of 90% ethanol. Species identification and classification of Day 0 and Day +42 were performed by the engineering office © 2021 SAGE Environment (Annecy, France). To save costs accurate classification was done for all the mesocosms at Day+42 while the data *per* noise condition at Day0 was pooled. At Day+10 and Day+26, only the numbers of cladocerans and *Chaoborus flavicans* larvae was quantified as it was the most structuring trophic link expected in the communities. At the end of the experiment, a multiparameter probe (YSI ExO-2) was used to assess the main physicochemical parameters (temperature, pH, conductivity, turbidity, chlorophyll).

## 3. Functional response and behavior of *Chaoborus* larvae

The functional response (FR) of *Chaoborus* larvae feeding on five densities (3, 6, 12, 24, 48) of *Daphnia* sp. coming from the storage lake has been derived with four replicates *per* density and *per* noise condition. To account for potential habituation to the noise condition and better explain what happened in the mesocosms, larvae from the control and noisy mesocosms were collected and exposed to the same noise condition (see 4.4) during the FR tests. The experiment took place in two 90-L rectangular tanks (75 x 60 x 20 cm, one *per* noise condition) filled with filtered (50- $\mu$ m mesh size) water from the storage lake. A UW30 underwater loudspeaker was positioned in the center of each tank 20 cm above the bottom. A single larva was presented to the water fleas at one of the five densities (3 to 48) for eight hours in a 150-mL glass beaker (height = 7.2 cm, diameter = 7 cm) covered with a 0.03 mm mesh allowing water flow only. A total of 20 beakers *per* mesocosm were used and placed at 10 cm all around the speaker. At the end of the experiment, each larva was removed and put

into 90°C alcohol to be measured under binocular loop and using a rule. The number of remaining prey was counted to determine the number of prey eaten.

The behaviour of the *Chaoborus* larvae was studied in a 50-L aquarium (length×width×height: 60×25×35 cm) filled with filtered water from the mesocosms and equipped with an UW30 underwater loudspeaker in the center and 20 cm above the bottom. A 150-mL glass beaker containing 20 larvae and covered with a mesh allowing water flow only was positioned inside the aquarium at 10 cm of the loudspeaker. The number of body rotations performed by each larva was counted over a 20-min period of ambient noise (recorded in one of the mesocosm) or ambient noise supplemented with motorboat noise (see 4.4).

#### 4. Playback tracks

An Aquarian Audio H2A-HLR hydrophone (frequency response from 10 Hz to 100 kHz) connected to a ZOOM H4next Handy recorder was used for all the recordings and a UW30 underwater speaker (Electrovoice) connected to a Dynavox CS-PA 1MK amplifier itself connected to a ZOOM H4next Handy player for all the playbacks.

Natural background noise did not differ between the mesocosms and was around 90 dB re 1  $\mu$ Pa. In the control mesocosms, a 1-hr audio track of silence was looped continuously. To make the audio tracks of the noisy mesocosms, 25 sounds from commercial vessels and recreational boats were recorded from the river Seine after the lock of Champagne sur Seine (48°22'1.348 N. 2°29'37.401 E) at 1-m depth. The 25 original sounds were duplicated, changing a bit the intensity between the two replicates, and the resulting 50 sounds were distributed over 14 consecutive 1-hr audio tracks of silence so as to mimic the mean daily activity of the Champagne sur Seine lock (Table 1). The boat sound audio tracks were broadcasted from 6 am to 8 pm and silence the rest of the time. The intensity of each boat sound was modified with the Audacity 2.2.1 software to obtain realistic Signal-to-Noise Ratios (SNR) ranging from 25 to 30 dB (Fig. 1A), calculated after re-recordings in the mesocosms and using the *SNR* function of *Seewave* R package (Sueur et al., 2008) with:

$$\text{SNR} = 20\log_{10}(\text{RMS}_{\text{boat sound}} / \text{RMS}_{\text{ambient noise}})$$

where RMS corresponds to the Root-Mean-Square sound pressure level.

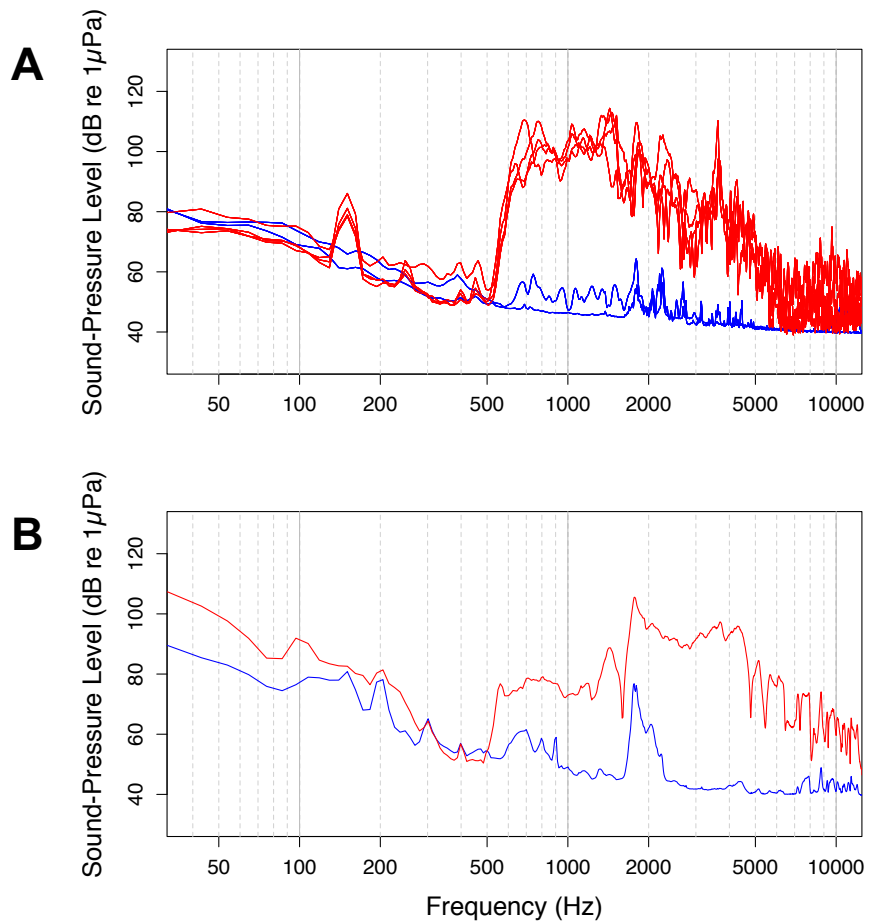
For the control condition of the FR experiment, an 8-h (playlist 1) audio track of natural background noise previously recorded in one of the mesocosm and whose level was adjusted to match that in the mesocosm around 90 dB re 1  $\mu$ Pa (Fig. 1A) was broadcasted. For the boat noise treatment, an 8-h recording (playlist 2) from a noisy mesocosm (Fig. 1A) was broadcasted using the same process than for control condition.

Concerning the behaviour of the *Chaoborus* larvae, a 20-min period of playlist 1 was randomly selected to be used for the control condition and a 20-min sequence of playlist 2 corresponding to the period with the largest number of boat sounds was used for the noisy condition (Fig. 1B).

**Table 1.** Composition of the 14-h playback track broadcasting silence supplemented with motorboat sounds during the mesocosm experiment.

Hour	Number of boat sounds	Boat ID	Duration in min	Start position in the 1-h track
6h	3	17	07'00	5'00"
		31	05'35	47'00"
		45	06'10	51'00"
7h	1	29	06'00	23'50"
8h	2	44	04'20	13'50"
		20	01'25	40'30"
9h	4	8	01'40	0'00"
		46	07'15	14'30"
		47	03'02	32'25"
		2	04'37	36'15"
10h	6	11	06'05	2'55"
		10	02'20	13'35"
		42	02'30	16'25"
		50	03'30	19'30"
		41	02'00	18'40"
		33	02'35	54'10"
11h	4	48	03'02	16'45"
		42	02'30	33'15"
		30	05'00	35'50"
		30	05'00	53'05"
12h	2	2	04'37	8'25"
		27	07'00	18'45"

13h	4	6 38 50 46	05'00 04'00 03'30 07'15	01'45" 17'40" 22'00" 40'50"
14h	6	40 17 24 20 25 10	04'15 02'00 03'02 01'25 06'30 02'20	01'45" 05'30" 07'45" 29'15" 35'10" 42'05"
15h	8	42 15 50 2 9 12 12 18	02'30 01'30 03'30 04'37 02'35 08'00 08'00 05'05	00'35" 07'00" 03'35" 14'21" 21'54" 26'45" 44'16" 54'55"
16h	4	20 44 23 35	01'25 04'00 07'15 06'05	00'00" 06'05" 20'52" 32'19"
17h	2	45 46	06'10 07'15	39'17" 46'22"
18h	1	13	03'30	27'07"
19h	3	31 30 42	05'35 05'00 02'30	24'03" 30'43" 49'29"



**Figure 1.** Sound spectra of the two noise conditions (ambient noise in blue and boat noise in red) in: A) the mesocosms used for the community investigation (each red lines correspond to a recording of the same boat noise made in four noisy mesocosm and each blue lines correspond to a recording of 3-min of ambient noise made in two control mesocosms); and B) the aquariums (50-L rectangular tank) used for functional response derivation.

## 5. Data analysis

The R software version 4.0.3 (R Core Team, 2018) was used for all the statistics with a significance level of 5%. A chi-square test of independence was performed to assess the homogeneity of taxa at Day+0 between both noise treatments. A generalized linear mixed models with a quasi-poisson distribution (GLMMTMB) was performed to explain the dynamic of cladocerans as a function of three fixed factors and their interactions: the noise condition (ambient or motorboat noise), the abundance of *Chaoborus flavicans* larvae, the sampling date, and considering the tank identity as random factor to account for repetitive measures. A Quasi-Poisson (or quasi-likelihood) distribution was used because it is recommended to consider the overdispersion (variance exceeds the mean) often found in



count data (Ver Hoef & Boveng, 2007). A Wilcoxon test was used to test for significance the difference in physicochemical parameters between the two noise conditions at Day+42.

For the FR experiment, a one-way ANOVA test was performed to detect heterogeneity in the size of *Chaoborus* larvae between the two noise conditions as the data met the normality and homoscedasticity assumptions. FR analysis was done with the *Frair* R package (Pritchard et al., 2017). The three main categorical FR types (linear type I, Rogers' type II, Hassel's type III) were modelled by maximum likelihood estimation (Bolker, 2008) with the *frair\_fit* function and the fits were compared using the second order Akaike information criterion (AIC). This allowed to exclude the types II and III whose AIC values were always the highest ( $\Delta\text{AIC} > 2$  with the type I). A type I FR is characterized by a linear increase of consumption rate as a function of prey density (Holling, 1959b). Both FRs being of type I, the delta method implemented by the *frair\_compare* function was used to perform pairwise FR comparison from parameter estimates with the null hypothesis that the difference in attack rates ( $D_a$ ) between the two FRs does not differ from zero (Pritchard et al., 2017). In addition, the overlaps of the 95% confidence intervals (BCa CIs) which correct for bias and skewness in the distribution of bootstrap estimates ( $a$  and  $h$  parameters) were inspected using the *frair\_boots* function (bootstrapping method,  $n=2,000$ ) (Pritchard et al., 2017).

Concerning the behaviour of the *Chaoborus* larvae, the total number of body rotations was compared between the two noise conditions using a generalized linear mixed models with a negative binomial distribution with the noise condition (ambient or motorboat noise), the sampling date as predictors and the tank where they coming as random factor to account for repetitive measures.

## 4. Results

At Day+0, communities between ambient noise and ambient + motorboat noise did not differ in taxa density (Chi-square test = 63.333,  $df = 56$ ,  $p\text{-value} = 0.2336$ ). At Day+42, no significant differences in the physicochemical parameters between the two noise conditions (Table 2 and 3) was found.

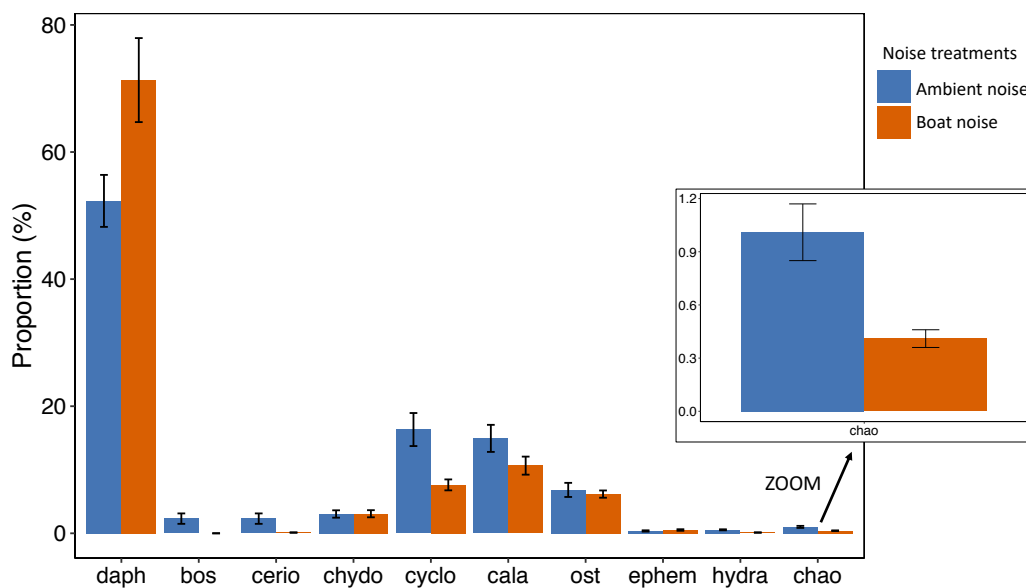
**Table 2.** Physicochemical parameters (mean  $\pm$  SD) in the control (ambient noise) and noisy mesocosms (boat noise) at the end of the experiment, with the results of the Wilcoxon tests performed to test the difference between the two noise treatments.

<b>Parameters</b>	<b>Ambient noise (mean <math>\pm</math> SD)</b>	<b>Boat noise (mean <math>\pm</math> SD)</b>	<b>W</b>	<b>p-value</b>
<b>pH</b>	7.60 $\pm$ 0.59	7.70 $\pm$ 0.37	266.5	0.665
<b>Temperature °C</b>	15.66 $\pm$ 0.08	15.66 $\pm$ 0.13	257.5	0.536
<b>[Chlorophyll] <math>\mu</math>g/L</b>	1.49 $\pm$ 0.87	1.71 $\pm$ 1.68	331	0.38
<b>ODO mg/L</b>	9.64 $\pm$ 0.32	9.62 $\pm$ 0.33	277.5	0.836
<b>Conductivity uS/cm</b>	165.32 $\pm$ 8.11	167.66 $\pm$ 5.74	212.5	0.121

**Table 3.** Physicochemical parameters obtained at Day+0 and at Day+42 for all outdoor mesocosm.

Tank	Noise condition	Temperature (°C)	pH	Conductivity (us/cm)	Green algae (µg/L)	Cyanobacteria (µg/L)	Diatoms (µg/L)	Chlorophyll concentration (µg/L)	Turbidity (FNU)
1	Ambient	15.57	9.2	159.33	6.14	2.02	0.48	0.85	1.44
2	Boat	15.79	9.71	180.33	6.81	0	0.33	0.75	0.97
3	Ambient	15.68	9.76	172.9	7.55	0.92	0.3	0.88	1.15
4	Boat	15.73	9.55	165.63	7.58	1.65	0.87	0.45	1.1
5	Ambient	15.69	9.56	165.87	7.69	0.22	0.34	1.17	1.36
6	Boat	15.62	9.22	171.4	7.73	0.62	0.18	0.87	1.32
7	Ambient	15.71	9.37	181.07	7.76	0.25	0.24	1.05	1.18
8	Boat	15.59	9.96	166.23	7.95	1.08	0.43	0.96	0.99
9	Boat	15.39	9.86	161.8	7.91	6.21	0	5	6.04
10	Ambient	15.72	9.37	154.33	7.82	3.88	0.37	3.65	3.65
11	Boat	15.77	9.43	161.7	7.8	1.13	0.41	0.98	1.14
12	Ambient	15.73	9.92	161	7.92	0.76	0.16	1.36	1.26
13	Boat	15.65	9.32	167.5	7.9	0	0.21	0.79	0.86
14	Ambient	15.63	9.72	160.97	7.89	0.07	0.14	0.97	0.93
15	Boat	15.7	9.93	166.7	7.93	0.55	0.19	0.83	1.29
16	Ambient	15.53	10.21	167.17	8.05	0.26	0.07	0.66	0.95

The zooplankton communities of the noisy and noiseless mesocosms included Cladocerans (*Daphnia* sp., *Bosmina* sp., *Chidorus* sp. and *Ceriodaphnia* sp.), Copepods (especially Calanoïda and Cyclopoïda), Ostracods and Dipterans (especially *Chaoborus* larvae). Cladocerans species and more particularly *Daphnia* sp. were the most abundant at the beginning and the end of the experiment in the control mesocosms (57.31% and on average 52.11% respectively) whereas in the noisy mesocosms, Copepods and Cladoceran were more abundant at Day+0 (48.25% and 39.84% respectively) but Cladocerans increased to reach 71.24% of the whole community at the end of the experiment (Table 4, Fig. 2).

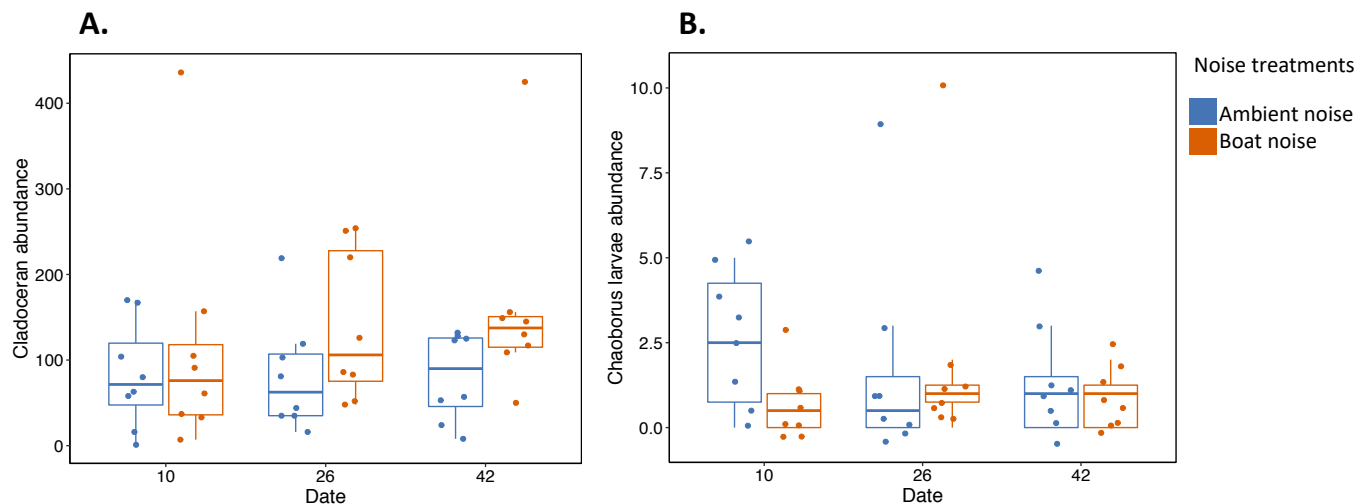


**Figure 2.** Frequency distribution (mean  $\pm$  SD) of the zooplankton taxa found in the control (blue) and noisy (orange) mesocosms at the end of the experiment with a focus on *Chaoborus flavicans* larvae, the main predator (daph: *Daphnia* sp., bos: *Bosmina* sp., cerio: *Ceriodaphnia* sp., chido: *Chidorus* sp., cyclo: Cyclopoids, cala: Calanoïds, ost: Ostracods, ephem: Ephemeroptera, hydra: Hydracarina and chao: *Chaoborus flavicans* larvae (Diptera)).

**Table 4.** Count of taxa at Day+0 and at Day+42 for all outdoor mesocosm (n=16) in both noise conditions (ambient noise, n=8 or ambient noise with boat noise, n=8).

Order	taxa	Day+0 ambient noise (total, n=8)	Day+0 boat noise (total, n=8)	Day+42 ambient noise (total, n=8)	Day+42 boat noise (total, n=8)	Day+42 ambient noise (mean $\pm$ SD per mesocosm)	Day+42 boat noise (mean per mesocosm)
Copepods	Cyclopoïds	79	73	177	131	22.13 $\pm$ 28.2	16.38 $\pm$ 14.86
Copepods	Calanoïds	158	162	162	183	20.25 $\pm$ 23.06	22.88 $\pm$ 24.47
Cladocerans	<i>Bosmina</i> sp.	0	0	25	0	3.13 $\pm$ 8.84	0
Cladocerans	<i>Ceriodaphnia</i> sp.	2	0	25	2	3.13 $\pm$ 8.84	0.25 $\pm$ 0.71
Cladocerans	<i>Chydorus</i> sp.	10	5	33	53	4.13 $\pm$ 6.33	6.63 $\pm$ 9.65
Cladocerans	<i>Daphnia</i> sp.	439	189	567	1226	70.88 $\pm$ 44.32	153.25 $\pm$ 113.55
Crustacean	Ostracods	76	25	74	106	9.25 $\pm$ 12.08	13.25 $\pm$ 9.84
Insect	Ephemeroptera	11	0	4	9	0.5 $\pm$ 1.07	1.13 $\pm$ 2.10
Insect	<i>Chaoborus flavicans</i>	7	16	11	7	1.38 $\pm$ 1.77	0.88 $\pm$ 0.83
Insect	Hydracarina	2	1	6	2	0.75 $\pm$ 0.89	0.25 $\pm$ 0.71

The abundance of Cladocerans was significantly increased by noise (p-value = 0.044, Table 5, Fig. 3A) but was not influenced by the abundance of *Chaoborus*, the date and the interactions between predictors. The abundance of *Chaoborus* larvae did not differ between the two noise conditions (GLMMs, Estimate = 0.026, Std.Error = 0.501, z-value = 0.050, p-value = 0.960, Fig. 3B).



**Figure 3.** Variation in the abundances (median and interquartile range) of Cladocerans (A) and *Chaoborus* larvae (B) in the control (ambient noise, blue) and noisy mesocosms (ambient noise supplemented with boat noise, orange) at days 10, 26 and 42.

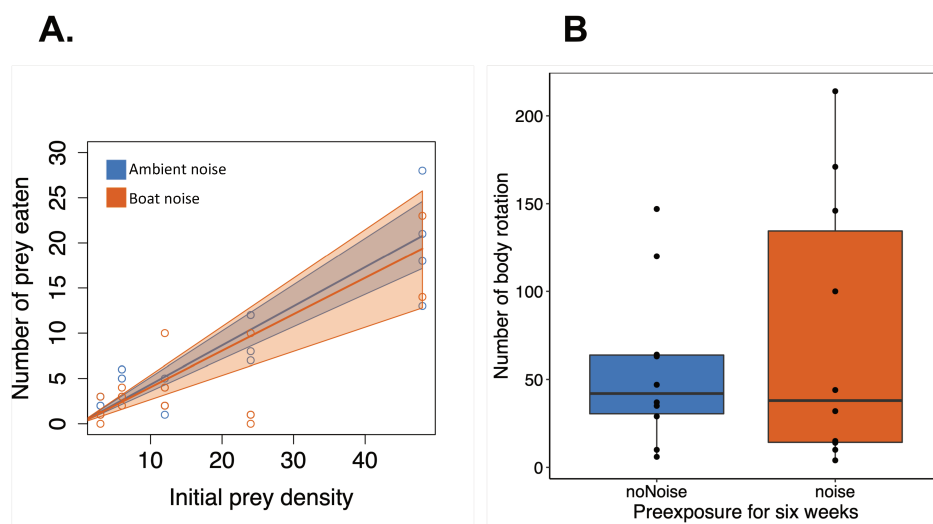
**Table 5.** Model-averaging coefficient estimates for the predictors included in the model selected explaining the amount of cladocerans species. Predictors correspond to the noise condition broadcasted in mesocosm (silence or chronic motorboat noise), the presence of *Chaoborus flavicans* larvae, the date, and interactions between all predictors.

	Estimate	Std.Error	Z value	P-value
Intercept	4.35259	0.19096	22.793	<b>&lt;0.001</b>
Noise	0.49052	0.24385	2.012	<b>0.0443</b>
Chaoborus	-0.06774	0.15784	-0.429	0.6678
Date	0.06991	0.13999	0.499	0.6175
Noise* <i>Chaoborus</i> larvae	0.20685	0.19719	1.049	0.2942

Noise*Date	0.19450	0.21705	0.896	0.3702
<i>Chaoborus</i> larvae*Date	-0.18475	0.17620	-1.049	0.2944
Noise* <i>Chaoborus</i> larvae*Date	0.41613	0.41402	1.005	0.3148

Concerning the FR experiment, there was no difference in the size of the *Chaoborus* larvae between the two noise conditions (one-way ANOVA:  $F_{1,18} = 0.269$ ,  $p\text{-value} = 0.61$ ). Irrespectively of the noise condition, the FR was a type I (linear increase of *per capita* consumption rate in function of prey density). No significant difference in attack rate (fixing the slope) was found between the two noise conditions (Estimate = 0.087, Std.Error = 0.108,  $z\text{-value} = 0.817$ ,  $p\text{-value} = 0.413$ ) supported by a strong overlap of the 95% BCa CIs, suggesting similar FRs (Fig. 4A).

No significant difference in the number of body rotations was found between the two noise conditions (noise: Estimates = 0.2957, Std.error = 0.4268,  $z\text{-value} = 0.693$ ,  $p\text{-value} = 0.488$ , Fig. 4B). However, inter-individual variability in both FR and behaviour was greater with boat noise than for controls.



**Figure 4.** A: Number of water fleas eaten by single *Chaoborus flavicans* larvae as a function of initial water flea density (functional response) under ambient noise (blue) or chronic motorboat noise (red).

Dots indicate the raw data and shaded areas the confidence intervals. B: Number of body rotations (median and interquartile ranges) made by the *Chaoborus flavicans* larvae exposed to recordings of ambient noise (blue) or chronic motorboat noise (red).

## 5. Discussion

In this chapter, a mesocosm investigation was conducted to assess the effect of chronic motorboat noise on the dynamics of freshwater zooplankton. Predation tests were also performed in microcosms through the functional response (FR) derivation to test the prediction that in case of a noise-induced alteration in community dynamics, this would be linked with a change in the foraging behaviour of invertebrate predators, focusing on *Chaoborus flavicans* as the main predator within the zooplanktonic community.

No marked effect of chronic motorboat noise on the zooplankton community was found except for water fleas (*Daphnia* sp.), which represented the most abundant taxon and were significantly more numerous in the noisy mesocosms. This apparent positive effect could be indirect, considering that noise has no or a very limited direct negative effect on water fleas but negatively influences their natural enemies. Although no investigation on the response of water fleas to noise was made, the absence of direct effect is partially supported by the little literature available. Sabet et al. (2016) did not find any alteration in mobility in *Daphnia magna* exposed to either continuous or intermittent 300-1500 Hz band-pass filtered white noise, a result that was also obtained working on motorboat noise (Rojas et al., unpublished data). More recently, (Yağcılar & Yardımcı (2021) found that exposure to 432 Hz and 440 Hz frequency sounds resulted in lower egg numbers and heartbeats in *D. magna*. However, the use of pure tones that do not refer to any kind of noise pollution in nature as well as the absence of information on sound levels make these results difficult to compare with the results of this chapter and also difficult to extrapolate to natural populations.

Concerning water fleas' natural enemies, it was reasonable to expect from the FR results that water fleas had experienced predation by *Chaoborus* larvae in the mesocosms. However, contrary to this assumption, noise did not alter the FR of *Chaoborus* larvae nor their behaviour assessed through the number of body rotations. The main difference between this chapter and the study by Rojas et al. (2021), where *Chaoborus* larvae displayed more body rotations with motorboat noise, is that we accounted for repeated exposure (i.e., chronic noise), what Rojas et al. (2021) did not. So, it might be that *Chaoborus* larvae show more body rotations when exposed to noise for the first time and then resume normal behaviour with repeated exposure, a phenomenon also referred to as "habituation" that has not been



addressed in the present chapter as the response of “naïve” larvae was not tested. Habituation to noise has been reported in many species including fishes (Johansson et al., 2016; Kusku, 2020; Rojas et al., 2021) and aquatic invertebrates (Hubert et al., 2022), and could result from sensory or motor fatigue, or associative learning between the repetition of a given stimulus and the absence of any threat.

Similar FRs irrespectively of the noise condition does not support the hypothesis that the water fleas of the noisy mesocosms benefited from a noise-induced reduction in *Chaoborus* predation. Surprisingly, the FR of *Chaoborus* larvae was of type I (linear increase of *per capita* predation rate with increasing prey density) whilst they were found to display a type-II FR (decelerating rise to an asymptote) in previous studies (Cuthbert et al., 2019; Krylov, 1992; Spitze, 1992; with *Daphnia pulex*, *D. longispina* and *Culex pipiens* as prey, respectively). Regarding the *Chaoborus* and *Daphnia* populations used in this chapter, the highest prey density used ( $n = 48$ ) was not enough to reach saturation and it is not possible to exclude an effect of noise at higher prey densities. Another reason why it was difficult to use the behaviour of the *Chaoborus* larvae to explain the increase in cladocerans in the noisy mesocosms could be that predation tests in small and highly-controlled experiment units are not representative of the foraging patterns occurring in more complex systems (i.e., the mesocosms used in this chapter). For instance, many zooplanktonic species including *Chaoborus* larvae and *Daphnia* show vertical migrations (Dawidowicz et al., 1990; Haupt et al., 2009). Noise might disturb trophic links within zooplankton through alterations in the species-specific spatial patterns. In other words, the tests performed in aquariums might have underestimated the negative effect of noise on *Chaoborus* predation.

To understand how noise influenced the zooplanktonic communities of the mesocosms, a focus was made on the trophic link between *Chaoborus* larvae and *Daphnia* and no work was made on the other ecological interactions, and in particular competition. Cladocerans are known to compete with rotifers and copepods for common food resources (Gilbert, 1988; Lehtiniemi M & Gorokhova E, 2008), copepods being the second planktonic group (after cladocerans) in terms of abundance in the mesocosms. The response of freshwater copepods to noise remains unknown but a negative effect could make the competition even more asymmetric in favor of cladocerans. The three groups are also engaged in apparent competition by sharing *Chaoborus* larvae as predator (Elser et al., 1987; Swüste et al., 1973). An interesting perspective would be to assess their respective contribution to *Chaoborus*' diet under chronic noise.

To conclude, this chapter suggests that chronic motorboat noise is likely to disturb the composition and dynamics of freshwater zooplankton without providing evidence for any alteration in the trophic link between *Daphnia* sp. and *Chaoborus* larvae. The effects of chronic motorboat on freshwater zooplankton probably involves the modulation of ecological interactions but this remains to be further investigated. This chapter also illustrates how scaling up individual responses obtained in highly controlled conditions to the level of communities remains tricky. Additional research on the long-term effect of noise on freshwater zooplankton, as well as on fish-dominated planktonic communities, is needed.

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## General discussion

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# I. Overview of the thesis results

The main objective of this thesis was to characterize the response of several aquatic species to anthropogenic noise at integration levels ranging from individuals to communities, in a context of biological invasions. We worked on three invasive species: the pumpkinseed sunfish *Lepomis gibbosus*, the Asian topmouth gudgeon *Pseudorasbora parva*, and the round goby *Neogobius melanostomus*; one native fish: the roach *Rutilus rutilus* and three native invertebrates: the phantom midge *Chaoborus flavicans*, a chironomid larvae and the cladoceran water flea *Daphnia magna*. Individual responses were assessed in microcosms using behavioral measurements together with derivation of the functional response (FR) while community responses were assessed in mesocosms through the monitoring of population dynamics under the trophic cascade concept.

## 1. First exposure to noise can induce changes in predator foraging success and in prey escape

In this project, we assessed the response to short-term (i.e., first) exposure to noise and showed that the instantaneous effect of noise can generate various responses.

When a particular sound stimulus is within the sensory capabilities of an organism, extra sensory noise led to less capacities in processing information with changes in behavioral responses under noisy environment (i.e. mobility reduce or masking conspecific cues). Supporting literature studies, we found that first exposure to noise can also reallocate an animal's finite attention preventing it from responding to their environment (Chan et al., 2010). In the context of foraging activity, a distraction effect led to less effective attack rates and/or longer time to handle prey (i.e., pumpkinseed sunfish, topmouth gudgeon, roach). Our results are consistent with the recent studies on noise pollution, for example, in the absence of auditory element to predator cues, road-noise playback distracted dwarf mongooses' response to predator feces (Morris-Drake et al., 2016). Motorboat noise playback also suppressed the anti-predatory response to conspecific chemical alarm cues in the fathead minnows (*Pimephales promelas*) (Hasan et al., 2018), as well as in the crab where it induces a delayed reaction to an impending silent looming object (Chan et al., 2010).

Additionally, we showed that the response to noise of invasive species cannot be generalized. Contrary to our expectation we found that some species displayed symptoms of the distraction effect (i.e pumpkinseed sunfish) as the native species studied whereas the response of the invasive round goby was an improvement of its predation rate with an increase in mobility. We showed for the first time that short-term exposure was likely to increase the predation rate of an invasive species. Considering how serious is the round goby invasion, this result could explain its success in invading new environments even if they are subject to human impacts. Yet, further investigations should be carried out to know if this response persists with repeated exposure before concluding that noise would enhance the trophic impact of round goby.

One of the particularities of this thesis was to study the response to noise of the invertebrates used as prey during the predation trials. We found that first exposure to noise increased the anti-predator behavior (body rotation) of the phantom midge larvae (chapter 1). These movements increase its visibility to predators but can also reduce the probability of capture by predators (increased handling time). In a natural context, this response to noise could induce changes in the structure of food webs as it is an important invertebrate predator as well as a resource in freshwater systems. Indeed, when we presented roach to phantom midge larvae and water fleas simultaneously under boat noise, they consumed preferentially water fleas suggesting that the body rotations as anti-predator movements might be effective. This result is also consistent with the absence of effect of noise on the mobility of daphnia (chapter 2).

Considering all the results obtained, it is clear that species (fish and invertebrates) respond in different ways when first exposed to noise, whether invasive or not. It is thus difficult to generalize about the response of different species to anthropogenic noise.

## **2. Responses to noise do not necessarily weaken with repeated exposure**

Short-term experiment showed a distraction effect of noise whereas long-term exposure showed different type of responses. The pumpkinseed sunfish showed that long-term exposure to noise changes the baseline response during foraging with a habituation to the stimulus. This response corresponds perfectly to an associative form of learning defined as a progressive response decreasing due to repeated stimulation and that cannot be explained by

sensory adaptation or motor fatigue (McDiarmid et al., 2019) as we did not find any change in body length, mobility, and social attraction.

We expected to find such habituation in the subsequent invasive species studied, but we found that responses to noise did not necessarily fully weaken with repeated exposure. In the topmouth gudgeon even after three week of noise pollution, they still showed negative effect of noise on their mobility resulting in reduced predation at low prey densities. But the presence of a conspecific led them to return to their basal behavior and resume predation. This species demonstrated an ability to tolerate noise when in group but their individual response when alone did not weaken with repeated exposure. We also observed in the native roach that exposure to six weeks induced an acceptance of boat noise during foraging activity in group, but they continued to show less group cohesion. Alteration of behaviour but a restoration of feeding activity suggested that noise continue to mask congeners signals after long-exposure but not prey as they continue to forage.

Social aggregation in fish is extremely common in nature: group cohesion allows protection from predators and enhances foraging ability (Tien et al., 2004). Generally, at a small spatial scale abiotic factors can enhance social interaction by increasing the aggregation of individual (Bartolini et al., 2015). We found an opposite effect with a decrease of aggregation. This result could be due to masking effect or noise (i.e., reducing vibrations of potential predators, prey, congeners) that can impair the ability of animals to detect information about neighbors' positions through the lateral line and could have implications for the functional benefits of a group's collective behaviour (Herbert-Read et al., 2017).

Even if we did not significantly demonstrate it, we found that noise could alter the behaviour of some zooplankton species (phantom midge) and this effect seems to be visible on the long-term as we observed changes in community composition. We demonstrated for the first time that noise affects lower trophic levels over time when fish were not present. Although repetitive exposure to a stimulus often causes a weakening of individual responses (Bejder et al., 2009), we found that it was not a general pattern with noise pollution.

### **3. The change of scale showed no strong effect on communities**

Chapter 1 focused on individual responses to noise, whereas chapters 2 & 3 assessed the long-term effect on more complex interactions (i.e., pair of predators, cascading effects) and in

more realistic conditions in microcosm and mesocosm experiments. As mentioned before, the change of temporal scale (long-term exposure) led to weaken noise stress responses or to habituation.

We showed that changing biological scale through producing more realistic contexts modified individual responses to noise in both microcosms and mesocosms. The introduction of a conspecific during topmouth gudgeon predation resulted in a tolerance to noise. Conspecific attraction is known to occur in other situations such as habitat selection where species locate conspecific with social cues (especially chemical cues in fish) to settle in an environment (V. L. Buxton et al., 2020; Reed & Dobson, 1993; Stamps, 2001). The studies on multiple predator effects (MPE) also demonstrated the importance of conspecific presence even when the species don't show shoaling behavior such as in the solitary mouthbrooder that displayed antagonistic interactions with conspecific during feeding activity resulting in less prey eaten than expected (Wasserman et al., 2016). Therefore, our result showed that social interactions modulate trophic interaction and dilute individual response to noise. Multiple predator studies highlight how the responses expected from individual ones are not reliable for predicting group interactions and thus predictions at larger spatial and biological scales. The combination of functional response and MPE investigations provided relevant information in the effect of noise pollution in microcosm experiment bringing complementary interpretations to mesocosm studies.

Moreover, in the mesocosm experiments we assessed a global response (predator-prey, predator-pairs) to noise by assessing cascading effects. Short-term exposure to noise distracted fish and even if long-term exposure induced persistent effects with less group cohesion these effects did not propagate along the trophic chain as the planktonic communities had the same dynamics as with ambient noise.

Overall, in this thesis, we showed that responses to noise effect was diluted by changing temporal, biological and spatial scales. The impact of other stressors (i.e presence of predators, competing species) could be interesting to investigate in the future.

## **II. The efficiency of the methods used to assess underwater noise effects**

### **1. Can we trust in acoustic playback in microcosm?**

Sound propagation is complex in aquariums because of physical constraints resulting in reflection and diffraction processes that induce differences between the playback and the original sound. Reflection is a phenomenon where a wave reaches the boundary between one medium and another medium, a portion of the wave undergoes reflection, and the other portion undergoes transmissions across the boundary. Reflection leads to echo or reverberation, especially in glass tanks where inversion of sound phases occurs when the sound wave reaches the boundaries. Diffraction is a modification of the propagation of the wave direction when reaching boundaries and depends on the size of the tank: when tanks are smaller than the wavelength of the sound it results in distortion (re-emission of the incident wave in many directions from discontinuity) of the sound (Akamatsu et al., 2002; Gray et al., 2016; P. H. Rogers et al., 2016).

Signal quality represents another challenging issue. Working in small tanks (aquariums) induces high-frequency (e.g., oscillating and collapsing air bubbles, filter pumps) highly absorbed and attenuated due to the small space of transmission which contribute to distort original signal emitted. While low-frequency (e.g., water flows, ground vibrations, aquariums wall vibration) are reflected and diffracted when they are in contact with the walls. To obtain reliable results, it is needed to verify whether the noise broadcasted is like the original one by assessing some physical characteristics: the propagation properties of sound, the distribution of the amplitudes and phases of each frequency component (frequency spectrum), the particle motion velocity and the sound pressure level. Particle motion and sound pressure are not related in shallow water and should be considered at depths of less than 100 m and frequencies less than 1 kHz (Nedelec et al., 2016). It is recommended to measure particle motion in small tank as resonant frequencies and reflections lead to a complex relationship between particle motion and pressure (Nedelec et al., 2016). However due to a lack of equipment, we did not measure it and worked with sound pressure levels.



To reduce reflection, various materials for sound absorption (bubble paper, fibers) exist and during this thesis we decided to use foam rubble panel positioned at the opposite side of the speaker. We also surrounded the speaker with foam to avoid vibrations from direct contact with the glass wall. The foam helped to reduce reverberation mainly on high frequencies and the type of substrate can also contribute to this reduction such as the utilization of sand (Akamatsu et al., 2002). However, in underwater bioacoustics laboratory studies no standard design exists. More precision about the location of the hydrophone to record sound could improve standardization because depending on the distance to the loudspeaker, the substrate and the walls, the noise characteristics and especially intensity and frequency spectrum can differ.

To reduce the sound frequency spectrum, to reduce the distortion of frequencies distortion I opted for a modification of the input signal so that the re-recording was more faithful to the original sound spectrum. I changed the frequency-ranges of the input signal when the spectrum of the broadcasted signal showed differences with the original spectrum using a graphical frequency equalizer of a digital audio data processing software. Moreover, we were limited in the choice of the equipment: underwater loudspeakers are not good to broadcast low frequencies.

## **2. Is functional response a useful tool to study the impacts of noise?**

A feature of my research work was the diversification of the contexts during functional responses (FR) derivation: with one or two predators, different preys, and under different acoustic treatments. The type-II FR was the model that fitted best most of the data and allowed to interpret predation under noise pollution through the attack rate (initial slope) and prey handling time (asymptote).

This is a relevant tool to be used on a small scale and to interpret the direct effects of noise but increasing complexity requires denser logistics and is difficult to achieve in terms of space. Moreover, FR experiments oversimplify the real-world context which makes extrapolation of results difficult. It allows to rule on the predation on only one prey species while in real context fishes are most often opportunistic and feed on a range of prey items. FR can be very different from one prey to another. For example, in the FR of four North

American crayfish invaders, different FR types were found depending on the type of prey suggesting species-specific patterns (Chucholl & Chucholl, 2021). We only used one type of prey per predator in our FR experiments and it would be very interesting to expose predators to different prey species and observe potential changes under different noise conditions, especially testing preys that are or not affected by noise as in the case of the phantom midge.

Linking behavioral measurements to FR derivation helped us to find the origins of alterations in FR parameters. For instance, swimming distance and attack rate were often positively correlated as both are related to the pattern of spatial use. Higher mobility provides more opportunity to find and capture prey. Behavioral variables bring more precisions to the characterization of a predation strategy and appear to be useful when combined with the FR. However, interpreting handling time can be trickier as it is not directly linked to mobility.

Handling time reflects the amount of time required to process a single prey item (Holling, 1959a) and is thus expected to depend only on anatomical constraints. Noise is not expected to affect the morphological process of prey manipulation. However, we found in the round goby that fish had a shorter handling time under boat noise than under ambient noise, suggesting improved prey processing. This surprising result might be explained by the duration of our experiments. According to Li et al. (2018), when experimental duration increases, handling time could include other activities than processing prey, like resting or moving. These activities that could be decreased by boat noise.

Another issue of the FR approach is when both FR parameters suggest antagonist effects on *per capita* predation. To solve this problem, Cuthbert et al. (2019) proposed a novel metric through the functional response ratio (FRR), which is attack rate divided by handling time ( $a/h$ ). It reduces FR to one dimension and thereby facilitates result interpretation and promotes between-species and between-studies comparisons (Chucholl & Chucholl, 2021; Cuthbert, Al-Jaibachi, et al., 2019; Haubrock et al., 2020; McCard et al., 2021). FRR values increase with trophic impact, and vice versa. For example, Chucholl et Chucholl (2021) compared four invasive species with one native crayfish, and the FRR showed that the impact of invasive crayfish was very species-specific and can differ according to the type of prey. This method could potentially help FR method to be used for ecological prediction.

### 3. Is silence a good control?

As mentioned previously (see section II.1), broadcasting acoustic signals as close as possible to the originals is not a straightforward task in experimental units. Broadcasting natural signals of low quality might be as stressful as artificial noise. Villalobos et al. (2017) used ‘anthropogenic boat noise, natural noise from river, and silence’ as acoustic treatments, and they found that natural noise had a negative impact on the functional response of the larvae *I.elegans*, greater than anthropogenic noise. One explanation was the presence of nonlinearities in the audio cues used in the experiment with more differences in amplitude in the low frequencies of the natural noise than in anthropogenic noise. These nonlinearities could be more stressful than anthropogenic noise. In addition, natural sound recordings are generally made for short periods of time during which certain biological sounds may be missing or accentuated (vocalizations depending on the context, i.e., defense of territory, presence of predators, etc.) potentially inducing a stress reaction.

Natural ambient noise is a background noise (above 100 dB 1 re  $\mu$ Pa, Amoser & Ladich 2005, personal observation) composed of biotic and abiotic sounds, and varies with time, location, and depth. There is no consensus on the better choice as “control noise condition” between broadcasting the natural background noise or silence to let the ambient noise of the laboratory. In all the experiments of the thesis, fish were transported to the laboratory several weeks before to be tested. We broadcasted silence from the loudspeaker in their breeding aquarium but they were still exposed to artificial sounds (pump, flow water, air bubble) and biotic sound (those of congeners if the same aquarium) with an overall sound level close to what is found in the field (around 100-110 dB 1 re  $\mu$ Pa). We consider that the arrival of the individuals in the laboratory could be assimilated to an arrival in a new environment, and that the equipment used together with the presence of conspecifics could be a less stressful background noise than trying to reproduce a natural soundscape that would overlap with the background noise of the laboratory. However, this raises questions about the reliability of the responses obtained under ambient laboratory noise, and whether playback of natural sounds would be a better alternative. Yet all the fish were bred under the same conditions until the experimental treatments such that any difference in behavior was due to the experimental treatments.

#### **4. Are mesocosms the ideal scale of investigation?**

In natural conditions, fish can move away from the source of noise suggesting that microcosms may represent an extreme exposure to noise. To solve this issue, studies in mesocosms appear to be a good complementary approach as they serve as realistic surrogates of natural ecosystems and allow to expose populations and communities to stressors. Mesocosms have become increasingly popular in ecology as an important intermediary between microcosm experiments, and the greater biological complexity of natural systems in which cause, and effect relationships are difficult to identify. However, replication, which is of importance to detect the effect of a factor, often decreases with the size of the experimental unit due to logistical and financial limits. Small numbers of replicates can result in huge variability within the same treatment that could mask a potential significant effect. Indeed, when increasing the number of replicates in mesocosm the effect of noise found in the cascading experiment (tendency) had been enhanced in the second mesocosm experiment (chapter 2, article 5). Nevertheless, we were able to detect effects of noise on zooplanktonic communities which would have been difficult to apprehend in the laboratory.

Result interpretation can be difficult when working on complex communities. Our investigations have shown that it is useful to supplement mesocosm experiments with microcosm experiments to test specific predictions and better interpret the results.

### **III. Perspectives**

Invasive species are known to have better tolerance to environmental changes compared to native species. In this thesis we demonstrated that even if short-term responses could be totally different (e.g., improved predation of round gobies vs. distraction effect on pumpkinseed sunfish when exposed to noise), long-term experiment led to habituation process or tolerance during feeding. A result also found in the native roach but with persistent negative effect of noise on their group behavior. This thesis summarizes the many efforts to assess anthropogenic underwater noise effect and pointed out aspects that would improve

current noise effects and help develop effective conservation plans. This last part will present three perspectives arising from the experiments in this manuscript.

## **1. Scaling up the effects of noise to food-web structure**

The main objective of the thesis was to characterize the effect of noise on individual responses and community dynamics over time. We, thus, started by using one type of prey to focus on the direct effect of noise on predator foraging behaviour. However, we know that predators face to a multiple choice of prey species in their natural environment, and that noise could induce changes in prey preference (Chucholl & Chucholl, 2021). Indeed, in the microcosm experiment on roach submitted to two different species (*Daphnia* sp. and *Chaoborus* larvae, chapter 3, article 3), fish showed a preference for water flea under noise exposure whichever its noise preexposure. Therefore, it raises the question of the effect of noise when multiple prey is present, do they turn away from one resource to consume another? To assess this question, adding other ecological approach to our studies especially the isotopy approach would be very interesting.

Isotopy is an approach consisting in measuring the stable isotope ratios of nitrogen and carbon to know the trophic level and the food sources respectively, of a consumer and identify its functional role within an ecosystem (Pingram et al., 2014; D. M. Post, 2002; Vander Zanden et al., 1997, 1999). Stable isotopes give information on species movement, habitat use (Rasmussen et al., 2009), seasonal food web pattern (Herwig et al., 2007) and especially track resource assimilated by individuals. It would be very interesting to use isotopy to identify direct and indirect ecological interactions between invasive species and native communities under noise pollution as it was not tested during this thesis and is not supported by previous research. This approach will be useful to assess long-term effect, therefore, it will be interested to combine it with gut content analysis at specific moment to have an idea of what has been consumed. Combining isotopy and gut content to our work would be a relevant perspective to assess noise effect of an entire food webs.

## **2. Decreasing its response to noise: a threat for survival?**

We demonstrated in the thesis that long exposure to noise can result in habituation (chapter 1). This raises many questions about the consequences of a weakened response. It is known that animal developed mechanism to escape predators and in fish a fast-start escape response

occurs during the first millisecond of a predator attack (Killen et al., 2015). Therefore, weakening the response to noise stimuli during feeding exposed them to more threatened situation because they may not respond normally to predator signals. Consequently, an interesting approach could be to assess impact of noise pollution combined with predatory cues (odors, visual, physical).

In addition, this habituation to noise raises a second question: does the habituation process continue with each chronic exposure in the life of the fish or does the fish have to get accustomed again after a long exposure without noise? Therefore, a second perspective will be to assess how individual accustomed to noise react to another noise exposure after a long period of ambient noise.

### **3. Effects of long-term exposure in reproductive success?**

Animals must constantly negotiate trade-offs in sensory and motor performance, therefore how it cost to an animal to increase mobility under noise exposure (as in the study of round goby). Does this trade-off last over time? The consequence of an increase energy demand could impair reproductive process and thus survival.

Reallocation in energy needs could induce a decrease of responsiveness to threatening situation and have detrimental consequences in the reproduction. Stress plays a key role to perform essential biological functions, including reproduction (Schreck, 1981), it is a physiological cascade of events that occur when the organism attempts to resist death or restore homeostatic standards in the face of a stressor (Schreck, 1981). During this thesis we did not quantify stress level through physiological measurements, but we assessed it through behavioral responses. Studies demonstrated that elevated level of stress hormone resulted in retarded oocyte growth, reduced condition factor, and lowered serum testosterone and  $17\beta$ -estradiol in tilapia, *Oreochromis mossambicus* (Foo & Lam, 1993). Long-term exposure to noise showed that species could tolerate noise during feeding in non-threatened situation but continues to show persistent effect of noise on their behavior (i.e., decrease in attack rate in the single preexposed topmouth gudgeon, chapter 2) or can mask relevant biological signal from congeners (i.e., roach experiment, chapter 3). A long-term study (two years) on the wild Lusitanian toadfish (*Halobatrachus didactylus*), a species using advertisement calls for mate attraction, behavioural, physiological, and reproductive endpoints, demonstrated that males

depressed their metabolism and their activity (parental care and mate attraction) to cope with boat noise stressor (Amorim et al., 2022).

Invasive fish can be distracted or to improve feeding performance (i.e., pumpkinseed sunfish; round goby, chapter 1), assessing the effect of noise on their reproduction would be an interesting perspective to bring knowledge for their management and to be able to predict their impact on vulnerable freshwater system.

Otherwise, we observed that noise may change zooplanktonic communities, especially cladoceran species. My thesis was the possibility to collaborate in studies on the reproduction of the water flea *Daphnia* under noise exposure with Dr L.Prosnier.

# Abstract of the thesis

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**Multi-scale responses of freshwater communities to anthropogenic noise with a focus on invasive species.**

**Key words:** anthropogenic noise, freshwater, feeding, invasive species, planktonic communities

There are few natural soundscapes that are free of sounds associated with human activities. These anthropogenic sounds are now recognized as a source of pollution with effects on the anatomy, physiology or, more often, the behavior of exposed organisms, which can lead to a decrease in their selective value. However, while individual responses are well described, the effects on biodiversity and ecosystem functioning are still unknown. Also, ecosystems are unevenly documented and compared to terrestrial and marine environments, noise pollution in freshwater environments is only marginally studied and is not yet subject to any legislation.

This thesis is a multi-scale project (temporal, spatial and biological) on the effect of anthropogenic noise on trophic (feeding relationships between individuals in the same ecosystem) and non-trophic relationships in freshwater. The aim was to study the direct effects via behavioral alterations during feeding, and indirectly via top-down forcing exerted by the fish population and noise pollution on the dynamics of planktonic communities.

A widespread response was observed during short-term (min) exposure to noise with a distraction effect observed in fish accompanied by a decrease in feeding (sun perch, pseudorasbora parva, roach), except for the round goby, an increasingly common invasive freshwater species where an increase in feeding performance was observed. However, in the long term (weeks) individual responses did not ultimately predict feeding consequences given its recovery (habituation process, tolerance). We also found that interspecific interaction (interaction with conspecifics) had a stronger effect that it modulates and modifies the individual response. At the food web scale, long-term exposure also revealed that lower trophic levels (zooplanktonic communities) were affected by noise with respect to modification of community composition.

This thesis is the first study to combine laboratory and large-scale responses to understand the overall community response to stress induced by anthropogenic pollution in freshwater.



## Résumé de la thèse

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Réponses multi-échelles des communautés d'eau douce au bruit anthropogénique avec un accent sur les espèces invasives.

**Mot clés :** bruit anthropogénique, eau douce, alimentation, espèces invasives, communautés planctoniques

Rares sont les paysages sonores naturels qui sont exempts de sons associés aux activités humaines. Ces sons anthropogéniques sont aujourd'hui reconnus comme une source de pollution avec des effets sur l'anatomie, la physiologie ou plus souvent le comportement des organismes exposés, pouvant induire une diminution de leur valeur sélective. Cependant, si les réponses individuelles sont bien décrites, les effets sur la biodiversité et le fonctionnement des écosystèmes sont encore inconnus. Aussi, les écosystèmes sont inégalement documentés et comparativement aux milieux terrestres et marins, la pollution sonore dans les milieux d'eau douce n'est que très peu étudiée et ne fait encore l'objet d'aucune législation.

Cette thèse est un projet multi-échelle (temporelle, spatiale et biologique) menée sur l'effet des bruits anthropiques sur les relations trophiques (relations alimentaires entre des individus d'un même écosystème) et non trophiques en eau douce. L'objectif était d'étudier les effets directs via les altérations comportementales pendant l'alimentation, et indirects via le forçage top-down exercé par le peuplement piscicole et la pollution sonore sur la dynamique des communautés planctoniques.

Une réponse assez générale a été remarquée lors d'une exposition à court-terme (min) au bruit avec un effet de distraction observée chez les poissons accompagnée d'une diminution de leur alimentation (perche soleil, pseudorasbora parva, gardon), sauf chez le gobie à tâche noire, une espèce invasive d'eau douce de plus en plus répandues où une augmentation des performances alimentaires a été constatée. Cependant, au long terme (semaines) les réponses individuelles n'ont finalement pas permis de prédire les conséquences sur l'alimentation étant donné son rétablissement (processus d'habituation, tolérance). Nous avons également constaté que le contexte social (interaction avec des congénères) avait un effet tellement important qu'il module et modifie la réponse individuelle. A l'échelle du

réseau trophique, une exposition au long-terme a également révélé un changement de la composition des invertébrés zooplanctoniques en absence de grands prédateurs (poissons).

Cette thèse est une première étude qui combine les réponses obtenues en laboratoire et à grande échelle pour tenter de comprendre la réponse globale des communautés au stress induit par la pollution anthropogénique en eau douce.





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