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River soundscapes: the human-altered acoustic world of migratory fish

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Chapter 7:

Thesis Summary & General Discussion

Freshwater ecosystems in general, and migratory fish in particular are heavily threatened, with many species in danger of extinction because of a wide range of human stressors (Costa et al., 2021; Sayer et al., 2025; WWF, 2024). However, the contribution of anthropogenic noise in this decline is rarely considered, while numerous studies report adverse effects of noise on animals (Erbe et al., 2019; Mickle & Higgs, 2018; Popper & Hawkins, 2019). To understand how noise can impact aquatic animals, we must first understand how aquatic animals use sound for their survival and reproduction. And to understand how aquatic animals use sound for their survival and reproduction, we must first characterize and quantify natural sound sources and test their effects on behavioral decisions of aquatic animals. Furthermore, we must quantify and characterize anthropogenic noise to be able to assess the potential impacts of acoustic masking in aquatic ecosystems, and test the direct effects of noise on behavioral decisions of aquatic animals. In this thesis, I addressed these knowledge gaps by using outdoor soundscape studies to characterize and quantify natural soundscape information and anthropogenic noise in freshwater systems (Chapter 2-4), designing a swim tunnel to assess the effects of sound on fish migration behavior (Chapter 5), and carrying out a dual-tank experiment to test the response of a migratory fish species to natural and anthropogenic sounds (Chapter 6). Here, I first summarize and describe the main findings of my chapters and aim to answer the overarching research questions based on the findings in my chapters. Then I discuss several main topics in more detail and explore future research opportunities in the following order: Natural soundscapes (Chapter 2 & 4), Anthropogenic noise (Chapter 2-4) and Evidence for the use of sounds by freshwater animals (Chapter 5 & 6). For each topic I first describe what was known from other studies, then what I found, and then the advances made when put in the context of the literature and future research avenues. Finally, I discuss what we can do to quantify and mitigate the effects of anthropogenic noise pollution on aquatic animals, and how sound can be utilized to protect and preserve aquatic animals.

Across the Chapters of this thesis, I followed a conceptual framework for investigating how natural acoustic information is used

by aquatic animals in general, and migratory fish in particular. And aimed to answer 6 overarching research questions related to this conceptual framework. I was not able to fully realize the complete conceptual framework and answer all research questions, but below I describe the progress made towards addressing the knowledge gaps required to ultimately answer these questions.

1. What are the most common geophonic and biophonic sound sources in freshwater systems?

In chapters 2-4 I described several common sound sources of potentially biological origin in freshwater systems including aquatic insects, fish, amphibians and aquatic plants. Furthermore, I was able to identify several hydro-geomorphological river features that were reflected in the natural soundscape, such as river size, sediment type and water flow, which can likely be attributed to either direct geophonic sound production or indirect effects on sound propagation.

2. Which natural sound sources could serve as potential acoustic cues for migratory fish, based on their acoustic properties, occurrence, and relevance to fish life-history?

Due to their widespread availability, the potential to fall within the hearing range of fishes, and the relevance of the habitat features they reflect to fish life-history; I identified sediment and flow related geophonic sounds as high potential acoustic cues for migratory fish. Furthermore, biophonic sound events are generally more sparse (lower availability) but can be of high relevance to fish life-history. Both active calls and passive water or sediment disturbances can provide conspecifics with information on potential reproductive partners or competition but can also inform prey species on nearby predators. Furthermore, bubbles produced by aquatic plants could inform fish on suitable spawning habitats or shelter.

I must emphasize that identifying potential cues remains speculative, and there is no guarantee that these sounds are actually used in behavioral decisions of animals. The only purpose is to

generate new hypotheses and identify good candidates for later testing in behavioral experiments.

3. What are the most dominant anthropogenic noise sources in freshwater systems and how are they distributed in time and space?

The two most dominant sources of anthropogenic noise identified in chapters 2-4 were road traffic noise and shipping noise. Both sources are prominent during both day and night, but road traffic noise showed consistent diel and weekly patterns in terms of slightly reduced noise levels during nights and weekends. As expected, road traffic noise levels were higher and more prominent in cities and under bridges compared to rural locations, but may also propagate up to several hundred meters away from roads. Shipping noise levels and time contribution varied greatly among rivers, but show a consistent noise gradient from more noise in the river estuary to less noise with distance upstream.

4. To what extent does anthropogenic noise mask natural sound sources in freshwater systems?

By comparing the spectral intensity of the natural sound sources identified, with the spectral intensity of boats recorded in large European rivers we can expect that almost all natural sound sources in rivers are masked in the presence of boat noise. For road traffic noise I did not make a direct comparison, but by comparing city noise spectra presented in chapter 2 with sound spectra of natural sounds in chapter 4, we can expect that only low frequency sound types such as fish grunts will be (partially) masked by road traffic noise in cities. Directly under bridges sound level elevations are seen in frequencies up to 5 kHz, which could lead to (partial) masking of mid-frequency sound types.

5. How do migratory fish respond behaviorally to natural sound cues and anthropogenic noise in experimental conditions?

In chapter 6 I carried out a behavioral experiment in a dual-tank setup with three-spined sticklebacks from a migratory

population. This revealed that three-spined sticklebacks are capable of detecting and responding to playbacks of natural and anthropogenic sounds under laboratory conditions, revealing slight preference towards flow related sounds, and deterrence away from boat noise playbacks. Whether these responses scale up to migratory behaviors remains to be tested in experimental setups such as the MIGRADROME that facilitate more migration associated behaviors, and ultimately in the field with free swimming migrating fish.

Over the course of this PhD project, I spent considerable time together with our team to design, develop and test the MIGRADROME, an experimental swim tunnel designed to test the effects of sound on fish migration behavior. Due to several years of delays in preparing the room for housing the MIGRADROME facility, I was unable to apply it for behavioral experiments within the timeframe of this PhD thesis. However, the work done during the PhD resulted in an innovative research facility that is ready for carrying out experiments that can contribute to answering this research question in the near future. Furthermore, in chapter 5, I was able to investigate the sound fields in terms of sound pressure and particle motion that can be created in such an experimental facility and explored the potential research questions that can be answered by manipulating those sound fields. In chapter 5 I aimed to provide insights on tank acoustics that may help the broader research community in the design of experiments that can help answer this research question.

6. How do behavioral responses to anthropogenic noise, or lack of responses to natural sound sources due to masking, affect fish during migration?

This question cannot be answered based on the results of this thesis or the currently available literature. But based on the findings and literature comparison conducted in chapter 6, I hypothesize that anthropogenic noise reduces passage success or results in delays in time of arrival at the migratory destination. Either directly by acting as a deterrent, or indirectly by masking attractant sounds such as turbulent flow sound at river entrances or fish passages.

Natural soundscapes

What is known from other studies?

Freshwater soundscapes consist of a wide variety of sound sources with diverse spectral characteristics. Fish hearing ranges are generally below 1000 Hz, while species at the most specialized end of the range can detect frequencies of up to 5 kHz (Popper & Fay 2011; Putland et al., 2019a). Higher frequency sounds can still affect fish indirectly, through nearby species with broader hearing ranges that respond to them. Biotic sounds include fish calls, aquatic invertebrate chorusing, amphibian and bird calls and even aquatic plant respiration. These sounds have a wide variation in spectral and temporal characteristics and are often species specific (Narins et al., 2007; Parmentier & Fine, 2016). Some common soniferous river fish species in Europe are: European perch (*Perca fluviatilis*), Pikeperch (*Sander lucioperca*) and two species of sculpins: *Cottus rhenanus* and *Cottus perifretum* (Colleye et al., 2013). Common species of soniferous aquatic invertebrates include *Sigara striata* and *Micronecta scholtzii* and several species of dytiscid water beetles (Desjonqueres, 2016; Greenhalgh et al., 2021). Still, most species are yet to be investigated for sound production (Desjonqueres et al., 2024; Looby et al., 2022). The bubbles formed and expelled by plant photosynthesis and microorganism respiration, are suspected to produce short pulses with wide frequency bands (Feliberto et al., 2015a; Freeman et al., 2018; Kratochvil & Pollirer, 2017a; van der Lee et al., 2020). Sound from wind is broadband and increases with wind speed (Hildebrand, 2009a). Sediment transport also generates sound from interparticle collisions and was shown to dominate frequencies above 1000 Hz in a large gravel bed river (Geay et al., 2017). And the reflection of sound at different frequencies varies among sediment types (Greenberg et al., 2025). Increases in water velocity result in increased sound levels over a wide range of frequencies, and obstructions in flowing water create turbulence and bubble formation, which produce sound signatures most pronounced in frequencies between 125-2000 Hz (Tonolla et al., 2009). This short summary highlights just a fraction of underwater sound sources and already reveals the wide range of information that is available in underwater sound.

What did I find?

In chapter 2 & 4, I recorded soundscapes in rivers of varying sizes across Europe with the aim to disentangle the biophonic and geophonic sounds sources that make up the soundscape and evaluate their potential as acoustic cues to aquatic animals. By combining spatially replicated soundscape recordings with datasets on river morphology and water quality, I found that geophysical characteristics of the local river were reflected in the natural soundscape. Specifically, river size, water velocity and sediment characteristics explained most of the variation in spectral differences among river sections. I also demonstrated that variations in position across the river cross-section are reflected in the local soundscape. This shows that geophysical river characteristics can drive habitat specific soundscape variation within rivers that could be used by fish as navigational cues or to gain information on local habitat suitability. Especially sediment and waterflow are high-potential cues when you consider the life-history of migratory fish, as many fish have specific sediment and flow condition requirements to deposit their eggs (Kemp et al., 2011; Rosenfeld, 2003). River size and sediment typically changes gradually with distance, from upstream to downstream, which may provide a reliable acoustic cue about habitat as the geophysical nature of rivers is highly predictable and consistent. Turbulent flow from river entrances in particular, may act as acoustic beacons for navigation.

Although sometimes less predictable and consistent, biological sounds (biophony) can also provide high-quality information on habitat suitability, prey availability, potential mates, shelter and predation risk. Because simply the presence of another organism is linked to specific habitat features (Moenkkoenen & Forsman, 2002; Pupin et al., 2007; Slabbekoorn & Bouton, 2008). I found that acoustic communication signals are diverse and widespread in temperate river systems. I found sounds produced by animals from a wide range of species groups: Including amphibians, fish, insects and even sound from birds on and next to the water. Furthermore, there is a broad range of natural sound events not specifically linked to communication such as gas bubbles from aquatic plants or bubbles escaping from the sediment.

Advances made & Future Research

Previous studies rarely described soundscapes in both geophony, biophony and anthrophony in as much detail as I did. I believe it is of great importance to study them side by side to understand how they affect each other. Geophonic sounds can reflect physical aspects of the local river, but they can also produce noisy habitats that limit communication or other subtle sources of biophonic information. And animals are likely adapted to the acoustic environments they occupy (Amoser & Ladich, 2005; Ladich, 1999, 2000). It is important to quantify the intensity and spectrum of both natural and anthropogenic sounds to be able to predict masking impacts from anthropogenic noise sources. A noisy, high-flow, turbulent river environment is less likely to be impacted by noise than a quiet lake.

Chaper 2 & 4 add more examples of habitat specific soundscapes in rivers. And with regards to geophony, our findings validate and expand on the patterns found by Tonolla et al. (2010,2011). For instance, our flow sound findings are largely in line with findings by Tonolla et al. (2010,2011), but I show that flow induced sound is reflected in different frequencies in slow flowing rivers (Chapter 2), and there seems to be a water velocity threshold at which flow-induced sounds start to dominate the soundscape, potentially masking most other sounds (Chapter 4) (Tonolla et al., 2009, 2010, 2011). With regards to sediment, Tonolla et al. (2010), found that sediment size of different habitats in fast-flowing streams is positively correlated with sound levels across all frequencies in those habitats. While I found a significant negative relationship between sediment hardness and the sound pressure level at frequencies above 350 Hz in low-velocity sections of a large European river. Still, Tonolla et al. (2009, 2010, 2011) did not seem to correct for cross-correlations between sediment type and water velocity, and it is possible that water velocity may explain the largest part of soundscape variation in high-flow environments. It must be noted that Geay et al. (2020) found that bed load flux was a better predictor of sound pressure than water velocity or grain size in gravel bed rivers, which is something we did not measure directly. This suggests that particle collisions from moving sediment are the main

source of sound at gravel beds in rivers with a strong current (Geay et al., 2020).

Although our analysis helped disentangle different geophonic sound sources and explore how and at what levels they are reflected in the soundscape, just like prior studies, our findings were still correlative. Correlation is not necessarily a problem from a fish perspective, since causation is not required for a fish to gain information about their surroundings. Still, investigating causal effects of geophysical aspects on the soundscape through experimental manipulation of aspects like slope, sediment type and flow speed, could help us predict geophonic soundscapes in rivers across the globe with more confidence and precision. This could help us predict the masking impacts of noise on geophonic sounds without the need for field recordings. Furthermore, causality may be especially important in passive acoustic monitoring, and recording geophonic sounds has been proposed as a method for measuring fundamental river processes, important to human infrastructure and aquatic habitats, such as bed load transport, which could be of great use in river management (Geay et al., 2018, 2020).

I was able to make progress in our understanding of the available acoustic information in rivers. With regards to transient sound events, I was able to describe several sounds of potentially biological origin. Still, transient sound events can both be associated with physical and biological aspects of river habitats. The challenge with linking transient sounds to habitat features is that it would require long-term hydrophone deployments in many locations. And processing long sound files requires time and effort. Still, I believe it is an important part of the soundscape that requires further study. In the future, innovative sound processing methods such as machine learning algorithms can be of great benefit (Alcocer et al., 2022; Borowiec et al., 2022; Stowell, 2022). In a co-authored publication, I showed that machine learning algorithms can help detect unknown sound events in rivers and even classify them into different sound types based on unsupervised clustering of acoustic features (Parcerisas et al., 2024).

Studying acoustic communication in aquatic animals can help us better understand their acoustic ecology. I believe that acoustic communication may be widespread in freshwater animal taxa, but many species-specific sounds remain to be discovered (Desjonqueres et al., 2024; Greenhalgh et al., 2025; Looby et al., 2022). Communication is used by many freshwater animals in behaviors such as mate attraction and alarm calls (Aiken, 1985; Rountree et al., 2006, 2019, 2020). Characterizing and quantifying species-specific sounds, is necessary to evaluate masking impacts of noise on these signals that are vital to their survival and reproduction. There are most likely still thousands of undescribed species-specific freshwater sounds (Desjonqueres et al., 2024; Looby et al., 2022), and describing new sounds can be a time-intensive process. To make significant progress, international collaboration is required. Therefore, I have contributed the sounds of animals found in these studies to the newly initiated freshwater sounds archive and urge others to do the same (Greenhalgh et al., 2025).

Potential acoustic cues

In summary, in chapters 2 and 4, I aimed to identify potential acoustic cues to migratory fish based on their acoustic quality and availability. I herewith expanded on earlier studies in fast-flowing streams, lakes and large river segments (Geay et al., 2018; Kacem et al., 2020; Tonolla et al., 2009, 2010, 2011; Wysocki et al., 2007), showing habitat associated soundscape signatures linked to physical river characteristics such as river size, flow speeds and sediment in a slow flowing lowland river (Chapter 2), and at high spatial resolution in large European rivers (Chapter 4). River size and sediment typically change gradually from upstream to downstream, potentially offering reliable acoustic cues due to the predictable geophysical nature of rivers. Furthermore, I hypothesize that turbulent flow near river entrances may serve as acoustic beacons for navigation. I therefore suggest that flow, sediment, and river size present high-potential acoustic cues for migratory fish, as they are consistent across habitats, change gradually from downstream to upstream, and can provide discrete acoustic landmarks. Biophonic sound events are generally more sparse (lower availability) but can be of high quality. Both active calls and passive water or

sediment disturbances can provide conspecifics with information on potential reproductive partners or competition but can also inform prey species on nearby predators. Furthermore, bubbles produced by aquatic plants could inform fish on suitable spawning habitats or shelter. Still, I must emphasize that the identified potential acoustic cues remain purely speculative until they have been shown to affect fish behavior in controlled experiments.

Anthropogenic noise

What is known from other studies?

Shipping noise is generally composed of a broadband component and a set of tonals and are generally high in amplitude compared to natural soundscapes (Hildebrand, 2009b; Jansen & De Jong, 2017). Due to the broadband nature of boat noise, it largely overlaps with the hearing ranges of most animals (Duarte et al., 2021). Boat noise in the May River was shown to have 10-80% temporal overlap with fish chorusing depending on species and location (Smott et al., 2018b). Noise events from passing vehicles on bridges or in tunnels are generally low in frequency, ranging from 1-700 Hz (Holt & Johnston, 2015a; Song et al., 2020a; Zang et al., 2019a). The high energy at low frequencies in underwater recordings of traffic noise suggests that it mainly propagates through air or sediment, because low frequencies do not propagate far in shallow water environments. Road noise has been estimated to propagate as far as 12 km (Holt & Johnston, 2015b). A study that recorded freshwater soundscapes in the U.S. showed that traffic noise comprised more than 40% of the recording time on average across the 173 sites (Rountree et al., 2020). However, land-based traffic noise is rarely quantified or predicted across large spatial scales in freshwater systems.

What did I find?

In chapter 2 & 3, I found elevated sound levels and clear diel noise patterns in cities and under bridges, but even rural locations had diel patterns that are likely attributable to land-based traffic noise. With about 25 dB higher daily SPL between 10-50 Hz under bridges compared to rural locations. Weekends were slightly more quiet under bridges compared to weekdays, which reflects human activity patterns. Still, it was rarely quiet under bridges, even at night. Land based traffic noise was mainly

expressed in low frequencies between 1-100 Hz, and sometimes up to 2000 Hz under bridges. One rural location situated 300 meters from a highway had 20 dB higher sound levels at 20 Hz than other rural locations. This indicates that land-based traffic noise can propagate hundreds of meters, possibly up to kilometers away from roads into freshwater environments.

In chapter 4, I was able to quantify shipping noise from acoustic recordings in three large European rivers, The Elbe, Rhine and Gironde. Shipping noise was mainly expressed in frequencies above 50 Hz. The lower impact on frequencies below 50 Hz are likely due to propagation constraints by low frequencies in shallow water environments. I found a general pattern of higher shipping noise downstream near the estuaries compared to more upstream locations. Shipping noise was highest in the Rhine, both in terms of % time per day boat presence and in intensity. In contrast with road traffic noise, shipping noise persisted throughout the night in the river Rhine. AIS (Automatic Identification System) density data from commercial inland shipping was significantly correlated with noise in my recordings and could therefore be used to predict shipping noise across the entire length of the three rivers. This showed that the Rhine has 40-75% of the time at least one boat present over the whole length, the Elbe has 80-100% boat presence in the estuary, declining to 5-15% after Hamburg, and the Gironde has 7% boat presence before-, and 5% after Bordeaux. Showing large differences in boat noise among rivers and river sections. It should be noted that our model has a significant intercept, which means that it predicts 5% acoustic boat presence in rivers when there are no boats reported in the area with AIS on board. This is likely caused by the presence of recreational boats without AIS in recording locations with no commercial shipping traffic. Still, it is promising that AIS data has predictive value for boat noise in large rivers, potentially allowing us to roughly predict shipping noise in large rivers at a global scale.

Advances made & Future research

The % time contribution of boats throughout the Rhine and in the Elbe estuary was exceptionally high compared to findings in some other studies (Marley et al., 2016; Smott et al., 2018a;

Vieira et al., 2021). This can likely be explained by commercial boat traffic, because in terms of inland cargo transport volumes, the Rhine is one of the busiest rivers in the world, and the Elbe is the third busiest river in Europe (Central Commission for the Navigation of the Rhine, 2024). Similar levels of noise pollution from commercial inland shipping traffic may only be found in rivers such as the Yangtze, Pearl, Grand Canal and Mekong river in Asia, Mississippi river in America and Danube in Europe (Central Commission for the Navigation of the Rhine, 2024; Lu et al., 2023). However, I also showed that rivers with moderate cargo transport volumes such as the Elbe can still have river sections with extremely high % time contribution of boat noise.

Spatial boat noise patterns found were in line with Smott et al. (2018), who found a higher incidence of boat noise at locations closer to the river mouth (Smott et al., 2018b). In the past, strong temporal patterns in boat noise occurrence have been found with higher boat noise during the day, weekends and summer (Haviland-Howell et al., 2007; Marley et al., 2016; Smott et al., 2018b; Vieira et al., 2021). Although our 24-hour spectrograms suggested slightly lower boat presence during the night, this was less pronounced than other studies, especially in the Rhine. Furthermore, comparing monthly AIS shipping density data over the year in the Elbe, Rhine and Gironde, showed no significant seasonal patterns in commercial shipping densities. I believe that commercial boat traffic may be more persistent across day, week and season, while recreational boat traffic, not captured in AIS data, may have stronger diurnal, weekly, and seasonal patterns.

In terms of land-based traffic noise, our findings are largely in line with the literature, showing that traffic noise is most prominent in low frequencies and can propagate over large distances (Holt & Johnston, 2015b; Rountree et al., 2020; Song et al., 2020b; Zang et al., 2019b), and I showed that rivers had significantly elevated sound levels under bridges and when flowing through cities. The temporal patterns found below bridges of lower sound (or ambient noise) levels during the nights and weekend were in line with those under a bridge in the Hudson River (Martin & Popper, 2016). The consistency of these findings

suggests that noisy conditions from land-based traffic could potentially be predicted relatively easily.

Still, field measurements would be required to characterize noise spectra and improve sound propagation modeling from different noise sources such as road traffic, bridges and inland boating. I believe there may be ample resources on car and commercial boat traffic densities, that can help predict global road traffic and shipping noise output in freshwater environments through noise maps, once sound propagation models are developed for shallow freshwater systems (Deng et al., 2022; Rakowitz et al., 2008) However, quantifying recreational boat traffic densities would also be required to get a full sense of anthropogenic noise output in freshwater systems.

Evidence for the use of sound by freshwater animals

What is known from other studies?

Fish have been shown to respond to natural and anthropogenic sounds in a variety of ways. Responses to sound can be expressed into two broad categories: Spatial responses, and up- or downregulated behaviors (Slabbekoorn et al. 2025). Spatial responses can be grouped by direction, fish either swim towards the sound source (attraction), away from the sound source (deterrence) (also referred to as positive and negative phonotaxis), or displacement is found not specifically linked to the position of the sound source, such as adjustment of their vertical position, or displacement in another direction. Sound can also increase (upregulate) or decrease (downregulate) the occurrence or intensity of certain behaviors, such as activity, swimming speed or anti-predator responses. Table 1 presents several examples of the behavioral responses expressed by a wide range of species to natural and anthropogenic sounds.

Fish typically show deterrence, displacement or no response to anthropogenic noise (Beach et al., 2025; de Vincenzi et al., 2021; Leduc et al., 2021; Matos et al., 2024; Shafiei Sabet, Van Dooren, et al., 2016; Waddell & Širović, 2023), while natural sounds can elicit both deterrence, displacement and attraction (de Vincenzi et al., 2021; Holt & Johnston, 2011; Kowal et al., 2023; Liu et al., 2019; Moynan et al., 2016; Parmentier et al.,

Table 1; Summary of behavioural responses of fishes to natural and anthropogenic sounds. Spatial responses describe movement relative to the sound source. Up- and downregulated behaviours indicate increased or decreased behavioural expression. N.T. = not tested or not reported; empty cells indicate no reported effect

Spatial response	Upregulated behaviours	Downregulated behaviours	Sound type	Captive / Free swimming	System	Species	Reference
Natural							
<i>Both</i>	<i>N.T.</i>	<i>N.T.</i>	Vocalizations	Captive	Freshwater	Round Goby	(Moynan et al., 2016)
<i>Deterrence</i>		<i>Swimming speed</i>	Predator sound	Captive	Freshwater	Flower fish	(Liu et al., 2019)
<i>Deterrence</i>	<i>Swimming speed</i>		Predator sound	Captive	Freshwater	Tu-fish	(Qin et al., 2020a)
	<i>Activity</i>		Vocalizations	Captive	Freshwater	Lake Victoria cichlid	(Estramil et al., 2014)
<i>Displacement</i>	<i>Directional changes, Acceleration, Group cohesion</i>		Flow sound	Captive	Freshwater	Chub & Brown trout	(Kowal et al., 2023)
<i>Attraction</i>	<i>Swimming speed</i>		Feeding sound	Captive	Freshwater	Flower fish	(Wang et al., 2021)
<i>Attraction</i>	<i>N.T.</i>	<i>N.T.</i>	Rock shuffling	Free swimming	Freshwater	Several	(Holt & Johnston, 2011)
<i>Both</i>	<i>N.T.</i>	<i>N.T.</i>	Reef soundscapes	Captive	Marine	Several	(Parmentier et al., 2015)

Both						
<i>Deterrence & No-response</i>	<i>N.T.</i>	<i>N.T.</i>	Boat noise & Estuary sound	Captive	Estuary	Several (Waddell & Širović, 2023)
<i>Deterrence & Attraction and Diving down</i>	<i>Activity & No response</i>		Boat noise & Biophony	Captive	Marine	<i>Small-spotted catshark</i> (de Vincenzi et al., 2021)
<i>Deterrence & Attraction</i>	<i>Group cohesion</i>		Boat noise & Flow sound	Captive	Freshwater	Three-Spined Stickleback Chapter 6, This thesis
Anthropogenic						
<i>Deterrence</i>	<i>Activity & Swimming speed</i>		Boat noise	Captive	Freshwater	Brook trout (Beach et al., 2025)
<i>N.T.</i>	<i>Startle responses</i>	<i>Feeding</i>	White noise	Captive	Freshwater	Three-Spined Stickleback (Purser & Radford, 2011)
<i>N.T.</i>	<i>Anti-predator response</i>		Boat noise	Captive	Freshwater	Three-spined stickleback & European minnow (Voellmy et al., 2014)
<i>Displacement</i>		<i>Vocal activity</i>	Boat noise	Free swimming	Estuary	Meagre & weakfish (Matos et al., 2024)
<i>Deterrence</i>		<i>Swimming speed</i>	Intermittent	Captive	Freshwater	Zebrafish (Shafiei Sabet, Van Dooren, et al., 2016)
<i>N.T.</i>	<i>Swimming speed & Group cohesion</i>		Intermittent & continuous	Captive	Freshwater	European minnow (Currie et al., 2020)
<i>N.T.</i>	<i>Anti-predator response</i>	<i>Feeding, Anti-predator response</i>	Carnaval noise	Free swimming	Marine	Brazilian damselfish (Leduc et al., 2021)
			Boat noise	Free-swimming	Marine	Brown meagre (La Manna et al., 2016)

2015; Qin et al., 2020b; Wang et al., 2021). When deterrence was found away from natural sounds, authors argued that the sound reflected unfavorable conditions such as predators, male competitors or unsuitable habitat (Liu et al., 2019; Moynan et al., 2016; Parmentier et al., 2015; Qin et al., 2020a). Attraction towards natural sounds can generally be linked to beneficial conditions such as potential mates, food availability or suitable habitat (de Vincenzi et al., 2021; Holt & Johnston, 2011; Moynan et al., 2016; Wang et al., 2021). Which suggest that fish can use natural sounds to select favorable and avoid unfavorable areas and typically associate anthropogenic noise sources with unfavorable conditions.

Several up- and downregulated behaviors in response to anthropogenic noise can also be interpreted as unfavorable for fish. For instance, noise has been found to upregulate startle-, and anti-predator responses, and downregulate feeding rates and vocal activity (La Manna et al., 2016; Leduc et al., 2021; Matos et al., 2024; Purser & Radford, 2011; Voellmy et al., 2014). Upregulated anti-predator responses and downregulated feeding rates and vocal activity could be linked to increased vigilance, because the sound is interpreted as a potential danger, or maybe the fish does not interpret the sound as a danger but needs to increase visual vigilance to compensate for the loss of acoustic information due to masking. Distraction has also been suggested as an explanation for reduced feeding rates (Leduc et al., 2021; Purser & Radford, 2011; Rojas et al., 2021). But to my knowledge the effect of natural sounds on these responses has not been tested to date. Furthermore, noise can both up- and downregulate activity and swimming speeds, making it harder to interpret. With regards to unfavorable natural sounds, different species can respond differently in different contexts such as freezing to try to avoid detection by a predator, or increased swimming to escape predation (Estramil et al., 2014; Liu et al., 2019; Qin et al., 2020b; Wang et al., 2021).

When designing experiments to test the effects of sounds on fish it is important to consider that laboratory tanks and aquaria can create complex acoustic environments that are fundamentally different from open water (Campbell et al., 2019). All boundaries

in tanks are highly reflective, inducing amplified resonant frequencies and reverberations that smear out sounds in the time domain (Duncan et al., 2016; Jézéquel et al., 2022; Rogers et al., 2016). Furthermore, sound pressure and particle motion do not show the same relationship in tanks as they do in open field conditions (Campbell et al., 2019; Rogers et al., 2016). At frequencies above the minimum resonant frequency, pressure and particle velocity have spatial maxima and minima in the tank that vary greatly across frequencies (Duncan et al., 2016). This makes interpretation of spatial responses to sounds in small tanks harder to interpret at higher frequencies but still allows for comparison of responses among sound types. Due to reflections at the air water boundaries and tank wall vibration, tank walls can act as a secondary sound source, making acoustic fields near the walls especially complex (Carbajo et al., 2025; Gray et al., 2016). Frequencies below the minimum resonant frequency are strongly attenuated because the wavelength is larger than the tank size (Duncan et al., 2016; Jézéquel et al., 2022; Rogers et al., 2016). However, tanks still provide a controlled environment that can be used to evaluate behavioral responses to different sound types within a species, and if carefully used, tanks can provide a stable, easily modeled acoustic field (Rogers et al., 2016). At frequencies below the lowest resonant frequency, sound is attenuated quickly, producing steep particle motion and sound pressure gradients (Duncan et al., 2016). It should be noted that although there is an acoustic gradient, the direction of particle motion is affected and often even inverted (Rogers et al., 2016). Which is important to consider when fish are observed to swim towards or away from a sound source in an aquarium setup.

What did I find?

In Chapter 6, I conducted a two-phase laboratory experiment in which groups of five wild-caught migratory three-spined sticklebacks (*Gasterosteus aculeatus*) were exposed to three acoustic treatments: turbulent flow playback, no-flow control, and boat-noise playback to assess both stress-related behavioral changes and spatial deterrence or attraction. Contrary to my hypothesis that anthropogenic noise would up-regulate stress related behaviors, I observed no significant alterations in

thigmotaxis, overall swimming activity, or group cohesion during boat-noise exposures. Instead, playback of flowing-water sounds led to increased group cohesion, a response often interpreted as heightened anxiety (Blaser et al., 2010; Johnson et al., 2023). Still, Kowal et al. (2023) also]found increased group cohesion of Chub (*Squalius cephalus*) and Brown Trout (*Salmo trutta*) in response to playbacks of a high flow river soundscape, which he interpreted as a response to anticipated changes in flow conditions (Kowal et al., 2023). So it is possible that the fish in my experiment also increased their group cohesion in response to flow sound to gain hydrodynamic benefits to expected high-flow conditions.

Spatially, three-spined sticklebacks swam towards the sound of flowing water (attraction) and avoided boat noise playbacks (deterrence). During flow-sound playback, fish significantly reduced their average distance to the active speaker in Phase 1, demonstrating attraction to natural flow sound, whereas in Phase 2, individuals spent less time in the start tank under boat-noise playback, indicating aversion when given the option to escape to quieter waters. These spatial responses reveal that three-spined sticklebacks are capable of perceiving and responding to flow-induced soundscapes and boat noise, suggesting the potential use of geophonic sound in orientation and potential adverse effects of boat noise.

In chapter 5 I discussed the importance of considering tank acoustics when designing playback experiments and interpreting results in laboratory setups and how we applied this in the MIGRADROME. And in chapter 6 I thoroughly measured the particle motion and sound pressure fields created by the playback treatments in a dual-tank experiment. To improve interpretability, we avoided exposing fish to the complex nature of sound fields near tank walls by utilizing an inner tank in the MIGRADROME and a plexiglass tube in phase 2 of the dual tank setup to keep fish away from the tank walls. Furthermore, in the MIGRADROME I showed that low frequency acoustic gradients can still be created over greater distances by utilizing multiple speakers, if they are spaced close together. As stated earlier, at frequencies below the lowest resonant frequency, sound is attenuated quickly,

producing steep particle motion and sound pressure gradients (Duncan et al., 2016) that allow testing for intensity-dependent spatial preferences in response to different sound types, as shown in chapter 6. Furthermore, I showed that high levels of attenuation can also be utilized to test how fish may respond to acoustic barriers in a swim tunnel setup. I believe that complex acoustics in tanks make interpretation challenging, but not impossible, and if well understood, acoustic fields can be carefully manipulated to create acoustic fields suitable for testing the hypothesis of interest.

Advances made & Future research

My findings in chapter 6 contribute to a growing body of research that shows that fish can detect and respond to geophonic sounds, supporting the idea that geophonic sounds could be used as cues for orientation by migratory fish. At the same time, the deterrence we observed in response to boat noise adds to concerns about the potential impacts of anthropogenic noise on migratory routes, habitat use, and the energy budgets of freshwater species. I urge for more research on fish responses to natural sounds, because I believe that studying how fish respond to natural sounds that are linked to unfavorable conditions, will allow for better interpretation of the impact, and mechanisms behind responses to anthropogenic sounds. And studying how fish respond to natural sounds linked to both favorable and unfavorable conditions can help predict potential impacts of masking by noise pollution.

In marine systems, fish have been shown to orient and swim towards or away from habitat associated soundscapes (soundscape orientation) and induce settlement in response to habitat associated soundscapes (habitat selection) (Gordon et al., 2018; Huijbers et al., 2012; Montgomery et al., 2001, 2006; Parmentier et al., 2015; Radford et al., 2011). And the attraction and deterrence responses of freshwater fish to sounds associated with predators, food and conspecifics described above can also be seen as selection and orientation towards or away from favorable or unfavorable habitat conditions. I argue that soundscape orientation and habitat selection may be especially important to migratory fish, that must travel large distances,

experiencing a wide range of acoustic information, and are constantly faced with decisions on whether to stay or leave, or change direction of travel. I suggest several potential acoustic cues that could be used by fish during their migration but remain to be tested. Furthermore, as shown in chapter 2-4, migratory fish are likely to experience adverse effects from many sources of anthropogenic noise during their migration, as they travel under bridges, though cities and along shipping routes.

I suggest that one of the highest potential acoustic cues for orientation and habitat selection to migratory fish is flow sound. I hypothesized that flow sound attracts migratory fish because it indicates potential river entrances or side branches they can explore, and it can reflect suitable habitats for rheophilic fish species. Febrina et al. (2015) found the first experimental evidence for attraction in migratory Ayu toward playbacks of flow sound recorded in a fish passage and deterrence away from playbacks of recordings in an unpassable weir, but it is unclear whether they accounted for pseudo replication of sound stimuli (Febrina et al., 2015). Kacem et al. (2020) also found some support for this theory in small streams in Canada, where they found that brook trout densities were positively correlated with sound pressure levels (likely linked to flow) when comparing habitats of the same type (Kacem et al., 2020). And Kowal et al. (2023) found that acoustic playbacks of high flow and sediment transport environments changed the shoaling behavior, swimming patterns and longitudinal position in groups of Chub and Brown Trout, which they interpreted as a response to anticipated changes in flow conditions (Kowal et al., 2023). In chapter 6, I found that wild-caught three spined sticklebacks reduced their distance to the speaker in response to flow sound playbacks recorded in high turbulent flow environments when compared with playbacks from nearby low-flow environments, supporting our hypothesis. To validate whether flow sound attracts three-spined stickleback under natural conditions, I suggest that playback experiments should be carried out in the field on free ranging fish during the migratory period. Furthermore, sound playbacks in the controlled swim tunnels should be carried out to test how anthropogenic sounds affect fish during their migration, measuring potential delays or energetic costs. Because understanding how

fish respond to their acoustic environment could help mitigate the impacts of human activities and inform the design of more effective fish guidance systems, particularly around fish passages and other critical migration bottlenecks.

I showed that single, and dual-tank setups as used in chapter 6 can reveal attraction toward and deterrence away from natural and anthropogenic sounds. And I suggest that this should also be carried out for land-based noise and other potential natural acoustic cues such as sediment associated soundscapes, aquatic plant bubbles, or sounds linked to predators or available food. But I also believe that swimming motivation may play an important role during migration in flowing waters. If migratory fish are stressed or unsure of the proper direction of travel, this could greatly affect their energy expenditure and time of arrival, ultimately affecting their fitness. I therefore designed the migradrome (Chapter 5), a swim tunnel specifically designed to test the effects of natural and anthropogenic sounds on fish migration behavior. The migradrome contains 10 underwater speakers that can be used to create a wide range of acoustic fields and scenarios such as sound pressure and particle motion gradients, acoustic barriers, or even a looming acoustic stimulus. The swim tunnel can be tilted to induce a water velocity gradient that allow the fish to travel at their preferred swimming speed, which can be used as a measure of swimming motivation. This will allow us to test the behavior of migratory fish in response to a wide range of controlled sound exposure conditions.

I am not the first to describe land-based traffic noise and concerns about its effects on aquatic animals have been raised by others (Holt & Johnston, 2015b; Zang et al., 2019b). Still, I could only find three studies on the effects of land-based noise on fish, of which only one experimentally investigated the effect of road traffic noise (Crovo et al., 2015). They showed elevated cortisol levels in exposed fish, but did not test for behavioral responses (Crovo et al., 2015). Another study found elevated ventilation rates and decreased swimming velocity in response to railway bridge noise in 3 out of 4 tested freshwater fish species (Friebertshauer et al., 2020). And Leduc et al. (2021) showed that elevated land-based noise during the Brazillian carnival was linked

to reduced feeding rates and flight initiation distance (Leduc et al., 2021). This shows that several land-based noise sources can induce behavioral and physiological changes in fish. However, given the omnipresence of car traffic noise from roads and bridges encountered in our recordings, I believe there is a severe lack of experimental research towards the effects of land-based noise on fish.

Conservation with limited knowledge

Unlike the EU's Marine Strategy Framework Directive (MSFD), which has included underwater noise as a pollutant since 2008 and requires Member States to monitor and set thresholds for it, the Water Framework Directive (WFD) incorporates no legislative protection for freshwater ecosystems against anthropogenic noise (Bolgan et al., 2016). There is much to be discovered about how freshwater animals use natural sound for their fitness and survival. But it is known that most if not all aquatic animals can detect sound and vibrations (Budelmann, 1992; Narins & Feng, 2007; Popper et al., 2019; Popper & Hawkins, 2018; Putland et al., 2019b; Yack et al., 2020). Therefore, it is likely that they will be affected by noise. Although some animals can adapt well to human-induced changes, sometimes even to their benefit (Lipp et al., 2004), noise can negatively affect animals in many ways. It can mask natural acoustic information, distract, induce behavioral changes and sometimes even cause physical harm (Duarte et al., 2021; Mickle & Higgs, 2018; Rako-Gospić & Picciulin, 2019; Slabbekoorn et al., 2018; Weilgart, 2018). Therefore, anthropogenic noise will likely result in a net loss for most animals, and I believe noise monitoring and mitigation measures should be taken up in international freshwater legislation such as the WFD.

How animals use natural sound cues, how they are affected by especially vessel noise in freshwater river systems, and how important natural sounds are to their survival and fitness, varies among species, life stages and contexts (Egner & Mann, 2005; Forlano et al., 2015; Shafiei Sabet, Wesdorp, et al., 2016), and can only be determined through experiments. However, experiments take time, and given the current threats to freshwater ecosystems, immediate conservation measures are required to

prevent further degradation. Therefore, I urge for a precautionary approach with regards to noise pollution in freshwater. If we consider that all natural sounds have the potential to be an important source of information to an aquatic animal, we should strive to limit masking of all natural sounds where possible. Especially in vulnerable habitats and for endangered species.

Quantifying potential impact

The potential masking impact of noise sources can be predicted by comparing the spectral intensity of anthropogenic noise with those of natural sounds. If the noise source overlaps with a natural sound in terms of spectrum, it will negatively affect the audible distance of the natural sound source. In chapter 4, I found that boat noise in rivers overlaps in terms of spectrum with most natural sound sources. In the presence of boat noise, most natural sounds encountered in our recordings during boat absence, would be fully masked. Therefore, we can assume when boats are passing by in rivers, almost all acoustic information is lost to nearby aquatic animals, and our predictions of % time boat presence is virtually the same as % time masked for all natural sound sources.

When considering acoustic masking it is important to note that all fishes are sensitive to particle motion and, so far, I only addressed sound pressure, just audible to those fish that have a swim bladder (Popper & Fay 2011). Masking and disturbance will likely not be the same if taking particle motion into account as signal-to-noise ratios will be different. Chapman and Johnstone (1974) showed that the masking effect of noise on the detection of a pure tone by Atlantic cod (*Gadus morhua*) was significantly decreased by about 7 dB when the masker was positioned at an angle of more than 10° in relation to the pure tone signal (Chapman, 1973; Chapman & Johnstone, 1974). For sound pressure, masking noise will accumulate omnidirectionally, while the signal of interest is likely to come just from one particular direction. This means the masking problem is likely less for those sensitive to particle motion, for which masking noise is likely just the noise arriving from the same angle as the signal. A potentially disturbing sound can therefore also be detected over longer ranges in particle motion, as it will be less quickly masked by ambient

noise from the same direction, in comparison to the omnidirectional signal-to-noise ratio as expressed in sound pressure.

Aquatic habitats can vary greatly in terms of soundscapes (Kacem et al., 2020; Tonolla et al., 2011; Vračar & Mijić, 2011; Wysocki et al., 2007). Therefore, they are likely to be impacted to a variable extent by anthropogenic noise. Natural sounds in naturally noisy high-flow environments limit detection of more subtle sounds, and therefore, artificially noisy conditions will lead to less acoustic masking. Animals in more quiet habitats such as stagnant waters, typically have more sensitive hearing to listen to subtle sounds of relatively low level (Amoser & Ladich, 2005; Ladich, 1999), which makes them more vulnerable to masking, and potentially disturbing noise is also audible to them at greater distances. Still, having more sensitive hearing does not mean that hearing specialists are more likely to be affected in terms of behavioral or physiological changes compared to hearing generalists, as the potential for responsiveness starts when the sound falls within the audible range (Shafiei Sabet, Wesdorp, et al., 2016). Nonetheless, the intensity variation of biologically relevant sound events and natural ambient background levels in different habitats should be considered when estimating masking impacts.

At larger distances, shipping and other noise sources may not fully overlap in spectrum with some natural sounds or can still be below natural sound spectra in terms of intensity when the animal is close to the natural sound source (referred to as the zone of audibility by (Richardson et al., 1995)). In those cases, noise does not cause masking of signals of interest but can still induce behavioral or physiological changes in aquatic animals. The zone of audibility is often considered as larger than the zone of responsiveness, since animals can choose not to respond to the sound, and it is commonly thought that animals are more likely to respond to sounds of higher intensity (Moretti & Affatati, 2023; Richardson et al., 1995). However, I would argue that the only prerequisite for behavioral response to a sound is that it falls within the audible range of an aquatic animal and is above ambient sound levels. I therefore propose that % time above ambient should also be a measure that is used to quantify

potential noise impact on aquatic animals. The frequency bands for which the noise is above ambient can be adjusted through frequency weighted curves of hearing groups for species in those habitats, to predict what animals are affected most (Lucke et al., 2024).

Noise is often a transnational problem, spanning multiple borders, but has a fragmented regulatory framework in the EU (Pouikli, 2025). Regional or global noise maps can help emphasize the need for collective action and can be used as a starting point for broader international environmental assessment procedures (Pouikli, 2025). Field measurements and noise modeling can be used to produce noise impact maps, and several projects have created noise maps in marine environments, providing insights into highly impacted areas (Bosi et al., 2023; Erbe et al., 2014; Farcas et al., 2020). However, currently no noise maps have been created for freshwater systems. Furthermore, I believe that % time masked and % time above ambient may better predict potential impacts on animals than the monthly or yearly average excess noise levels that are typically used in noise maps (Farcas et al., 2020). Because behavioral responses to anthropogenic noise are highly dependent on species and context, received sound pressure level alone is likely a bad predictor of impact on animals (excluding physical damage impacts for extreme intensity sounds) (K. de Jong et al., 2020; Ellison et al., 2012; Erbe et al., 2025). These noise maps can then be overlaid with maps of vulnerable habitats, and distribution maps of endangered species, to identify acoustic bottlenecks to migratory fish and pinpoint high-risk areas and species, while correcting for hearing sensitivity (Erbe et al., 2014; Lucke et al., 2024). The resulting maps can help identify areas where anthropogenic noise may have an above-average impact on species habitats, and where mitigation measures may be most effective (Erbe et al., 2014). Which can in turn help raise awareness, prioritize research avenues and inform management interventions.

Possible mitigation measures

Anthropogenic noise is often a byproduct of the actions we perform and not an intended aim. There are various ways to reduce noise; this can be done by limiting sound transmission through

material choices when constructing roads and bridges (Ling et al., 2021) or through modifications to ship propellers (Lafeber et al., 2022), but also with speed limits, rerouting shipping lanes, requiring ships to travel in convoy, incentivising less boats with larger transport capacity (Heise et al., 2017; Merchant, 2019) or enforcing closed seasons or times for boat traffic in important seasons or habitats. Ships produce more noise when they travel faster, so speed limits result in a smaller affected areas with lower noise levels (Findlay et al., 2023). We may therefore be able to help aquatic animals by reducing or prohibiting shipping in vulnerable areas or seasons, such as during spawning or migration. The effectiveness, cost and applicability of these noise mitigation measures can be evaluated using modelled noise maps by comparing different noise mitigation scenarios (Bosi et al., 2023).

Fish guidance

In the past, acoustic guidance systems to deter fish away from harmful anthropogenic hazards such as hydropower turbines or pile driving has received considerable research attention (Hubert et al., 2024; Popper et al., 2020; Putland & Mensinger, 2019). Acoustic deterrence has been shown to have varied efficacy among species, stimuli and contexts, but can be used along with other deterrents such as light or physical screens (Deleau et al., 2020; Putland & Mensinger, 2019). Like many other studies, I showed that boat noise can also be used to deter fish. Boat noise is broadband but consists of many components that are produced by onboard machinery and propeller movements, including narrow frequency tonals and cavitation induced amplitude modulations (C. A. F. de Jong, 2023; Jansen & De Jong, 2017). Investigating how fish respond to these different sound components could support the development of effective stimuli for acoustic deterrent devices and inform improved ship and propeller design. Furthermore, the attraction of fish towards natural sounds also provides opportunities for fish passages, many of which have low passage successes or cause migratory delays because fish are insufficiently attracted to the entrance (Hershey, 2021; Noonan et al., 2012). For instance, flow sound could potentially be used to attract fish to the entrances of fish passages, either through acoustic playbacks, or by designing

passages that naturally generate these sounds. Furthermore, masking of natural sounds at fish passage entrances by anthropogenic noise, large weirs or pumps should be investigated and considered in the design of passages.

Passive acoustic monitoring

Monitoring freshwater fauna is essential for assessing water quality, population trends and evaluating the efficacy of restoration and mitigation efforts. Based on the findings in this thesis, I believe that acoustic communication may be widespread across freshwater taxa. Passive acoustic monitoring (PAM) provides a tool in which the species-specific sounds from fish, aquatic insects, amphibians, and birds can be detected and quantified from underwater recordings (Linke et al., 2018). PAM could also enable continuous monitoring of dynamic bio-physical ecosystem processes such as flow rates, sediment transport, and possibly even primary production and decomposition of organic material by microbial activity (Desjonquères & Linke, 2020; Felisberto et al., 2015b; Geay et al., 2018; Kratochvil & Pollirer, 2017b; Linke et al., 2018). Traditional monitoring methods can be invasive and, in many cases, only provide snapshots of species presence. PAM allows for continuous, long-term, non-invasive monitoring of animal activity and movement. Permanent monitoring stations could provide real-time ecological insights, both seasonal and in response to sudden disturbances and could help detect more cryptic and high movement species that are missed in traditional snapshot surveys. The same technology can also be used in short-term projects, ranging from days to weeks, for targeted surveys. Despite the large gap in knowledge on species specific sounds in freshwater environments that should be addressed (Desjonqueres et al., 2024; Greenhalgh et al., 2025; Looby et al., 2022; Parsons et al., 2022; Rountree et al., 2019), I believe that PAM can already be applied in freshwater research to study behavior and distribution of animals in response to (human induced) environmental changes such as light and noise pollution.

Conclusions

In this thesis, I have raised awareness about and provided new

insights into the ecological significance of natural soundscapes in freshwater ecosystems and the potentially widespread impacts of anthropogenic noise, particularly on migratory fish. I demonstrated that geophysical features such as flow velocity, sediment type, and river size create distinct and consistent acoustic signatures, and hypothesise that these could serve as orientation or habitat selection cues for fish. Biophonic sounds could also offer information about habitat quality, predator presence, or reproductive opportunities. My studies also show that anthropogenic noise from shipping and land-based traffic is widespread and strongly overlapping in spectrum with natural sounds, leading to significant masking. Importantly, my experimental exposure study confirms that fish exhibit attraction towards natural cues like flow sounds and are deterred by boat noise. I hypothesise that natural sounds can play an important role for free-ranging fish as well and anthropogenic noise could disrupt key spatial behaviours such as migration.

Despite these advances, many knowledge gaps remain. Most natural sound sources, especially transient sounds such as species-specific biological sounds, remain undescribed, and experimental evidence on how free-ranging fish perceive and respond to both natural and anthropogenic sounds in the freshwater is still largely absent. I showed that noise from commercial inland shipping can be predicted from AIS data, but there is a lack of knowledge on noise propagation and other sources of anthropogenic noise for freshwater systems, particularly for land-based traffic and recreational boating. Future research should prioritize experimental validation of potential acoustic cues in the field, effects of anthropogenic noise sources on fish migration, the use of passive acoustic monitoring using machine learning to capture transient sound events, and development of predictive noise maps to assess masking impacts across freshwater systems. A precautionary approach to noise management is urgently needed, and soundscapes should be integrated into conservation planning, particularly at migratory bottlenecks and vulnerable habitats for migratory fishes. And I believe that noise monitoring and mitigation measures should be taken up in international freshwater legislation such as the European Water Framework Directive.

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