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

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Chapter 1:

General introduction

Freshwater ecosystems and migratory fish under threat

Freshwater makes up only 0.01% of water on Earth, while it harbors almost 6% of all described species (Dudgeon et al., 2006). The high diversity and levels of endemism in freshwater animals likely emerged from the highly fragmented nature of freshwater ecosystems (Arthington et al., 2016). Unfortunately, this also makes them vulnerable to human stressors. From 1970 to 2022, freshwater biodiversity has experienced a dramatic decline of 87%, compared to 69% in terrestrial and 56% in marine biodiversity, with one quarter of freshwater species threatened with extinction (Sayer et al., 2025; WWF, 2024). Freshwater fish are considered the most vulnerable group of all vertebrates, and migratory species are particularly threatened (Costa et al., 2021). Here, fish migration is defined broadly as the cyclic movements of fish between habitats, such as between feeding grounds and shelter, or between feeding- and spawning grounds. This includes long distance spawning migrations such as diadromous migration between sea and freshwater and potamodromous migration within freshwater, but also diel, tidal or seasonal migrations between habitats not specifically linked to spawning. The declines in migratory fish populations are caused by a wide range of stressors, including canalization and urbanization, migration barriers, habitat loss and degradation, invasive species, overfishing, chemical pollution and climate change (Costa et al., 2021). However, a source of pollution that is rarely listed as a stressor in freshwater ecosystems but may have contributed to this decline is anthropogenic noise (Mickle & Higgs, 2018; van Opzeeland & Slabbekoorn, 2012).

Over the past century, urbanization, population growth, technological advancements and expansion of transport networks have led to large increases in anthropogenic noise pollution around the world (Hildebrand, 2009; Mickle & Higgs, 2018; Morillas et al., 2018). And in the past decades, human-made noise is increasingly recognized as a stressor to both humans and animals (Morillas et al., 2018; Slabbekoorn et al., 2018). While the effects of noise on aquatic animals are relatively well studied in marine species, especially for marine mammals, studies on freshwater animals are scarcer (Mickle & Higgs, 2018). The

acoustic landscapes of marine and freshwater systems differ considerably in terms of sound propagation, background levels and types and distribution of sound sources (Wysocki et al., 2007). Moreover, there are considerable differences in environmental conditions and animal taxa between marine and freshwater systems. Therefore, freshwater ecosystems may be affected differently by anthropogenic noise. To understand how anthropogenic noise may contribute to population level effects of freshwater animals we must first understand how they use sound in their natural environment.

Use of sounds by aquatic animals

Most, if not all aquatic animals can detect and respond to sound and vibrations (Budelmann, 1992; C'okl & Theiss, 1987; R. R. Fay & Popper, 2000; Narins & Feng, 2007; Popper et al., 2019; Solé et al., 2023; Yack et al., 2020), but only very few studies have investigated natural soundscape information available in freshwater environments, and how this is used by animals. Still, aquatic animals of a wide range of taxa have been shown to use sound in a multitude of ways, including communication, predator- and prey detection, orientation, navigation and habitat selection (Gordon et al., 2019; Jansson, 1973; Popper & Hawkins, 2019; Simpson et al., 2011; Wilson et al., 2014). There is a large group of animals that can detect but not actively produce sound, although there also is a large proportion of fish and aquatic invertebrates that are believed to actively produce sound as a means of communication (Desjonqueres et al., 2024; Greenhalgh et al., 2025; Looby et al., 2022). It has been suggested that hearing threshold and ranges of fish are adapted to the background levels of their environment, and that this evolution was mainly driven by the necessity to detect abiotic sounds, predators, prey, and to a lesser degree communicative sounds (Amoser & Ladich, 2005). Furthermore, it is believed that the use of abiotic sounds, heterospecific calls and unintended sounds, may play an important role in the ability of animals to orient themselves and select appropriate habitats (R. Fay, 2009; Ladich, 2014; Slabbekoorn & Bouton, 2008).

Soundscape orientation and habitat selection

In marine systems, attraction and settlement in response to habitat associated soundscapes have been shown in a wide range of taxa and life stages, including corals, bivalves, crustaceans, and fish (Gordon et al., 2019; Huijbers et al., 2012; Lillis et al., 2013; Montgomery et al., 2001, 2006; Simpson et al., 2011; Vermeij et al., 2010). The same has been suggested for freshwater fish, and soundscape orientation may be especially valuable to migratory fishes that have to navigate long distances in environments limited in terms of other sensory cues (Slabbekoorn & Bouton, 2008; van Opzeeland & Slabbekoorn, 2012). In marine environments, habitat associated soundscape attraction studies have mainly been conducted by playing back recordings made on relatively discrete habitat types such as coral- and oyster reefs, or mangrove forests. But these natural soundscapes are made up of a wide range of sounds from biological sources (biophony) such as fish calls and arthropod snaps, and geophysical forces (geophony) such as wind, waves and waterflow (Bohnenstiehl et al., 2016; Hildebrand, 2009; Lindseth & Lobel, 2018). Generally, the most prominent sources that distinguish habitats have been suggested as the soundscape components to which animals respond, such as snapping shrimp snaps, and turbulence around oyster reefs (Bohnenstiehl et al., 2016; Volaric et al., 2025). But these potential cues about environmental properties are rarely tested on aquatic animals for their potency to trigger responses in separation.

In rivers, clear habitat associated soundscapes have been described in small streams. Showing that sub-habitats such as pools, glides and riffles can be characterized based on their sound signatures (Tonolla et al., 2010). And higher brook trout densities were found to be associated with habitat dependent soundscape differences (Kacem et al., 2020). While correlative, this suggests, that fish may have habitat preferences based on the acoustic features of those habitats. Some progress has been made towards disentangling and characterizing the most prominent geophysical sound sources (geophony) leading to habitat-associated soundscape variation in freshwater systems. The most notable drivers of habitat-associated soundscape variation seem to be water flow, sediment transport, and river size

dependent sound propagation. (Geay et al., 2020; Kacem et al., 2020; Tonolla et al., 2009, 2010, 2011; Wysocki et al., 2007). Furthermore, a wide range of freshwater organisms, including fish, aquatic invertebrates, amphibians, (semi-) aquatic mammals, reptiles produce sounds (biophony), while also bubbles from plants, decomposing bacteria, and physical disturbance of substrates or the water surface can make sounds (Aiken, 1985; Colley et al., 2013; Desjonqueres, 2016; Holt & Johnston, 2011; Kratochvil & Pollirer, 2017; Marian et al., 2021; Rountree et al., 2020). Simply detecting another organism can serve as a source of information for orientation and habitat selection, since organisms typically only occupy areas with certain habitat characteristics. However, only a select number of water types has been investigated in terms of natural soundscapes, and studies rarely investigate all sound types that make up the soundscape. To gain a better understanding of the range acoustic information available to aquatic animals in freshwater systems, and the threats of anthropogenic noise, systematic recordings of soundscapes are required to further disentangle the geophonic, biophonic and anthropogenic sources that make up the soundscape in a range of habitats.

In freshwater, only a few behavioral experiments have tested the response of animals to natural soundscape cues. Holt & Johnston (2011) showed attraction of several freshwater fish species to acoustic playbacks of sediment disturbances in the field (Holt & Johnston, 2011). Febrina et al. (2015) described how intensity-dependent sound preferences of adult and juvenile Ayu (*Plecoglossus altivelis*) varied for several pure tone frequencies and the dominant frequencies in the sounds from an unpassable weir and passable fish ladder (Febrina et al., 2015). Wadell & Širović (2023) showed no attraction of lab-reared settlement stage estuarine fish species to estuarine soundscape playbacks (Waddell & Širović, 2023). But Kowal et al. (2023) did show increased aggregation and changes in swimming patterns and longitudinal position of Chub (*Squalius cephalus*) and Brown Trout (*Salmo trutta*) in response to acoustic playbacks of a high flow and sediment transport environment (Kowal et al., 2023). Although the function of these responses is hard to interpret, it shows that fish species with a range in variable hearing abilities

can detect and respond to flow and sediment associated soundscapes.

In terrestrial environments, acoustic playbacks of turbulent river soundscapes were also shown to increase abundance of a wide range of terrestrial arthropod species, many of which have an aquatic larval stage (Gomes et al., 2021). And in one toad species, females preferred male calls when the playbacks were supplemented with river soundscapes (Zhao et al., 2017) These studies show that responses of animals to river soundscapes are widespread, but in order to gain a better understanding of the importance of sound in the life-history of freshwater animals, we require more studies on a wide range of taxa and contexts. Furthermore, experiments should be designed with care, avoiding pseudoreplication of acoustic stimuli (Hubert et al., 2024; Slabbekoorn & Bouton, 2008), making sure that outcomes are interpretable, and can be linked to behaviors vital to the fitness of aquatic animals (Council et al., 2005; New et al., 2014; Slabbekoorn et al., 2019).

Noise pollution effects on aquatic animals

Since most aquatic animals can detect sound and use acoustic cues for activities vital to their survival, most are likely affected by anthropogenic noise. The most severe impacts of noise occur close to loud sources such as explosions, impact pile driving and seismic surveys, leading to hearing damage or sometimes even death (Popper & Hawkins, 2019). If anthropogenic noise overlaps with the hearing range of aquatic species, it can invoke both behavioral and physiological changes, such as deterrence, attraction, activity levels, shoaling and elevated cortisol levels and heart rates, which can all limit the time-energy budget of animals (Graham & Cooke, 2008; Neo et al., 2014; Rojas et al., 2021; Wysocki et al., 2006). Furthermore, noise can distract animals, negatively affecting their foraging efficiency (Halfwerk & Van Oers, 2020; Rojas et al., 2021). If anthropogenic noise overlaps with biologically relevant sounds, it can lead to masking, reducing the range and time over which suitable mates, predators, prey and habitats can be detected (Codarin et al., 2009; Holles et al., 2013; Rogers et al., 2021; Voellmy et al., 2014). Although loud events of physical damage are the most

severe, lower intensity persistent sources such as boat noise are generally believed to have a larger cumulative impact on aquatic animals at a population level (Neo et al., 2014; Soudijn et al., 2020).

Anthropogenic sound can generally be considered a negative stressor, but animals may also have the capacity to evolve or learn and adapt to changes in the environment over time. For example, pigeons (*Columba livia*) have learned to use human made features as landmarks, and great tits (*Parus major*) increase their pitch by which they escape masking from highway noise at least to some extent (Lipp et al., 2004; Slabbekoorn & Peet, 2003). Fish have been seen to increase the amplitude of their vocalizations in response to noise (Brown et al., 2021; Holt & Johnston, 2014; Luczkovich et al., 2016). This is important to keep in mind when estimating the impacts of noise on animals. Still, we can expect through the loss of information through acoustic masking and based on the wide range of studies that have observed negative impacts, that anthropogenic noise will negatively affect animals in most cases, at least to some extent.

Acoustic conservation applications

Sound can also be applied as a tool for restoration and conservation. For instance, the attracting and deterring nature of different sound stimuli can be applied as a tool in restoration and conservation. For instance, sound is successfully used to deter marine mammals away from sites before damaging acoustic activities such as pile driving (Geelhoed et al., 2017; Voß et al., 2023). Furthermore, sound barriers have been applied with variable success to deter migratory fish from potential entrainment into harmful hydropower stations (Deleau et al., 2020; Putland & Mensinger, 2019). Acoustic enrichment can aid in reef restoration by attracting and promoting settlement in reef building larvae and beneficial reef fish (Gordon et al., 2019). Lastly, acoustic species communities and ecosystem processes can be monitored through Passive Acoustic Monitoring (PAM). PAM has great potential as a relatively cheap non-invasive tool for continuous biodiversity monitoring (Desjonquères & Linke, 2020). It can help upscale freshwater biodiversity monitoring programs,

allowing for better spatial and temporal resolution. And, it can help capture the presence of endangered species that are missed in brief snapshot biodiversity sampling. Which can help governmental organizations and NGO's make better informed management interventions. However, we lack sufficient insight into underwater soundscapes in freshwater systems and need studies about the correlation between acoustic soundscape features and hydro-acoustic properties of the waterbody and the presence of biotic sound sources. Furthermore, complementary investigations of soundfields in aquarium facilities could complement our insights and understanding and would provide testing opportunities in captive conditions (Akamatsu et al., 2002; Campbell et al., 2019).

Thesis outline

This thesis contains seven chapters: This general introduction chapter (chapter 1), followed by three soundscape studies (chapter 2-4), one methodological study (chapter 5), one behavioral experiment (chapter 6), and a summary and general discussion (chapter 7). In chapter 2 I investigated urban noise and natural soundscapes in river segments of various sizes within one slow-flowing temperate river system. In chapter 3 I further explored temporal noise patterns in traffic noise under bridges. In chapter 4 I expanded and validated our findings from chapter 2 and quantified boat noise in large rivers across Europe. In chapter 5 I described the development of the MIGRADROME swim tunnel to investigate effects of sound on fish migration behavior and discuss the opportunities and limitations of indoor laboratory setups, based on acoustic fields that can be created in such setups. In Chapter 6 I carried out a behavioral preference test in a dual tank setup to investigate spatial preference and deterrence of captive migratory three-spined stickleback to natural sounds and boat noise.

The overarching aim of this thesis was to evaluate the effects of anthropogenic noise in freshwater systems on aquatic animals in general, and migratory fish in particular. In order to achieve this, across the chapters of this thesis, I attempted to follow a conceptual framework for investigating how natural acoustic information is used by aquatic animals in general, and migratory

fish in particular, and evaluated the impacts of anthropogenic noise (Figure 1). This can help assess how animals may be affected by anthropogenic noise, in terms of how and why features of anthropogenic noise elicit behavioral responses. But also, how they may be affected when important acoustic cues are masked by noise pollution.

The first step is to record soundscapes through field recordings (chapter 2-4), identifying and quantifying natural sounds and anthropogenic noise sources. This can then already be used to make a precautionary impact assessment, by comparing the intensity of anthropogenic noise with natural sounds and predicting the spatial and temporal extent of masking. Furthermore, to study how fish use natural sounds, it is important to identify natural sounds that have high potential to be used as acoustic cues for aquatic animals, based on quality and availability. Once high potential cues are identified, they can be used in controlled laboratory playback experiments, to verify whether they elicit behavioral changes in fish (chapter 5&6). If they do, this should be followed up with field experiments, to investigate how they may affect free swimming fish. Once the importance of acoustic cues is identified, this can help inform more targeted impact mitigation measures.

The conceptual framework can be broken down in to 6 different research questions:

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

3. What are the most dominant anthropogenic noise sources in freshwater systems and how are they distributed in time and space?
4. To what extent does anthropogenic noise mask natural sound sources in freshwater systems?

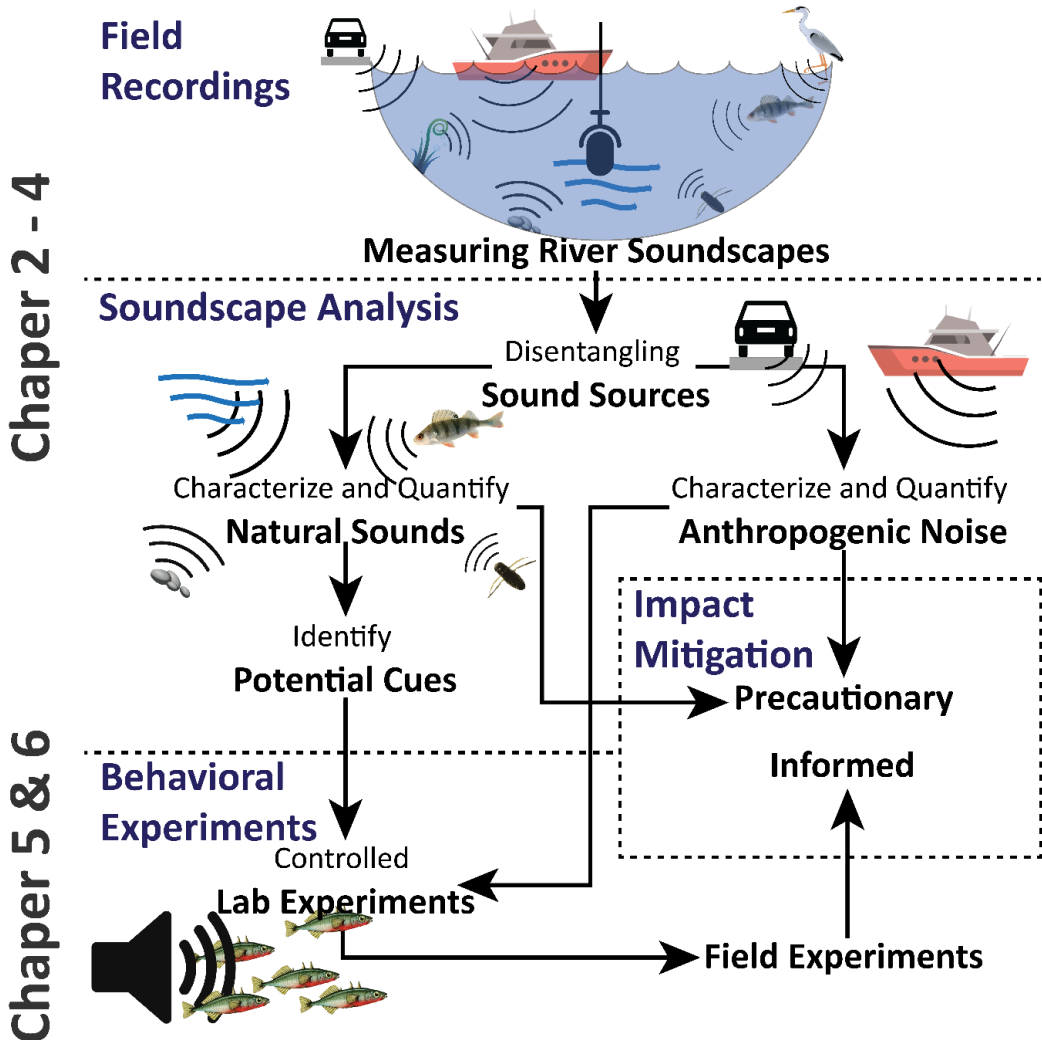


Figure 1; Framework for investigating how natural acoustic information is used by aquatic animals in general, and migratory fish in particular, and evaluate the impacts of anthropogenic noise

5. How do migratory fish respond behaviorally to natural sound cues and anthropogenic noise in experimental conditions?
6. How do behavioral responses to anthropogenic noise, or lack of responses to natural sound sources due to masking, affect fish during migration?

Outdoor studies (Chapters 2-4)

Chapter 2

In Chapter 2, I focused on characterizing the continuous elements of freshwater soundscapes in river segments of varying sizes in a lowland temperate river system through a combination of spatially replicated, short-term recordings and long-term stationary deployments. Sound sources can be roughly split into two groups: Continuous sound sources (typically geophonic) such as flow, wind, and sediment induced sounds, and transient sound events (typically biophonic) such as animal vocalizations, bubbles, and splashes. To capture habitat-dependent differences emerging from continuous geophonic sources I took spatially replicated snapshots at varying depths and distances from shore within each river type. This was analysed using a Redundancy Analysis (RDA), which allowed me to disentangle which local river features such as river size, water flow and water quality explained most of the variation in the sound intensity at different frequencies. To capture anthropogenic noise, I conducted 1-minute recordings at 1 km intervals along transects through two cities, allowing me to compare sound levels among urban and rural locations. Although short recordings are limited in duration, they enable extensive spatial coverage, revealing heterogeneity in continuous sound sources across and within freshwater ecosystems.

To complement this spatial approach, I deployed stationary hydrophones for at least 1 week in rural locations and in cities under bridges, ensuring capture of diel patterns and rarer transient events. I generated Long Term Spectral Average (LTSA) plots using a custom R script to visualize average spectral levels over time, which revealed clear diel and weekly patterns in traffic noise. LTSA imagery allowed me to distinguish geophonic from

biophonic sources, as well as to identify times of elevated road noise linked to human activity patterns. These long-term deployments were used to characterize biophonic sounds and explore diel road traffic noise patterns. By combining short and long recordings, Chapter 2 establishes a baseline understanding of how natural geophonic and biophonic sounds interact with human-generated noise in shaping river soundscapes.

Chapter 3

Building on the spatial sampling and exploration of temporal patterns of Chapter 2, Chapter 3 delves into the temporal structure of anthropogenic sounds. To quantify the temporal contribution of traffic noise, I applied threshold detection to the continuous 1-week recordings.

Chapter 4

Drifting hydrophones, boat noise impact, and cue identification
In chapter 4, spatial soundscape comparisons were made with a floating hydrophone passively drifting with the current in three large European rivers, to validate and expand on our findings in chapter 2. Furthermore, in high flow environments such as rivers, flow around the hydrophone can create turbulence resulting in low-frequency flow noise artifacts around the hydrophone that is not reflective of the natural soundscape (Lillis et al., 2018). Therefore, by drifting at the same speed as the river, flow noise artifacts are reduced, and recordings are more reflective of the true soundscape. I carried out another RDA to investigate whether the findings in chapter 2 held in other rivers across Europe and I was specifically interested in how sediment types affected the soundscape in a river with a more heterogeneous sediment distribution. Generalized linear models were then used to further understand the direct relationship between the soundscape and the features of interest.

I also utilized 24-hour stationary hydrophone recordings to capture transient boat passages and biophonic sound events. Manual screening of spectrograms and subsequent listening was used to detect short biophonic sound events. The spectral and temporal characteristics of the sounds were visualized through spectrogram images. Boat noise was quantified using adaptive threshold detection to the continuous 24 h recordings. This

technique corrected for fluctuating natural sound levels through a rolling minimum and provided robust estimates of the percentage of time during which boat noise was present. I described and quantified the spectrum and intensity of natural sound sources in the absence of noise and compared this with boat noise to estimate how likely it is for these sounds to be masked. Furthermore, we utilized a boat density map based on Automatic Identification Systems (AIS) carried by commercial inland shipping vessels to predict boat noise (and masking) over the full length of each river.

By combining knowledge on life-history requirements of fish with the quality and temporal availability of natural acoustic cues, I then selected high potential acoustic cues for future playback experiments aimed at testing behavioural responses in freshwater species.

Indoor studies (Chapter 5 & 6)

In chapters 2-4 I identified several high potential acoustic cues, which could then be used for experimental validation with acoustic playbacks. In ideal circumstances, properly replicated and controlled field experiments with wild fish are carried out to validate the use of acoustic cues, since the behaviour of captive fish in laboratory setups can differ significantly from natural contexts. However, field studies can be logistically challenging and expensive. Furthermore, indoor laboratory setups allow researchers to carefully control and manipulate experimental conditions to examine causal relationships. The reduced variability in controlled laboratory setups also often reduce the number of replicates required. Which will allow us to test more cues, at a faster pace in different species and contexts.

Chapter 5

In chapter 5, I therefore designed the MIGRADROME, an artificial river in which we can expose swimming fish to a wide range of acoustic scenarios, such as: An acoustic gradient, an acoustic barrier, or a temporally changing acoustic environment like a passing boat. We tested the possibilities and constraints of the MIGRADROME and similar setups in terms of the sound fields

that could be created in such a setup, with regards to particle motion and sound pressure.

Chapter 6

In chapter 6, I utilized a dual-tank setup to test the spatial response of fish to boat noise and flow sound. Migratory three-spined sticklebacks were caught in a fish passage during their migration, and exposed to boat noise and flow sounds to test anxiety related responses, and attraction or deterrence. The treatments were recorded using a drifting hydrophone thrown from the shore to collect sounds from high- and low flow environments.

I believe potential cues should first be tested in laboratory setups, to gain insights into underlying mechanisms, and recommend that these are thereafter tested for real world impacts in complementary field experiments. Once high potential acoustic cues have been identified and experimentally validated, extra care should be given to protecting these sounds from acoustic masking in vulnerable habitats and during vulnerable seasons and life stages of the species of interest.

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