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

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Chapter 4:

Human-altered Soundscapes in Large European Rivers: wide-spread potential for masking by boats

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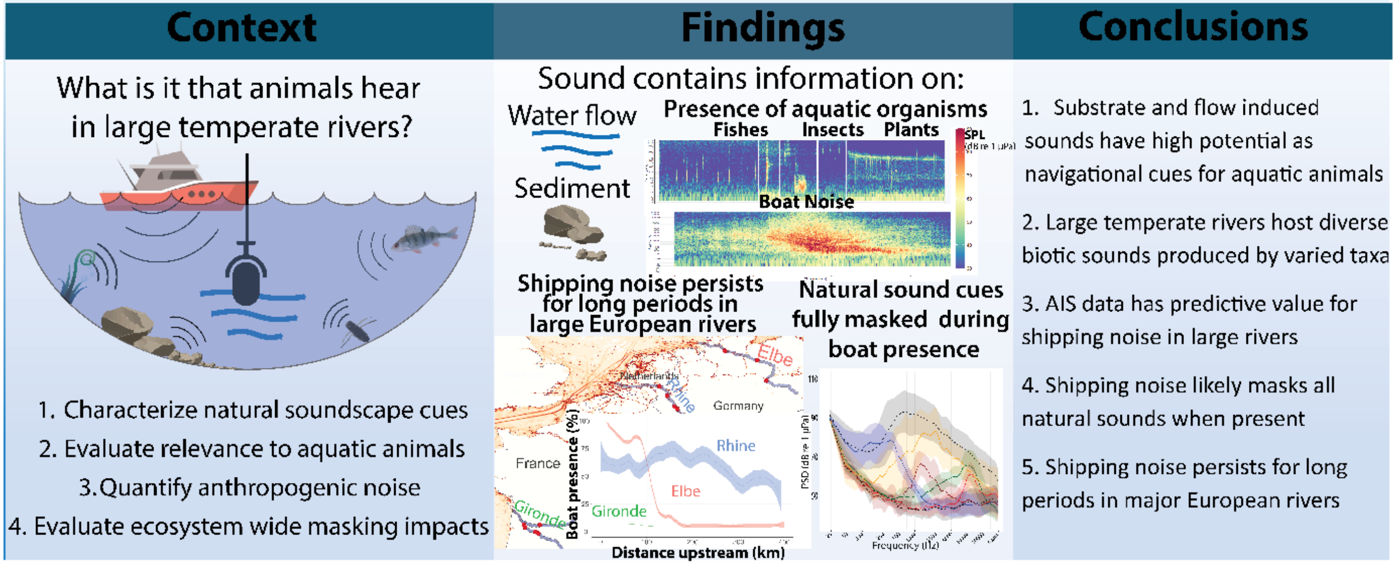
Abstract

Anthropogenic noise is increasingly recognized as a stressor to marine animals, but is rarely considered as a pollutant in freshwater ecosystems. We therefore characterized underwater soundscapes in three major European rivers (Rhine, Elbe, Gironde) to evaluate how natural soundscapes are shaped by river hydro-geomorphology and biotic sounds and the extent to which boat noise masks those cues. We (1) characterized biotic sounds in 24-h recordings; (2) assessed relationships between hydro-geomorphological features and the soundscape using drifting hydrophone recordings; (3) quantified boat noise in 24-hour recordings; (4) evaluated masking potential through sound spectrum comparisons between natural sounds and boat noise; and (5) assessed the value of Automatic Identification System (AIS) data to predict boat noise in rivers. River soundscapes contained biotic sounds from diverse taxa. Water velocity and sediment hardness explained a significant proportion of the variation in background sound levels at frequencies above 350 Hz, and sound levels sharply increased above 1.4 m/s. In the presence of boat noise, most natural sounds are expected to be masked. Boat noise occupied 42–86 % of recording time in the Rhine, 2–38 % in the Elbe, and 0–20 % in the Gironde. We found a significant relationship between AIS boat density and boat noise and extrapolated boat noise along each river. We conclude that: (a) river soundscapes reflect information on nearby physical river features and biota, providing information to aquatic animals, but (b) masking of these cues by boat noise is expected to be widespread and persists for long periods in large rivers.

Highlights

- Substrate and flow induced sounds have high potential as cues for aquatic animals
- Large temperate rivers host diverse acoustic signals produced by varied taxa
- AIS data are a good predictor for underwater shipping noise in large rivers
- High levels of boat noise persist for long periods in major European rivers
- Shipping noise likely severely limits aquatic animal sound perception in rivers

Graphical Abstract



Context

What is it that animals hear in large temperate rivers?

1. Characterize natural soundscape cues
2. Evaluate relevance to aquatic animals
3. Quantify anthropogenic noise
4. Evaluate ecosystem wide masking impacts

Findings

Sound contains information on:

Water flow

Sediment

Presence of aquatic organisms

Shipping noise persists for long periods in large European rivers

Natural sound cues fully masked during boat presence

Conclusions

1. Substrate and flow induced sounds have high potential as navigational cues for aquatic animals
2. Large temperate rivers host diverse biotic sounds produced by varied taxa
3. AIS data has predictive value for shipping noise in large rivers
4. Shipping noise likely masks all natural sounds when present
5. Shipping noise persists for long periods in major European rivers

1. Introduction

Underwater soundscapes contain a wealth of ecological- and geophysical information, as aquatic ecosystems are full of underwater sounds from biological sources such as fish, aquatic invertebrates, amphibians, (semi-) aquatic mammals, reptiles, bubbles from plants and decomposing bacteria, and physical disturbance of substrates or the water surface (Aiken, 1985; Colleye et al., 2013; Desjonqueres et al., 2024; Greenhalgh et al., 2025; Holt & Johnston, 2011; Kratochvil & Pollirer, 2017a; Marian et al., 2021; Rountree et al., 2020; te Velde et al., 2024; van der Lee et al., 2025), but also geophysical forces produced by the movement of water, air or substrates (Geay et al., 2017; Pijanowski et al., 2011; Tonolla et al., 2011). Furthermore, the sounds from the mixture of biotic and abiotic sources are altered by environment-specific propagation, and the source variety and propagation features together can provide critical information to aquatic animals on features of the local environment (Fay, 2009; Slabbekoorn & Bouton, 2008). Such habitat associated soundscapes have been shown to affect spatial behaviour in aquatic animals from a diverse range of taxa and life stages, especially in marine systems (Gordon et al., 2019; Huijbers et al., 2012; Montgomery et al., 2006; Radford et al., 2011; Simpson et al., 2011; Vermeij et al., 2010). However, studies investigating the importance of sound to freshwater animals are scarcer, and meanwhile, anthropogenic noise is ever increasing, and can severely limit the information animals have on which to base behavioural decisions vital to survival and reproduction.

In freshwater, habitat-associated soundscapes have been attributed predominantly to hydro-geo-morphological features. Wysocki et al. (2007) and Amoser and Ladich (2010) reported habitat-associated soundscape variation and seasonal diversity in Austria, especially between quiet stagnant waters and loud fast-flowing streams (Amoser & Ladich, 2010; Wysocki et al., 2007). Tonolla et al. 2010 & 2011 revealed that spatial heterogeneity of soundscapes within fast-flowing streams and in larger river segments, correlated directly with local hydro-geo-morphological characteristics such as flow speed, turbulence, depth and streambed sediment transport (Tonolla et al., 2010, 2011).

Te Velde et al. (2024) showed that spectral soundscape variation in segments of a relatively slow-flowing river system in the Netherlands were also partially determined by river size and flow velocities (te Velde et al., 2024). Kacem et al. (2020) investigated river soundscapes, but in addition reported a biased distribution of brook trout (*Salvelinus fontinalis*) within a specific micro-habitat, associated with higher broadband sound pressure levels (SPL) (Kacem et al., 2020). Acoustic responsiveness to natural river soundscapes could be responsible for this pattern, and Holt & Johnston (2011) indeed showed attraction of fish to playbacks of substrate disturbances (Holt & Johnston, 2011), while Kowal et al. (2023) revealed responses of fish to playback of flow and sediment transport sounds.

Descriptive studies of habitat-associated soundscapes, including those reporting acoustic responsiveness in aquatic animals, have typically focussed on relatively discrete habitat types in marine systems with abundant sounds of animals, such as coral- and oyster reefs and mangrove forests (Huijbers et al., 2012; Lillis et al., 2015; Radford et al., 2011; Vermeij et al., 2010). However, one can also look at gradually changing soundscapes and acoustic cues that are more dependent on gradually changing physical properties of the local environment, which may be particularly relevant for river systems. Migratory fish may use environmental cues for orientation and navigation from multiple modalities, including flow and olfactory cues, but at times they may have to rely on acoustic cues. Detecting suitable sediment and waterflow can be of critical importance for reproduction or shelter and may not have a particular smell or a very localized current (Erman & Erman, 1984; Gore, 1978; Kemp et al., 2011; Molokwu et al., 2014; Rosenfeld, 2003). In such cases a context-dependent acoustic signature may be critical (Holt & Johnston, 2011, Kacem et al., 2020). Besides the abiotic features that may affect this signature, there may be additional cues to habitat suitability for behaviours or life stages in the sounds from biotic sources from within (e.g. fish, frogs, or invertebrates) and outside (e.g. singing or calling birds) the water (te Velde et al. 2024).

Once high potential acoustic cues have been identified in rivers, it becomes important to understand to what extent they are still audible in the current state of human exploitation of river systems for transport of goods and people. This is particularly relevant as freshwater ecosystems are experiencing extremely high biodiversity declines due to a wide range of anthropogenic stressors (Deinet et al., 2024; Sánchez-Bayo & Wyckhuys, 2021). Freshwater fish are considered the most vulnerable group of all vertebrates, and migratory species are particularly threatened (Costa et al., 2021; Sayer et al., 2025; WWF, 2024). The current threats to freshwater ecosystems are diverse and many, including anthropogenic noise from road traffic and urban areas (te Velde et al., 2024; te Velde & Slabbekoorn, 2024) and likely even more dramatically from boat noise (Marley et al., 2016; Smott et al., 2018; Vieira et al., 2021). Still, we lack insight into the extent and severity of the masking and acoustic disturbance problem. In recent years, substantial efforts have been made to mitigate stressors affecting freshwater ecosystems, including dam removal, the implementation of fish passages, fisheries quotas, and reductions in nutrient loading (Forseth et al., 2017; Tamario et al., 2019). However, the potential importance of natural river soundscapes and the disturbance of aquatic animals by anthropogenic noise has received far less attention (Popper et al., 2020; van Opzeeland & Slabbekoorn, 2012). While Automatic Identification System (AIS) data are applied to assess distribution and intensity of shipping noise at sea, this has been rarely exploited for rivers. Any natural sound has the potential to be important to aquatic animal communities, including (migratory) fishes, amphibians, and invertebrates, and we therefore urgently need more recording data about natural rivers soundscapes, and more insight about the masking problem by anthropogenic noise.

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). Still, inland shipping traffic accounts for a significant proportion (6-8%) of total cargo transport in the EU, the US and China (Beyer, 2018), making it an important source of anthropogenic noise in freshwater systems. Large navigable waterways often coincide with areas of high ecological significance, as large rivers harbor a large diversity of fish, invertebrates and amphibians, and connect marine and freshwater ecosystems, critical for migration and dispersal of many aquatic species (Dudgeon et al., 2006; Pracheil et al., 2013; van Puijenbroek et al., 2019). Although there is a substantial amount of attention to the growing presence and potential for detrimental effects of boat noise on marine species of a wide range of taxa, the prominence and potential effects of anthropogenic noise in river ecosystems remain largely overlooked (Erbe et al., 2019; Havlik et al., 2022; Morley et al., 2013; Popper et al., 2020; Slabbekoorn et al., 2010; te Velde & Slabbekoorn, 2024).

Anthropogenic noise has been shown to affect behavior and physiology of aquatic animals in a multitude of ways. It can deter, attract, distract, affect activity patterns and reproductive success, and increase anxiety-related, or stress-induced physiological parameters in a wide range of taxa (Azarm-Karnagh et al., 2023; Nedelec et al., 2022; Neo et al., 2014; Rojas et al., 2021; Wysocki et al., 2006). Furthermore, anthropogenic noise can mask biologically relevant sounds, limiting availability of information critical for behavioral decisions of aquatic animals. Most, if not all aquatic animals can detect sound and use it for activities critical to their survival, such as habitat selection, navigation, predator avoidance, prey detection, and communication (Gordon et al., 2019; Jansson, 1973; Popper & Hawkins, 2019; Simpson et al., 2011; Wilson et al., 2014). To be able to understand how masking by anthropogenic noise can affect aquatic communities, we require more knowledge about the diversity and distribution of natural underwater soundscapes that are audible to aquatic animals.

When considering acoustic masking it is important to note that all fishes and likely many invertebrates and amphibians are sensitive to particle motion and sound pressure is audible to fish that have a swim bladder (Popper & Fay 2011). In addition, aquatic insects and many anurans can detect sound pressure, through pressure sensitive membranes and air bubbles or air-filled cavities (Čokl & Theiss, 1987; Simmons, 2025). While sound pressure and particle motion are related, their ratio can greatly vary in shallow water environments, especially near water-air or water-substrate boundaries. Furthermore, signal-to-noise ratios will be different between particle motion and sound pressure sensitive species. Chapman and Johnstone (1974) demonstrated that the masking effect of noise on a pure tone by Atlantic cod (Gadus morhua) was reduced by about 7 dB at angles greater than 10° between the masker and pure tone signal (Chapman, 1973; Chapman & Johnstone, 1974). Consequently, particle motion sensitive species may experience less acoustic masking and may detect potentially disturbing sounds over greater distances. In this study we provide the first quantitative estimates of sound pressure masking impacts on freshwater animals in large rivers but we acknowledge that these are likely somewhat overestimated due to directional unmasking in particle motion sensitive species.

In the current study, we investigated underwater soundscapes of three major European rivers; the Rhine (Netherlands, Germany), Elbe (Germany) and Gironde (France), to study the potential for acoustic identifiers of gradual habitat changes and the potential masking impact from boat traffic. We investigated natural soundscapes from geophonic sources by analyzing the relationship between spatially replicated acoustic recordings from a drifting hydrophone, and hydro geomorphological river features at those locations. And we explored the prevalence of acoustic communication signals of aquatic animals (biophony) in rivers in 24 hour stationary recordings at sites across the three rivers. Furthermore, we quantified the percent time contribution of boat noise in our 24-hour recordings using a threshold detection approach and investigated whether AIS boat density data has predictive value for boat noise in large rivers. Finally, we combined the results of these two analyses to make an assessment on the severity of masking of natural sounds by boat noise. We aimed to answer the following research questions about the distribution of and explanation for natural soundscape variation and about boat prominence and the extent of masking in time and spectrum: 1a) Do the three major European rivers vary among each other in amplitude and spectra of natural soundscapes? 1b) Do upstream and downstream river soundscapes vary consistently, taking water velocity, river size and bottom features into account? 2a) What proportion of the time are boats present in the Rhine, Elbe, and Gironde? 2b) To what extent is boat noise masking biophonic and geophonic sounds?

2. Methods

2.1 Research area

We collected underwater sound recordings in three large European river systems: the Elbe (Germany), Rhine (Netherlands & Germany) and Gironde (France) (Figure 1A). To explore and assess the potential value of natural sound cues to aquatic animals, and how they are affected by boat noise. These rivers harbor important habitats to diverse European freshwater taxa, including aquatic invertebrates, birds, plants and fish and provide valuable ecosystem services to humans including fisheries, transport, water supply, flood protection and recreation (Fenten & Dieperink, 2024; Fischer et al., 2019). Notably, the Elbe, Rhine and Gironde are especially important for several heavily threatened European migratory fish species, which are also often used as indicator species for good ecological status (Lasne et al., 2007; Schiemer, 2000). Between 7-9 anadromous migratory fish species inhabit these rivers, which is relatively high compared to most other European rivers (van Puijenbroek et al., 2019). The species include Atlantic sturgeon (*Acipenser sturio*), Allis shad (*Alosa alosa*), Twaite shad (*Alosa fallax*), Whitefish (*Coregonus maraena*), Houting (*Coregonus oxyrinchus*), River lamprey (*Lampreta fluviatilis*), Sea lamprey (*Petromyzon marinus*), Atlantic salmon (*Salmo salar)* and Sea trout (*Salmo trutta*). From these 9 species, 8 are included in the IUCN red list, and most notably, the Gironde contains the last surviving population of the critically endangered Atlantic sturgeon, while the feasibility of a restocking programme is being evaluated for the Rhine and restocking of Atlantic sturgeon is currently ongoing in the Elbe. The fish and other taxa in these rivers and the ecosystem services they provide are threatened by multiple stressors including pollution, reduced connectivity, channelization and invasive species (Fenten & Dieperink, 2024; Fischer et al., 2019; Leuven et al., 2009). In terms of boat traffic, the Rhine and Elbe are two of the most notable corridors for inland boat cargo

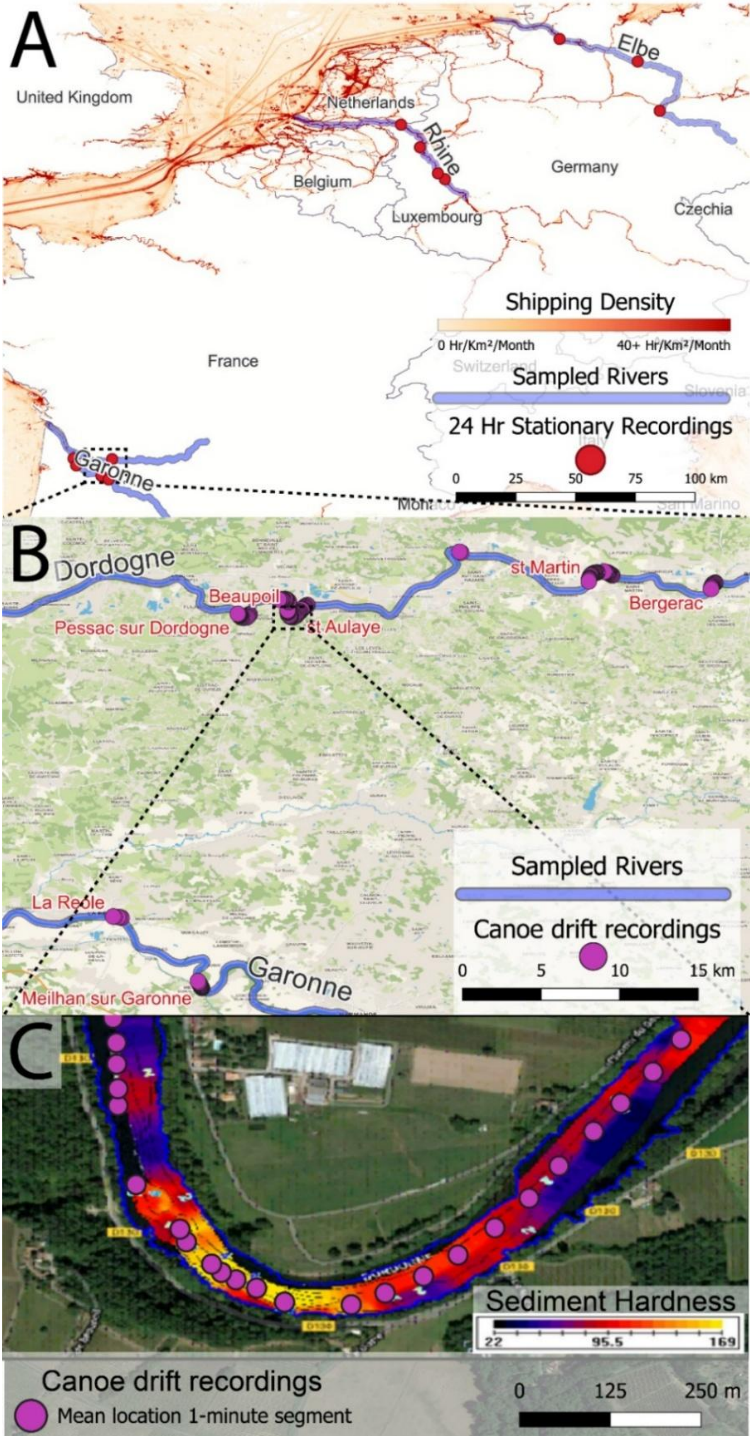


Figure 1; Sample locations in three large European river systems; Elbe, Rhine and Gironde (A) 24-hour acoustic recording locations including an AIS shipping density background map. (B) Canoe drift recording locations in the Garonne and Dordogne, (C) Zoomed in example of sample points including a background map of the sediment hardness.

transport in Europe, with the Rhine accounting for 58 billion t/km/yr, and Elbe 4.2 billion t/km/yr, while there is close to no inland cargo transport in the Gironde (Central Commission for the Navigation of the Rhine, 2024). Therefore, the Elbe, Rhine and Gironde provide us with three ecologically and societally important river systems affected by varied levels of boat traffic, suitable to compare in terms of shipping noise.

2.2 Natural soundscape analysis

To characterize geophonic and biophonic natural river sounds, and compare natural soundscapes among rivers, we collected two separate datasets. Geophonic sounds were characterized through canoe drift recordings in river sections in the Gironde and Rhine rivers for which maps were available on hydrogeomorphologogical river features such as sediment, depth and width. Biophonic sounds were characterized by screening 24-hour stationary recordings during boat absence. These 24-hour stationary recordings were also used to compare natural soundscapes among rivers.

2.2.1 Data collection

We made acoustic recordings in two different ways: Stationary with deployed hydrophones fixed to the substrate or repeatedly floating along with the current after throwing it in the water from the riverbank; and gently floating in the main current with the flow of the river in canoe drift recordings. All acoustic recordings were made using calibrated SoundTrap 300STD hydrophones. Soundtraps were set to record with a sample rate of 96 kHz, high preAmp gain, and high pass filter turned off. Below, we addressed the necessary details of the respective recording procedures and data processing.

Stationary acoustic recordings

To compare natural sound spectra of the three rivers during boat absence and to characterize biophonic sounds in large temperate rivers, 24-hour continuous stationary acoustic recordings were made by deploying hydrophones suspended between an anchor and sub-surface buoy at approximately 60 cm from the riverbed. Hydrophones were placed several meters from the shore, at least at 2 meters depth. In locations with tidal differences, hydrophones were deployed at low tide. Soundtraps were deployed in 3 locations in the Elbe, 4 in the Rhine, and 5 in the Gironde river system for a total of 12 recording locations (Figure 1A). These stationary recordings were also used to quantify boat noise, which is described further in section 2.3.1

Canoe drift recordings

To explore what local hydrogeomorophological river features are reflected in the soundscape, canoe drift recordings were made by deploying a weighted down soundtrap 50 cm below a floating surface buoy, at the end of a 5 m rope behind an inflatable canoe. To reduce the effects of flow noise artifacts, all recordings were made by drifting with the water current. The position of the canoe was recorded through gps tracking. Recordings were cut into 1-minute segments and linked to the mean gps location during that 1-minute timeframe. Any 1-minute segment with artifacts from hydrophone collisions or paddling when repositioning the canoe were excluded from the analysis. Drift recordings were made along 4 drifts in the Rhine and 5 trips in the Gironde. Only 1-minute recordings with boat absence and from locations with available sediment data were further used in the analysis. Since all recordings in the Rhine contained 100% boat presence, these had to be excluded from the analysis. This resulted in a total of 126 samples (Figure 1B&C).

Hydrogeomorphological river features

To investigate the relationship between hydrogeomorphological river features and the natural soundscape, we used data from a 2019 echosounder and sediment survey in the Gironde river system conducted by the French national National Research Institute for Agriculture, Food and the Environment (INRAE, unpublished data). In which sediment hardness and bathymetry maps were created using a Hummingbird Helix 9 echosounder, and collected substrate samples were passed through various square-mesh sieves after being dried in an oven to determine their composition based on 6 granulometric classes. Sediment hardness is a measure estimated from signal strength return of the echosounder, which has been shown to reflect sediment type, with lower grain size sediments such as silt having low signal strength, and higher grain size sediments such as gravel and bedrock having high signal return strength (Austin, 2012; Schooley & Neely, 2018; Winfield et al., 2015). The substrate size distribution at each site was used to explore the relationship between sediment hardness and substrate size and how the substrate changes with distance upstream of the river estuary.

At each 1-minute mean gps location from the canoe recordings, sediment hardness and bathymetry maps were used to extract the sediment hardness, depth at recording location and maximum river depth (Figure 1C). Furthermore, the water velocity was extracted from the mean distance moved in the canoe gps tracking data as the canoe was drifting with the water current this was indicative of the mean surface water velocity. River width at each location was determined from satellite images, and area of cross-section was calculated from the river width and max river depth.

2.2.2 Analysis

Biophony

To assess the prevalence and masking potential of underwater biological sound events, we visually screened spectrogram images in Audacity™ during boat absent time windows from the 24 hr recordings, for the presence of known and unknown biological sounds. Potentially biological sound events were saved and grouped into different classes after careful listening and visual inspection. Several known and unknown sound types were selected based on whether they were detected in at least 2 recording locations and a minimum of 5 sound events were available. Example spectrograms were made of representative samples from the different sound types using a custom R script with a window size of 8192 and 90% overlap.

Geophony

To explore the relationship between hydrogeomorphological river features and the natural river soundscape, we carried out a redundancy analysis (RDA) between the full octave band sound pressure level SPL and the hydrogeomorphological river features at each 1-minute recording location (c.f. te Velde et al., 2024). Since this typically results in a grouping of cross-correlated high- and low frequency octave bands, we calculated the mean SPL of all high frequency octave bands (350-45000 Hz), and low frequency octave bands (11-350 Hz). We then selected the hydrogeomorphological features that showed the strongest association with either high or low frequency mean octave band SPL and carried out a multiple linear regression with SPL as dependent variable and hydrogeomorphological features as explanatory variables.

2.3 Quantifying Boat Noise

2.3.1 Acoustic boat detection:

The 24-hour recordings that were used to compare natural soundscapes and characterize biophonic sounds, were also used to quantify percent time contribution of boat noise in the Elbe, Rhine and Gironde. Boat presence was quantified through a threshold detection method. First, long term spectral average (LTSA) spectrogram images were made of each recording using 1-minute average temporal windows and a 1 Hz frequency resolution (Figure 2). Then, acoustic boat presence was quantified from 5-minute rolling average power spectral density levels (PSD) between 1000-3000 Hz. Any timepoint where the 5-minute rolling mean exceeded 70 dB was classified as "Boat present". For rolling means lower than 70 dB, an adaptive threshold was used to correct for variation in the natural background level (adapted from Merchant et al., 2012). The adaptive threshold works on the assumption that the 1-hour rolling minimum SPL is representative for the natural background level. Any timepoint where the 5 minute rolling mean PSD between 1000 and 3000 Hz was >10 dB above the 1 hour rolling minimum, was also classified as "Boat present". To correct for the effect sound propagation from boats at larger distances, any timepoint that was below the threshold level for at least 5 minutes in both directions was labelled as "Boat absent". Any timepoint that was below the threshold, but still within 5 minutes before or after a Boat Presence detection, was classified as "Boat distant".

2.3.2 AIS data

To assess whether AIS boat traffic data has predictive value for boat noise in rivers, we obtained AIS boat density raster maps

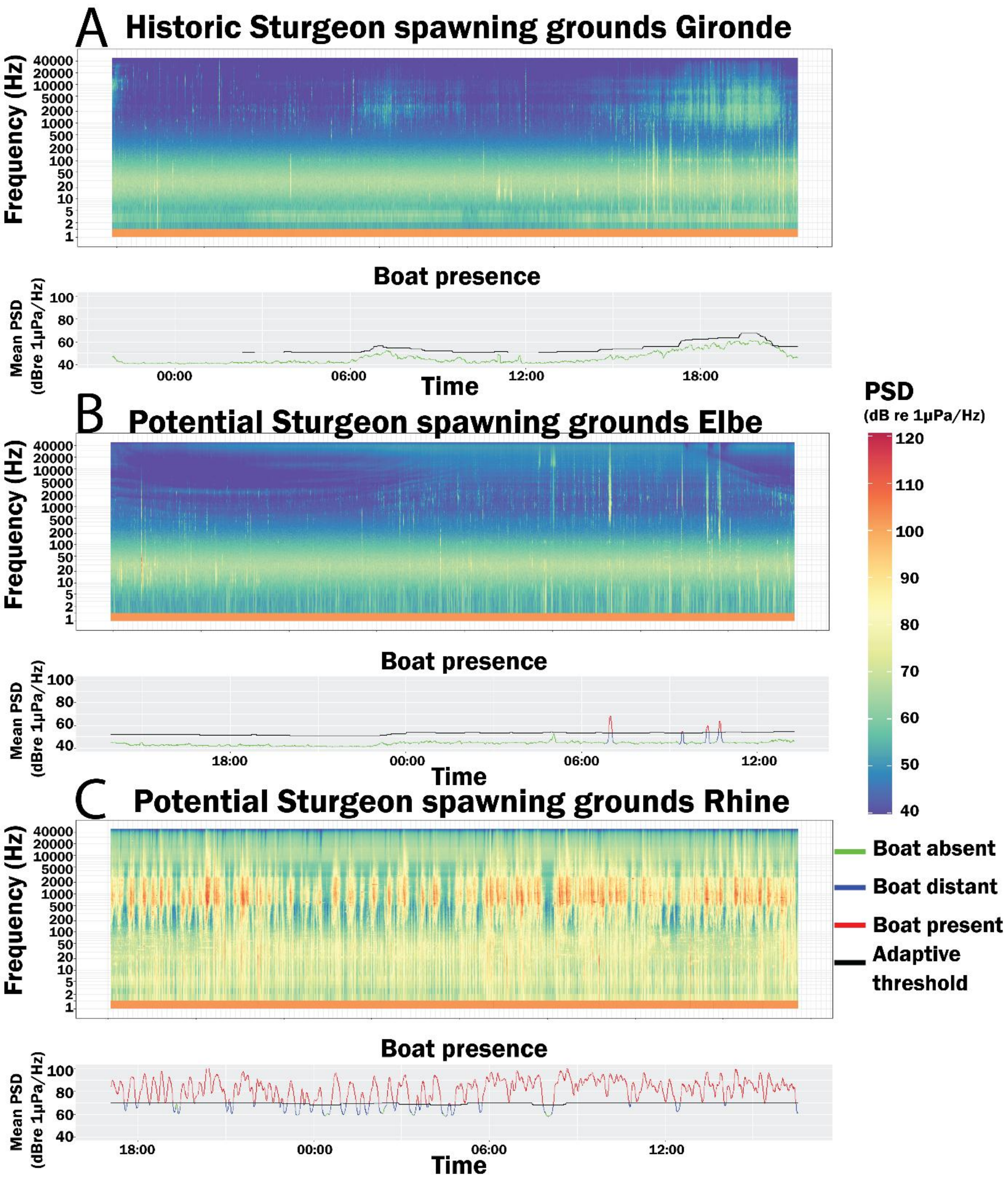


Figure 2; Example 24-hour long term spectral average (LTSA) images, with average SPL at 1-minute timesteps and boat detection threshold graphs below it, at historic and potential suitable spawning grounds for Atlantic sturgeon (A. Sturio) in the Gironde (A), Elbe (B) and Rhine (C). The Boat detection graphs show the adaptive threshold level in black that scales with a 1-hour rolling minimum SPL, the coloured line represents the mean power spectral density between 1000 and 3000 Hz. The line is coloured red (boat detected) when it is above the adaptive threshold, any timepoint that was below the threshold, but still within 5 minutes before or after a Boat Presence detection is coloured blue (Boat distant), and any time point below the threshold longer than 5 minutes before or after a Boat presence detection is coloured green (Boat absent).

in hours/month/km^2 via the Global Maritime Traffic Density Service (GTMDS), retrieved from GlobalMaritimeTraffic.org (a service of MapLarge 2021), using the ‘Export’ feature (GMTDS, 2024). Only data on non-loitering boats (spending less than 6 hours in 1 km^2 area) were used in the analysis.

We extracted the specific boat densities in the month and year of each 24-hour recording location to investigate the link between recorded acoustic boat presence and AIS shipping densities. Furthermore, to assess and predict the distribution of shipping noise over the entire river lengths, QGIS was used to extract the shipping density values from May 2023 at 1 km intervals along each river from the sea up to 400 km upstream. Figure 1A shows this shipping density map from May 2023. To explore seasonal changes in shipping activity, the mean monthly shipping density across the whole length of each river was investigated from January-December 2023.

2.3.3 Analysis

Acoustic boat presence detections as described above were converted into % time boat presence per 24-hours at each site. To investigate the relationship between acoustic boat presence and AIS shipping density, we applied a quasibinomial Generalized Linear Model (GLM) with acoustic boat presence in % time per day as dependent variable and cumulative AIS boat presence in hours/day/km^2 as explanatory variable. The resulting model was then used to predict acoustic boat noise presence across the entire length of each river based on the AIS shipping density data. To compare the natural background and boat sound spectra in each river, we selected 4 paired boat present, distant and absent recordings at each 24-hour recording location, spread out across the day, at approximately 6 hours apart. In some locations in the Gironde, fewer than 4 boat events were available. We then calculated the power spectral density (PSD) of each recording using a Fourier transform in R, using Hann windows with 50% overlap, and a window length equal to the sample frequency (96 kHz). The mean and standard deviation was calculated and visualized to compare the mean boat noise and background spectra among rivers.

2.4 Masking potential of Boat noise on Natural sounds

To evaluate the masking potential of boat noise on biophonic sounds, we compared mean and standard deviation PSD spectra of biophonic sound events with boat noise events from the same locations. Because several biophonic sound events were shorter than 1 second, PSD spectra were calculated using a window length of 4,096, using Hann windows with 50% overlap.
Furthermore, to evaluate the masking potential of boat noise on geophonic sounds, we compared mean and standard deviation PSD spectra of 1-minute recordings from locations within specific water velocity and sediment hardness bins, with 4 boat noise events from all locations. We calculated the PSD spectra using Hann windows with 50% overlap, and a window length equal to the sample frequency (96 kHz).

3. Results & Discussion

3.1 Natural Sounds and their potential as acoustic cues

3.1.1 Biophony

Manual screening of the 24-hour recordings yielded many sound events of potentially biological origin, including repeated occurrence of two sound types of known species: the Eurasian Perch (*Perca fluviatilis*) (Figure 3A), and the lesser boatman (*Micronecta sp.*) (Figure 3B). Perch sounds were detected in at least one location in all three rivers, for a total of 6 locations, while *Micronecta* was detected only at two locations in the Elbe. We selected the following three common unknown sounds and suggested the suspected organisms responsible for production of the sounds: Suspected aquatic plant (Figure 3C), Suspected Pikeperch (*Sander lucioperca*) snap (Figure 3D) (Kaschner, 2012; Tiepelt, 2005), and suspected fish grunt (Figure 3E). The biophonic sounds had diverse frequency characteristics, ranging from low frequency fish grunts to high frequency aquatic insect stridulation and broadband aquatic plant bubbles and Pikeperch snaps, but all fall within the same frequency spectrum as boat noise (Figure 3F).

As shown, acoustic communication signals are diverse and widespread in large temperate river systems. Furthermore, there is a broad range of natural sound events not specifically linked to

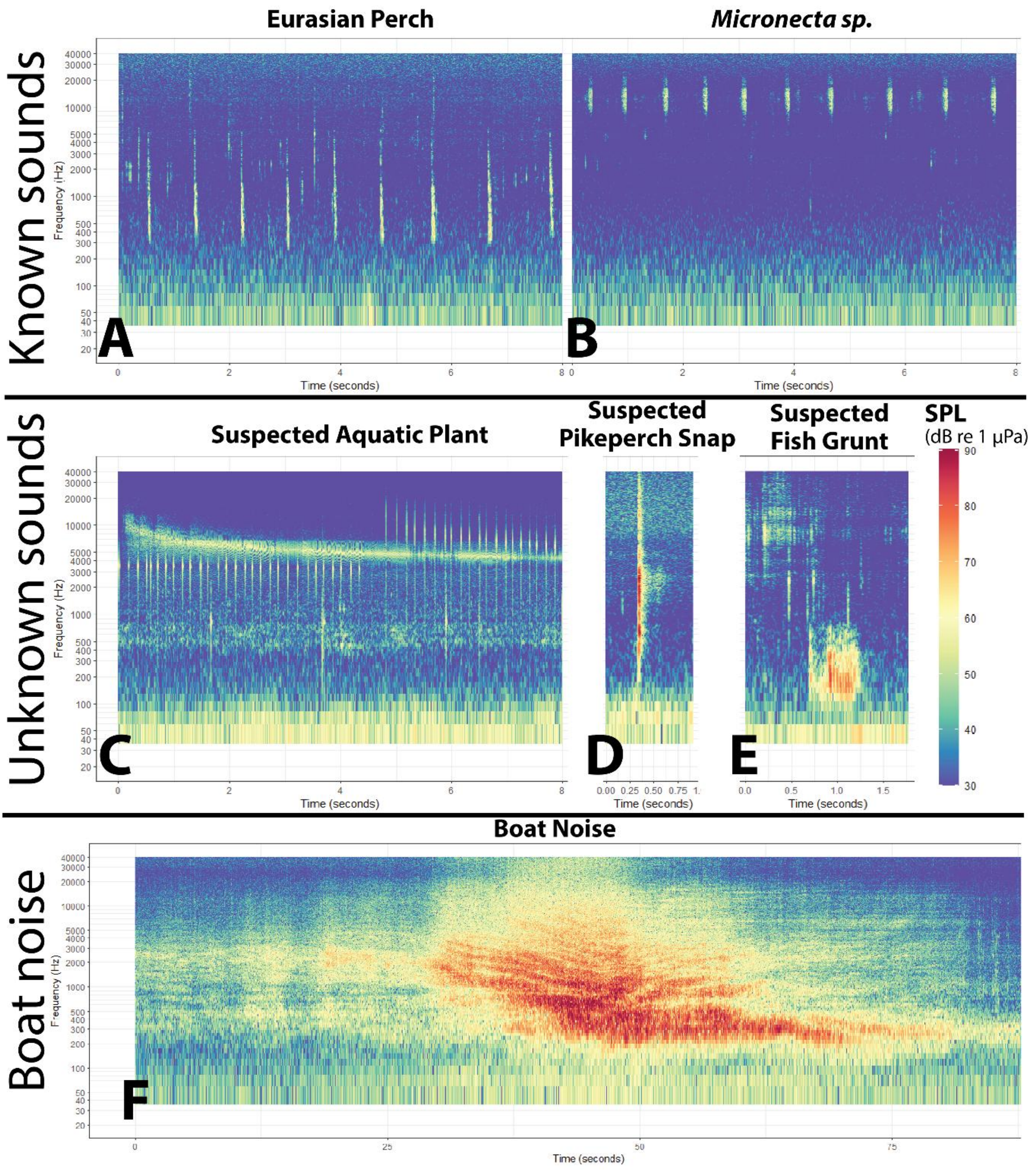


Figure 3; Example spectrograms of biophonic sounds from known and unknown aquatic organisms. Frequency axis and sound pressure level (SPL) color scale are proportional in all spectrograms, time axis differs among some spectrograms. A; European perch (Perca fluciatilis), B; Aquatic insect species of genus Micronecta, C; likely produced by O_2 *bubbles from an aquatic plant, D; Suspected Pikeperch (Sander lucioperca) snap, E; Suspected fish grunt (unknown species), F; Noise from a typical river boat* communication such as gas bubbles from aquatic plants and decomposing bacteria (Felisberto et al., 2015; Freeman et al., 2018; Kratochvil & Pollirer, 2017b) and disturbance of substrates or the water surface by aquatic animals (Holt & Johnston, 2011). Simply the presence of another species can tell an animal something about its surroundings, because the presence of an animal is typically associated with specific habitat features. Therefore, all these sounds can provide aquatic animals with information about their surroundings (Fay, 2009; Slabbekoorn & Bouton, 2008; te Velde et al., 2024). We provided a qualitative analysis of biophonic sound events, showcasing the diversity of underwater sounds, but much is still unknown, and longer recordings across seasons may yield many more biophonic sounds. Of the 7000 aquatic insect species that are predicted to produce sounds, less than 1% have been described (Desjonqueres et al., 2024; Greenhalgh et al., 2025). Furthermore, although almost 1000 fish species are known to produce sounds, only 96% of all fish species have been investigated for sound production (Looby et al., 2022). Automated analysis of known and unknown sound events may provide more insights into the availability and spatial and temporal distribution of acoustic cues. Innovative techniques using machine learning for sound event detection and unsupervised clustering based on acoustic features can aid in identifying novel biophonic sounds (Alcocer et al. 2022; Barroso et al. 2023; Aslam et al. 2024; Parcerisas et al., 2024).

3.1.2 Geophony

To investigate the effect of hydrogeomorphological river features on the natural river soundscape, we carried out a redundancy analysis (RDA) between the full octave band sound pressure level SPL and the hydrogeomorphological river features at each 1-minute recording location (Figure 6A). A forward selection yielded a model with water velocity ($p = 0.005$) as significant variable, and Area of cross-section as non-significant trend ($p=0.070$). Similarly, findings in other river systems show that water velocity and river size are likely reflected in the natural soundscape of rivers from a wide range of sizes and flow speed (Gu et al., 2022; te Velde et al., 2024; Tonolla et al., 2010, 2011; Vračar & Mijić, 2011).

The RDA plot shows a grouping of high- (350-45000 Hz) and low

(11-350 Hz) frequency octave bands, indicating that high and low frequencies may be affected differently by hydrogeomorphological variables. Water velocity, sediment hardness and distance from shore show the strongest association with higher frequency octave bands, while river width, depth recording and area of cross-section show the strongest associations with low frequency octave bands. To further explore this relationship, we calculated the mean octave band SPL of the grouped low- and high frequency octave bands. Data visualization revealed a strong increase in the high frequency octaveband SPL at higher water velocities (Figure 4B). A segmented regression (hockey-stick model) identified a breakpoint in the relationship between SPL and water velocity at 1.40 m/s (± 0.03 SE), indicating a threshold beyond which SPL increases steeply with water velocity. Two separate multiple linear regression models in the low- (<1.4 m/s) and high (>1.4 m/s) velocity range showed that both water velocity and sediment hardness were significant predictors of SPL below 1.4 m/s (Water velocity: $\beta = 1.51$, $p = 0.036$; Sediment Hardness: $\beta = -0.018$, $p = 0.025$, $R^2_{adj} = 0.09$), and only water velocity was a significant predictor above 1.4 m/s ($\beta = 68.99$, $p=0.010$, $R^2_{adj} = 0.64$). This suggests that sediment characteristics primarily influence SPL under low-flow conditions (Figure 4C), while high water velocities dominate SPL variation above this threshold (Figure 4D). Where mean high frequency octave SPL is best explained by the following regression models:

$$High\ frequency\ SPL = \begin{cases} 71.57 + 1.51 \cdot v - 0.018 \cdot h, & if\ v \leq 1.4 \\ -24.68 + 68.99 \cdot v, & if\ v > 1.4 \end{cases}$$

Where:

- High frequency SPL = Mean high frequency (350-45000 Hz) octave Sound Pressure Level (dB re 1µPa)
- v = Water Velocity (m/s)
- h = Sediment Hardness

Though earlier soundscape studies have revealed positive correlations between water velocity and SPL over a broad frequency range (Gu et al., 2022; te Velde et al., 2024; Tonolla et al., 2009, 2010, 2011), we showed that there is a steep increase in SPL at velocities above 1.4 m/s. This is relevant in the context

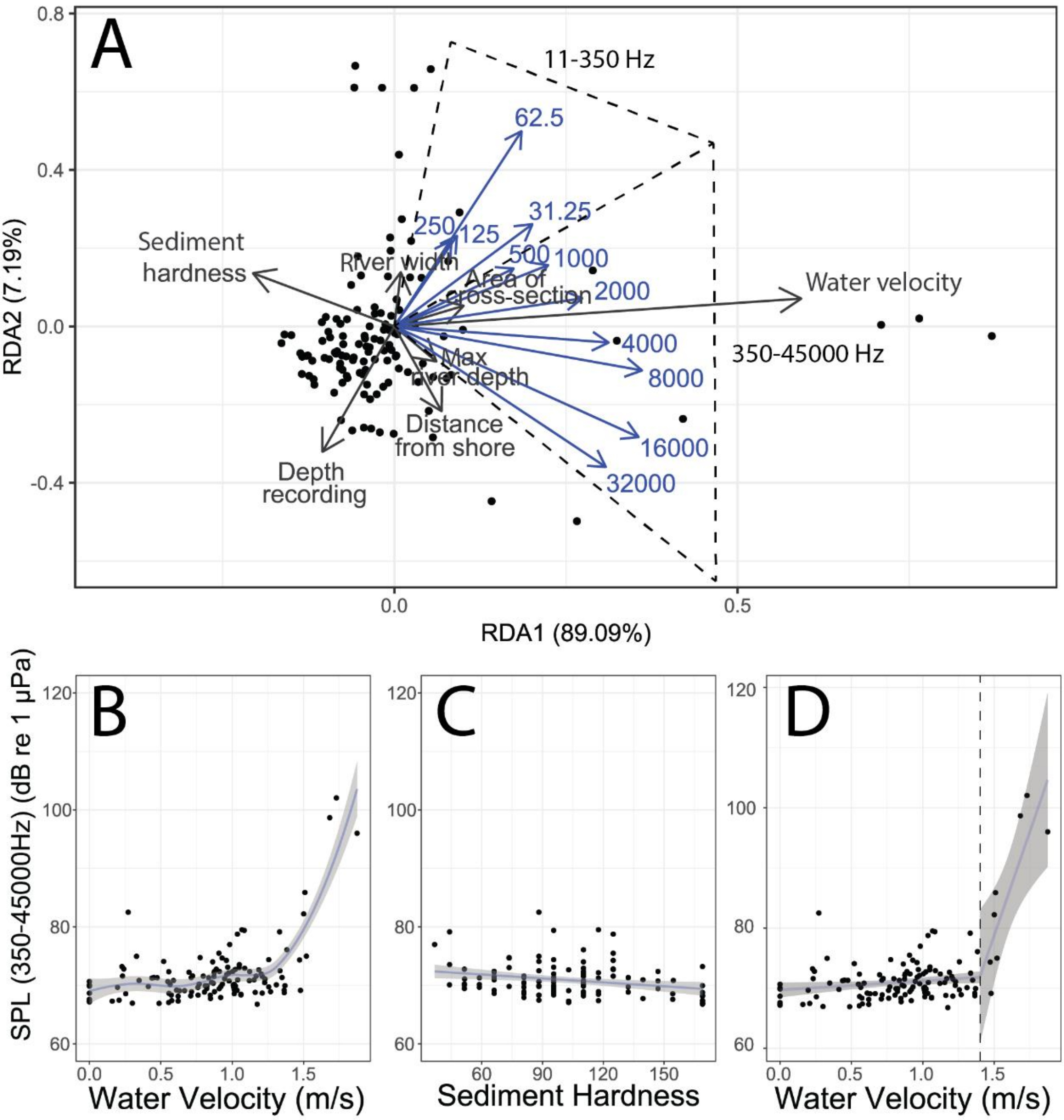


Figure 4; Relationship between hydrogeomorphological variables and Sound Pressure Levels (SPL) at different frequencies in the canoe drift recordings. A; Redundancy Analysis of full octave band SPL against hydrogeomorphological variables, dotted lines highlight a directional grouping of low- and high- frequency octave bands, B; relationship between mean SPL of high frequency octave bands (350-45000 Hz) and Water velocity with a loess smoothing line, C; relationship between high frequency octaves mean SPL and Sediment hardness for samples with water velocities below 1.4 m/s , D; relationship between high frequency octaves mean SPL and Water velocity, with a segmented (hockeystick) model prediction and 95% confidence margins if sediment hardness is kept constant.

of masking, since water velocity induced sound cues may be less vulnerable to masking in high flow conditions. However, flow induced sounds can also become a natural source of acoustic masking itself, limiting the perception of other natural acoustic cues by aquatic animals. During periods of high flow, hydropeaking induces higher sound levels across river habitats, making them harder to distinguish both in terms of acoustic signature, and by their hydrogeomorphological parameters (Lumsdon et al., 2018).

The negative association between sediment hardness and mean SPL between 350-45000 Hz in low flow conditions was contrary to our expectations, since higher hardness sediments such as gravel and rocks are expected to induce more sound from turbulent flow and particle collisions during bed load transfer (Geay et al., 2017). A possible explanation is that the low-flow conditions are not enough to cause sufficient bed load transfer of larger substrate particle sizes, while smaller substrate particles are more easily brought in motion. Nevertheless, our findings show that the underwater soundscape can reflect information on nearby substrate types, which may be audible and thereby available to aquatic animals.

The multiple linear regression between mean SPL of the low-octave bands (11-350Hz) and depth, width, and area of cross-section yielded no significant predictors. When exploring correlations between mean low octave band SPL and the other hydrogeomorphological variables, only water velocity had a significant positive correlation with mean SPL of the low octave bands (($r = 0.39$, $p < 0.001$). Earlier findings that showed this relationship, were conducted using stationary hydrophones, and could thus have been caused by flow noise artifacts due to turbulence created around the hydrophone (te Velde et al., 2024), but since our recordings were conducted using a drifting hydrophone, we can be more certain that water velocity is also reflected by the soundscape at lower frequencies.

River sediment type distribution

We examined how well sediment type distribution across river locations is reflected by the mean sediment hardness values at those locations as extracted from the echosounder data. There was a significant linear relationship between sediment hardness and the proportion of large grain size of substrate rocks & pebbles (>20 mm) ($\beta = 45.0$, $p = 0.002$, $R^2_{adj} = 0.41$), with the opposite relationship between sediment hardness and the proportion of low grain size of substrate clay & gravel (<20mm). Although strong statements on the relationship between sediment hardness and local grain size proportions would require

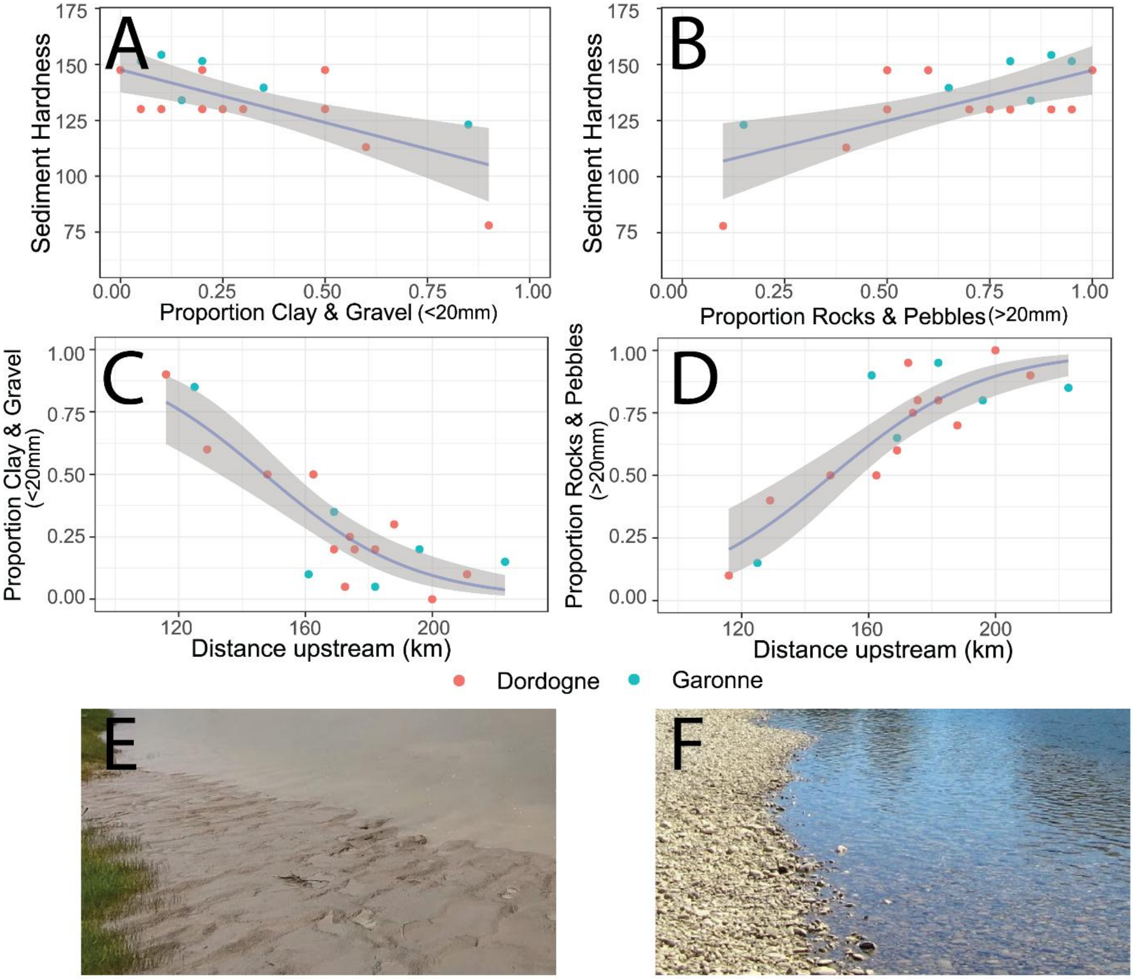


Figure 5; Relationships between mean location sediment hardness and proportion of low- and high grain size substrates in the Garonne and Dordogne, sampled at different distances upstream of the Gironde estuary. A&B; Shows the linear relationship between Sediment hardness and proportion low- and high grain size substrates, C & D Shows the distribution of low- and high grain size substrates with distance upstream with a negative binomial generalized linear model prediction. Pictures E & F show the riverbank along locations with small- (E) and large (F) grain size substrates.

more samples in locations with low grain size sediments, the general pattern found in this study is in line with expectations, where low sediment hardness is associated with small grain size substrates, and high sediment hardness with large grain size substrates (Figure 5A&B).

Furthermore, we explored how sediment is distributed over the length of the river. A quasibinomial glm showed that the proportion of high grain size substrate rocks & pebbles increased significantly with distance upstream of the estuary ($\beta = 0.042$, $p < 0.001$, pseudo$R^2 = 0.69$), with the opposite relationship between the proportion of low grain size substrate particles and distance upstream. Showing a distribution from low grain size sediment particles downstream, towards higher grain size sediment particles upstream of the estuary (Figure 5C&D). Consequently, local substrate type dependent soundscapes can also inform migratory fish on their position along the length of the river.

3.1.3 Potential relevance of acoustic cues to aquatic animals

For a cue to be useful to an animal it needs to be able to detect it. Therefore, it is important to consider the frequencies of potential cues and whether they fall within the hearing range of animal taxa. Fish typically have hearing ranges that are most sensitive in low frequencies with upper limits around 300-500 Hz, some hearing specialist species have hearing organs capable of detecting sound pressure, with limits up to 5000 Hz (Popper & Fay 2011; Popper et al., 2022). It should be noted that fish hearing ranges and threshold findings from the same species can vary greatly among studies, so should always be considered with care (Popper & Hawkins, 2021). Not much is known about aquatic insect hearing, but they likely have a broad hearing range like terrestrial insects, with the highest sensitivity in frequencies of their own communication signals (Čokl & Theiss, 1987; Prager & Streng, 1982; Yack et al., 2020). Therefore, most sounds in this study are expected to fall within the hearing range of aquatic insects. High flow rates affect a broadband frequency range and produce high sound levels. Therefore, high-flow conditions near rapids and waterfalls can likely be detected by most aquatic animals, while sediment hardness was mostly reflected in frequencies above 500 Hz, making it less likely that this is detectable by fish species with more modest hearing ranges such as salmon or sturgeon, but it should fall within the hearing range of more advanced hearing species such as shad and cyprinids (Harding et al., 2016; Hawkins & Johnstone, 1978; Mann et al., 1997; Popper et al., 2022; Popper & Calfee, 2023). Particle collisions from bed load transport may induce broadband peaks that have a low contribution to mean SPL, but could be detectable by fish species with low upper-frequency limits. Aquatic insects typically produce high-frequency sounds above 1000 Hz (Aiken, 1985; Desjonqueres et al., 2024; Greenhalgh et al., 2025), the majority of which are likely above the hearing range of most fish species. Aquatic plant sounds have many high-frequency components but also some broadband pulses, thereby having potential to fall within the frequency range of most aquatic animals. The fish sounds in our recordings varied from low frequency grunts to mid frequency perch sounds and broadband suspected pikeperch snaps. Interestingly, perch have most sensitive hearing at 300 Hz, with an upper limit at 1000 Hz, while the perch sounds in our recordings have highest energy above 1000 Hz.

As presented here, sound can carry a wealth of information. In aquatic environments, where visibility and chemical cues are often limited or variable, sound can provide a unique source of information for better informed behavioral decisions that can quickly travel over large distances and against the current. Still, for a sound to have potential as a cue for aquatic animals it is important to consider both its quality and availability. The quality may be reflected by the association strength between occurrence and a relevant resource such as food or spawning habitat. The availability refers to the actual presence of the sound where and when required to serve a purpose. Flow related geophonic sound sources are likely consistent, predictable and omnipresent (high quality and availability) (Geay et al., 2020; Johnson & Rice, 2014). They also vary with river discharge changes from meltwater and rain, thereby reflecting seasonal changes (Lumsdon et al., 2018). Detecting suitable sediment and waterflow can be of high importance to aquatic animals, many fish have specific sediment, oxygen, and flow condition requirements to deposit their eggs (Kemp et al., 2011; Rosenfeld, 2003). Furthermore, many animals have different strategies to avoid predators through shelter between rocks or burrowing in sand, which may also be found through hearing variation in flow conditions.

We also showed that the physical features reflected by the soundscape change gradually as you move upstream, allowing potential use as navigation and orientation cue, while more distinct local soundscape features such as waterfalls or rapids could act as landmarks during navigation (Murchy et al., 2024; Slabbekoorn & Bouton, 2008; Fay 2009). Several studies have shown significant effects of flow or sediment-related sounds on behavioral responses or spatial distribution of fish (Febrina et al., 2015; Holt & Johnston, 2011; Kacem et al., 2020; Kowal et al., 2023). Still, the extent to which and in what contexts these sounds are used by fish are still poorly understood. The high quality and availability of sediment and flow related sounds in rivers, and the relevance of this information to aquatic animals at various life stages warrant further behavioral studies. For if we want to understand how aquatic life may be impacted by masking from anthropogenic noise sources, we need to understand how they use sounds throughout their life cycle.

3.2 Quantifying River Boat Noise

At our 24-hour stationary recordings sites, the Rhine, Elbe and Gironde varied greatly in terms of boat noise, with daily boat presence in our recording locations ranging from 0-20% in the Gironde, 2-38% in the Elbe and 42-86% in the Rhine. The duration of detected boat presence varied greatly among single boat passes in all rivers, with boat pass durations ranging from 2 to 20 minutes.

3.2.1 Predictive value of AIS shipping density data

There was a significant positive relationship between the AIS boat density (in hours/km^2/day) and acoustic boat noise presence (in % time per day), as assessed by a quasibinomial GLM ($\beta = 0.181 \pm 0.037$, $t = 4.89$, $p < 0.001$) including a significant intercept ($\beta = -2.974 \pm 0.592$, $t = -5.02$, $p < 0.001$) (Figure 7A). This yielded the following model (with Boat presence in %, and Boat Density in hours/km^2/day):

$$Boat\ Presence = 100 \times \frac{e^{-2.97 + 0.181 \times Boat\ Density}}{1 + e^{-2.97 + 0.181 \times Boat\ Density}}$$

This model was used to predict the % Boat presence based on data extracted from an AIS shipping density map (Figure 1A) sampled along 400 km river length in each of the three rivers (Figure 6B). Predicting 80-100% boat presence in the first 100 km of the Elbe, rapidly declining after Hamburg (at 100 km from the sea) towards 5-15%, in the Rhine 40-75% boat presence over the whole length, and in the Gironde 7% boat presence Bordeaux, declining to 5% after Bordeaux (Figure 6B).

3.3 Masking Effects of Boat Noise on Natural Sounds

3.3.1 Differences among rivers

The sound spectra during boat absence in the Gironde and Elbe are relatively similar, while the Rhine has higher SPL above 500 Hz (Figure 7). Boats in the Rhine had generally higher SPL across the whole spectrum compared to boats in the Elbe and Gironde (Figure 7). Furthermore, above 50 Hz, boats in the Rhine have distinctly higher SPL compared to boat absence (Figure 7A), while boats in the Elbe & Gironde start to show distinctly higher sound levels above 100 Hz (Figure 7B&C). Boat distant spectra do not show distinctly elevated levels compared to boat absence, except for a slightly higher mean SPL between 400 Hz – 2000 Hz (Figure 7). Indicating that boats may still be audible by some animals with sensitive hearing in those frequencies, but are unlikely to cause much masking at larger distances.

3.3.2 Masking potential of biophonic & geophonic sounds

To evaluate the masking potential of boat noise on natural sounds in rivers, we compared the mean boat noise spectra with mean spectrum levels of biophonic and geophonic sounds encountered in our recordings (Figure 8). Only water velocities of 1.75 m/s produced sound spectra that exceeded boat noise below 75 Hz and above 1500 Hz (Figure 8B) and the suspected fish grunt produced mean sound spectra that exceeded boat noise between 100 and 200 Hz (Figure 8A). All other sounds had mean sound spectra below mean boat noise levels across the whole spectrum. Suspected aquatic plant, pikeperch, and *Micronecta sp.* have upper-level standard deviations that are above lower-level standard deviation of boat noise in some frequencies,

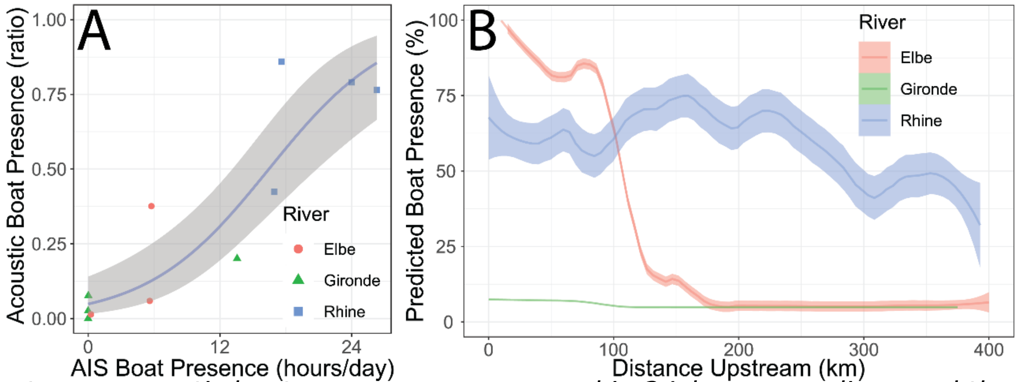


Figure 6; A; Relationship between acoustic boat presence as measured in 24-hour recordings and the AIS boat presence extracted from monthly AIS density maps (GMTDS, 2024). The line indicates the negative binomial regression model with 95% confidence margins. B; Predicted acoustic boat presence from the sea to 400 km upstream in the Elbe, Rhine and Gironde rivers based on AIS shipping density maps.

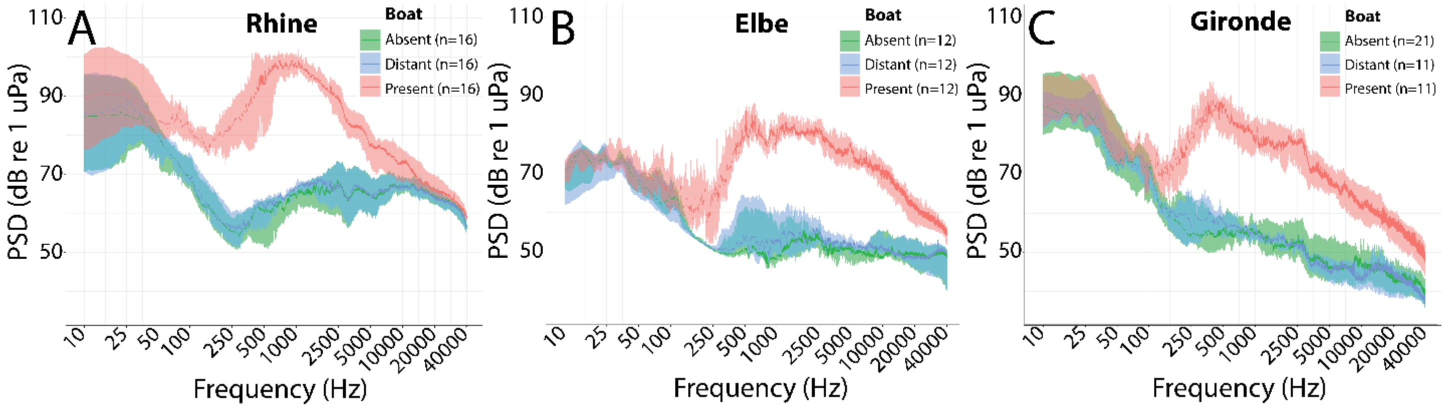


Figure 7; Mean Power Spectral Density (PSD) values of boat absent, present and distant samples in the Rhine (A), Elbe (B) and Gironde (C). Error margins indicate standard deviation. Sample sizes refer to the number of boat passes analysed: Four boat passes with paired boat distant and absent sections were selected in each recording location, several locations in the Gironde had less than 4 boat passes, leading to fewer boat present and distant than absent samples.

indicating that these sounds can sometimes exceed the more quiet boat events. Still overall, most natural sounds have sound spectra below that of boat noise in most frequencies, indicating large potential for masking of natural sounds in the presence of boat noise.

Our findings show that most natural river sounds are masked in the presence of boat noise. Only few natural sound events

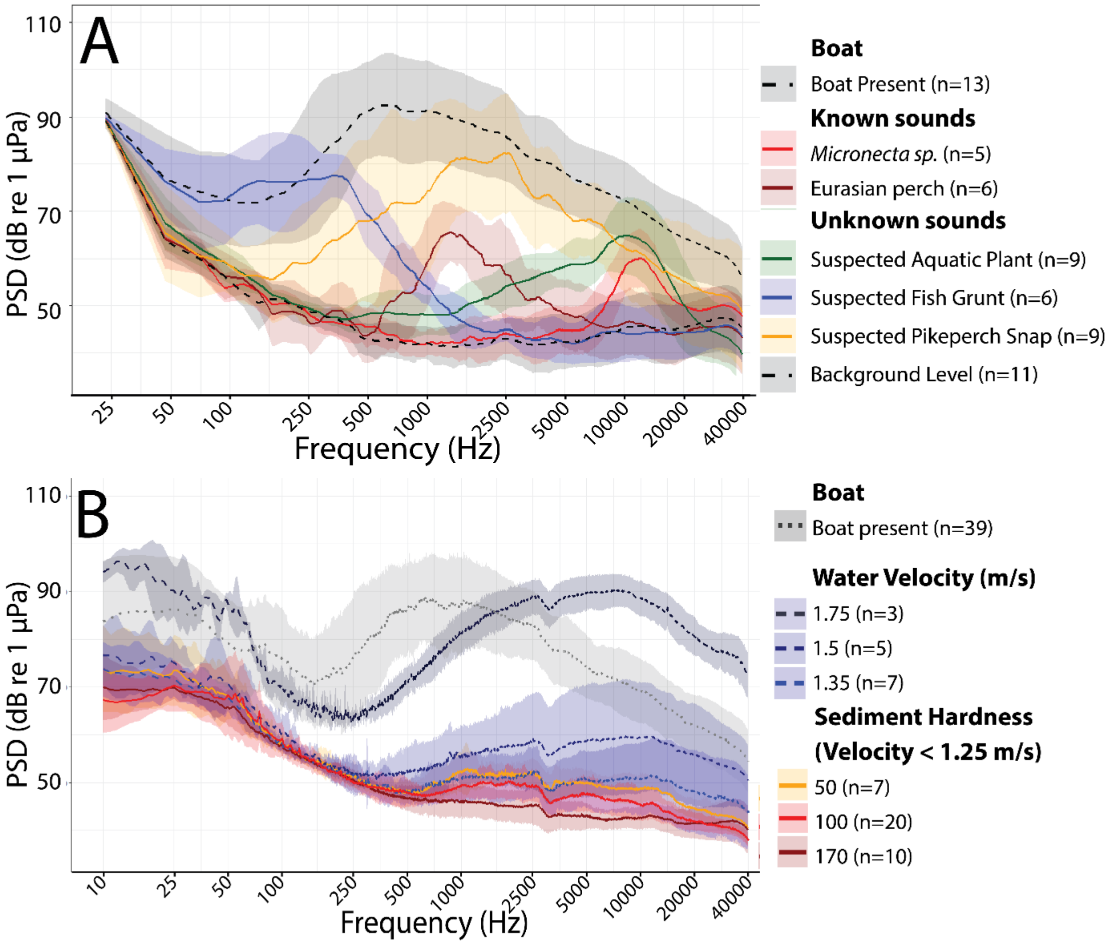


Figure 8; Masking potential of natural sounds by boat noise in rivers, A; Biophonic sound spectra, B; Geophonic sound spectra. Note that PSD of biophonic sounds were calculated using a window length (wl) = 4096, and geophonic sounds wl equal to the sample frequency (96000), so dB values should be interpreted differently.

exceeded boat noise spectra at some frequencies on some occasions. In general, one can assume that most of the natural river soundscape is masked during boat presence, limiting acoustic communication and perception of natural acoustic information by aquatic animals. Still, boat passes can vary greatly in duration and intensity, indicating that some boats contribute more to masking than others. Notably, boat spectra in the Rhine had higher average SPL and lower frequency cutoff compared to boat spectra in the Elbe and Gironde (Figure 7). These differences may be explained by boat type, river features affecting sound propagation, and distance of the boat to the receiver (Jansen & De Jong, 2017; Macgillivray & de Jong, 2021). Due to the high shipping densities in the Rhine, more than one boat often affected the soundscape during acoustic boat presence, which leads to more time during boat presence in which at least one boat is close to the receiver, and this could also explain why mean SPL is higher in the Rhine. Still, research into designing more quiet ships, and management interventions such as slowdowns are vital, since even moderate source level reductions can significantly lessen the area impacted by anthropogenic noise (Findlay et al., 2023). Although this effect may be lower in rivers, since lower source levels of boats will likely reduce the area affected in longitudinal direction, it would still be worth investigating the effects of source level reductions on masking in rivers.

We showed that in many locations in the three large European rivers, animals are severely limited in their ability to perceive sounds for long periods of time. This raises concerns about the effects of boat noise on freshwater animals and anadromous fish in rivers at a global scale. When comparing large European rivers in terms of inland cargo transport, most notable corridors include the Rhine (58 billion t/km), Danube (23 billion t/km), Elbe (4.2 billion t/km), Seine (3.1 billion t/km), Rhone (0.8 billion t/km) and Po (0.1 billion t/km) (Central Commission for the Navigation of the Rhine, 2024). Evidently, the Rhine is exceptional in western Europe in terms of the amount of shipping traffic, and similar values of acoustic boat presence may only be found in Rivers such as the the Yangtze, Pearl, Grand Canal and Mekong river in Asia, the Mississippi river in the United States of America and the Danube in eastern Europe (Lu et al., 2023). Still, our predictions of acoustic boat presence in the Elbe based on AIS density data showed that even moderate shipping intensity rivers can have river sections with near 100% acoustic boat presence. We found a general pattern of higher acoustic boat presence in estuaries, potentially disturbing or limiting anadromous fish in their ability to navigate towards and through river entrances during migration. Furthermore, acoustic masking of near 20% may still be impactful for animals relying on acoustic information, and these levels of boat presence are likely prevalent in moderate shipping intensity rivers such as the Seine, Rhone and Po.

As final remarks, our acoustic boat presence predictions were based on AIS density data which only included commercial boats. Therefore, AIS shipping density maps may underestimate boat noise in areas of high recreational activity (Hermannsen et al., 2019). Moreover, other anthropogenic activities such as city noise, and land-based traffic noise from bridges and roads can also significantly affect the underwater soundscape (Holt & Johnston, 2015; Rountree et al., 2020; te Velde et al., 2024; te Velde & Slabbekoorn, 2024). Thus, although we showed that AIS density data can roughly predict boat noise in large rivers at an international scale, we require more studies on the levels and spatial extent of land-based traffic noise and recreational boating traffic to get a sense of the full extent of noise pollution in freshwater systems around the world.

4. Conclusion

We here reported on human-altered soundscapes in Large European Rivers and widespread potential for masking by boats. The three large rivers were similar in the presence of hydro-geomorphological determinants of specific parts of the underwater soundscapes, on top of which a high diversity of biotic sounds provided further potential to aquatic animals to acoustically access the extent to which they find themselves upstream, away from the sea, above particular substrate and in proximity of specific underwater and above water habitat characteristics. The three rivers varied in natural background sound levels, biophonic sound types, and boat noise levels and duration.

The investigations into the presence of boats included long-term recordings and processing of AIS boat density data. These approaches revealed that boat noise may severely limit the acoustic information received by aquatic animals in large rivers, particularly when their habitats or migratory routes overlap with boat transport corridors. We showcased the first study to quantify and predict the extent of boat noise in rivers over a large geographic area. Showing that AIS density maps have predictive value for the presence of underwater noise in rivers and we provided a model that may serve as a starting point to identify high impact areas in rivers. Although noise maps created from AIS data and noise propagation modelling as often applied in marine areas could provide more accurate predictions.

While soundscapes offer rich information for freshwater fauna on local habitat characteristics and location, pervasive boat traffic increasingly obscures these natural signals. A precautionary approach to noise management is urgently needed, and soundscapes should be integrated into conservation planning, particularly at migratory bottlenecks and vulnerable habitats. And we 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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