Environmental Pollution 359 (2024) 124517

Contents lists available at ScienceDirect

Environmental Pollution

journal homepage: www.elsevier.com/locate/envpol

Natural soundscapes of lowland river habitats and the potential threat of urban noise pollution to migratory fish☆

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ARTICLE INFO

Keywords:
Anthropogenic noise
Bridge impact
Freshwater ecology
Migratory fish
Underwater acoustics
Water quality

ABSTRACT

Migratory fish populations have experienced great declines, and considerable effort have been put into reducing stressors, such as chemical pollution and physical barriers. However, the importance of natural sounds as an information source and potential problems caused by noise pollution remain largely unexplored. The spatial distribution of sound sources and variation in propagation characteristics could provide migratory fish with acoustic cues about habitat suitability, predator presence, food availability and conspecific presence. We here investigated the relationship between natural soundscapes and local river conditions and we explored the presence of human-related sounds in these natural soundscapes. We found that 1a) natural river sound profiles vary with river scale and cross-sectional position, and that 1b) depth, width, water velocity, and distance from shore were all significant factors in explaining local soundscape variation. We also found 2a) audible human activities in almost all our underwater recordings and urban and suburban river parts had elevated sound levels relative to rural river parts. Furthermore, 2b) daytime levels were louder than night time sound levels, and bridges and nearby road traffic were much more prominent with diurnal and weekly patterns of anthropogenic noise in the river systems. We believe our data show high potential for natural soundscapes of low-land river habitat to serve as important environmental cues to migratory fish. However, anthropogenic noise may be particularly problematic due to the omnipresence, and relatively loud levels relative to the modest dynamic range of the natural sound sources, in these slow-flowing freshwater systems.

1. Introduction

Freshwater ecosystems are among the most vulnerable in the world, with a third of freshwater fish species in danger of extinction (Deinet et al., 2020; Tickner et al., 2020; WWF, 2020). According to a IUCN assessment, freshwater fish may be the most vulnerable group of all vertebrates (Reid, Contreras Macbeath and Csatádi, 2013). The protection of especially migratory fish species is a major challenge, because their decline is often caused by multiple stressors (Parrish et al., 1998). These stressors include blockage of migratory routes, overfishing of populations, water quality changes and habitat deterioration (Allan et al., 2005; Brevé et al., 2014; Forseth et al., 2017; Grill et al., 2019; Tamario et al., 2019; Belletti et al., 2020). In recent years, much effort has been put into reducing these stressors through dam removal, fish passages, fisheries quotas and nutrient load reductions (Forseth et al., 2017; Tamario et al., 2019). However, very little attention has gone to the potential effects of the deterioration of natural river soundscapes and disturbance of migratory fish by anthropogenic noise (van Opzeeland and Slabbekoorn, 2012; Popper et al., 2020).

Natural soundscapes are increasingly recognized as an important ecological feature of critical importance to animals (Slabbekoorn & Bouton, 2008; Fay, 2009; Pijanowski et al., 2011). There are many studies in especially marine environments reporting habitat type and quality dependent soundscapes (e.g. Staaterman et al., 2013; McWilliam & Hawkins., 2013; Buscaino et al., 2016). Freshwater systems are less investigated, but soundscapes of rivers and lakes may also be rich and diverse. Sounds audible to freshwater fish may include sounds of (semi) aquatic mammals (estuaries), fish, frogs, and aquatic invertebrates

☆ This paper has been recommended for acceptance by Pavlos Kassomenos.

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https://doi.org/10.1016/j.envpol.2024.124517
Received 8 April 2024; Received in revised form 18 June 2024; Accepted 7 July 2024
Available online 11 July 2024
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(Colleye et al., 2013; Desjonqueres, 2016; Marian et al., 2021), gas bubbles produced by aquatic plants and decomposing bacteria (Felisberto et al., 2015; Kratochvil and Pollirer, 2017; Freeman et al., 2018), but also physical disturbance of the substrate or water surface by animal activity (e.g. Holt and Johnston, 2011) or other natural forces such as water, wind and sediment transport (e.g. Geay et al., 2017).

Over the last decades, aquatic soundscapes worldwide have been increasingly affected by anthropogenic noise, especially due to an increase in the number and size of shipping vessels (Hildebrand, 2009; Kaplan and Solomon, 2016). The presence of anthropogenic noise can cause disturbance, deterrence, and distraction of aquatic animals, and mask signals for communication and cues for orientation and navigation (Slabbekoorn et al. 2010; Duarte et al., 2021). While there is increasing research attention toward anthropogenic noise and soundscape deterioration in marine systems (Havlik et al., 2022, Lamont et al., 2022), river systems remain largely overlooked. Rivers often receive high levels of shipping traffic and aquatic recreational activity, and most rivers flow through noisy urban areas (Holt and Johnston, 2015; Zang et al., 2019; Song et al., 2020).Fish that rely on these rivers as migratory pathway may be affected through masking and disturbance, but we still know very little about these anthropogenic influences on freshwater soundscapes.

Migratory fish are constantly faced with spatial decisions on their journey and use information about their environment from a variety of senses (Lucas and Baras, 2008). Chemical cues may provide information about upstream conditions (Nordeng, 1977; Hasler et al., 1978; Huijbers et al., 2012), while the spatial details, temporal dynamics, and directionality of auditory cues can help fish decide whether to stay or move on, especially under dark and low-visibility conditions (Montgomery et al., 2006; Slabbekoorn and Bouton, 2008; Fay, 2009; Radford et al., 2011; Holles et al., 2013; Gordon et al., 2018, 2019). Tonolla et al. (2010, 2011) revealed that different stretches of fast-flowing rivers in Switzerland have distinct sound profiles correlated to hydro-geomorphological characteristics. Furthermore, Kacem et al. (2020) reported similar correlational data from Canadian streams and found higher brook trout densities in pools and riffles associated with higher broadband sound pressure levels (SPL). Migratory fish typically also pass through slow-flowing rivers and lowland streams, for which there are very few studies on underwater soundscapes (te Velde & Slabbekoorn, 2023).

Audibility is an important pre-requisite for underwater soundscapes in order to be beneficial or harmful to fish. Fish hearing ranges are generally below 1000 Hz or even 500 Hz, with some species that can detect frequencies of up to 4000 Hz (Popper and Fay, 1993; Ladich, 2000; Putland et al., 2019). Long-distance migrants, such as salmon, eel, and sturgeon, typically have relatively high auditory thresholds and restricted high-frequency sensitivity (Jerkø et al., 1989; Mann et al., 2001; Popper, 2005; Harding et al., 2016), However, broad hearing ranges and low absolute thresholds are generally more common among freshwater than marine species, and the sensitivity of some diadromous species such as shad and smelt extends to exceptionally high frequencies for fish. Although hearing thresholds do not translate directly into disturbance sensitivity (Shafiei Sabet et al., 2016), hearing abilities of freshwater fish suggest plenty of opportunity for exploitation of the auditory information provided by underwater soundscapes of river systems.

In the current study, we investigated natural soundscapes of a Dutch low-land river system and we explored the presence of anthropogenic noise. We investigated the relationship between natural soundscapes and local river conditions, through many short-term recordings with a manually operated hydrophone at the same locations, at different depths and distances from the shore. Furthermore, we explored the presence of human-related sounds in these natural soundscapes via sampling of spatial variation, through short-term recordings with a manually operated hydrophone along rural, suburban and urban transects, and via sampling of temporal variation in diurnal and week-long patterns, through long-term, continuous recordings at selected urban and rural sites. We aimed to answer the following research questions: 1a) How do natural river sound profiles vary with river scale and cross-sectional position, and 1b) how do local river or weather characteristics explain the variation? Furthermore, for the audible human activities: 2a) Do urban, suburban, and rural underwater soundscapes vary due to anthropogenic noise, and 2b) are day- and night-time sound levels different in urban and rural sites?

2. Methods

2.1. Research area

We collected underwater sound recordings in the Valleikanaal-Eem river system in the central part of the Netherlands (52°05′N, 5°27′E) (Fig. 1A). The Valleikanaal-Eem river system is a relatively small and highly modified low-land river system in the Netherlands, with river segments of various dimensions and flowing through urban and rural areas. It is fed partially by water from the river Rhine at its source and has a catchment area of 93000 ha (Koopmans and de Vries, 1982) (Fig. 1). The sampled river segments were (in order from upstream to downstream): Two parts of the small slow-flowing river Valleikanaal (upstream and downstream from Veenendaal), two small brooks, the Barneveldse Beek and the Lunterse beek, and the relatively large slow-flowing river Eem, north of Amersfoort (Fig. 1B). We measured the dimensions and flow velocity of each river segment in at least four sampling locations, which summarized in Table 1. The Eem is the only part of the river system in which motorized boat traffic is allowed.

2.2. Sampling sets

We collected three different recording sets at different spatio-temporal scales in the Valleikanaal-Eem river system to answer 4 different sub questions. For clarity, the link between the sampling sets and the corresponding research question for which they were used was indicated with: part 1a, 1b, 2a & 2b. Firstly, we investigated the natural soundscapes and variation related to local river conditions and weather through acoustic recordings at multiple positions in river cross-sections of 5 types of river segments with varying river conditions (Fig. 1B) (part 1a & 1b). Secondly, we explored the acoustic presence of human activities in these natural soundscapes via spatial variation in acoustic recordings from transects crossing two cities (Fig. 1C and D) (part 2a). And thirdly, we explored the acoustic presence of human activities via temporal variation in long-term recordings at high traffic density sites under bridges in two cities and low traffic density sites in nearby rural areas (Fig. 1C and D) (part 2b).

2.2.1. River cross-sections to study natural soundscapes (part 1)

Between October and December 2021, water quality, hydro-geomorphology and acoustics were investigated throughout river cross-sections in 5 river segments of varying sizes (Fig. 1B). This was done at 4 locations in each of the 5 river segments. The sample points were spread out over the river segments and had a minimum of 1 km distance between them. At each location, recordings were made in different positions of the river cross section (part 1a), depending on the size of the cross-section. Furthermore, this was done in 3 cross-sections, that were 3 m apart. This resulted in a total of 20 locations, 90 cross-sections, and 273 1-min recordings. Water quality and hydro-geomorphological variables were measured once per location, (part 1b), while each 1-min recording was associated with a different position in the cross-section.

2.2.2. City transects to study spatial variation (part 2a)

In January and February 2022, acoustic recordings were made every 500 m along a 10 km transect through the city of Veenendaal (January 2022) and every 1000 m along a 15 km transect through the city of

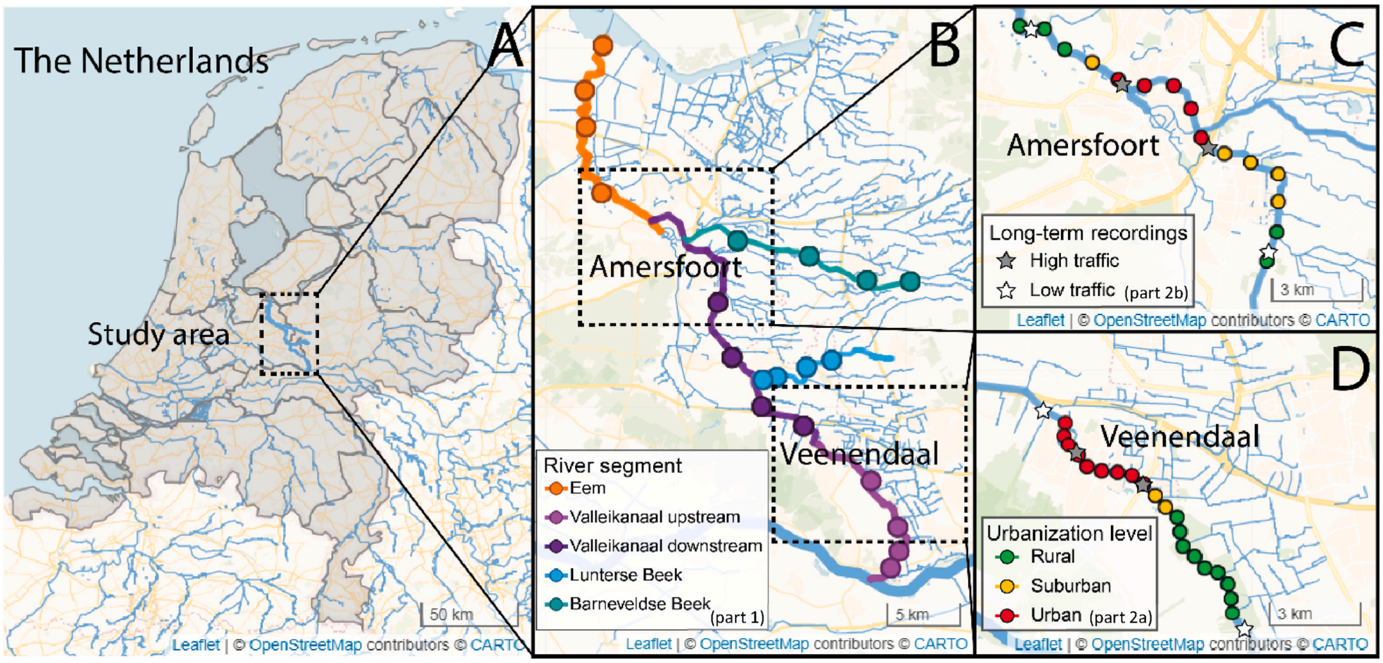

Fig. 1. Sample Locations in different river types in the Valleikanaal-Eem river system. Blue lines indicate all flowing waters in the area, and the three investigated river types are marked with different colors (see legend). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

Table 1
Average river segment dimensions and flow speeds at time of sampling with standard deviations.

	Width (m)	Depth (m)	Area of cross-section (m^2)	Water velocity ($m\ s^{-1}$)
Valleikanaal upstream	12.1 ± 2.1	1.5 ± 0.2	9.4 ± 2.3	0.05 ± 0.02
Valleikanaal downstream	16.4 ± 2.3	1.9 ± 0.2	15.3 ± 3.0	0.09 ± 0.04
Lunterse Beek	7.3 ± 2.3	0.8 ± 0.4	2.8 ± 1.7	0.04 ± 0.04
Barneveldse Beek	9.0 ± 1.1	0.7 ± 0.2	3.1 ± 0.8	0.08 ± 0.04
Eem	44.5 ± 3.7	3.9 ± 0.4	85.8 ± 8.2	0.14 ± 0.04

Amersfoort (February 2022) (Fig. 1C and D). This was done twice for each city: Once during the day (after sunrise 10:00–17:00) and once during the night (after sunset 20:00–2:00). This resulted in a total of 66 recordings. Sample locations were classified into three levels of urbanization: Urban (building coverage on both sides), Suburban (building coverage on one side) and Rural (no building coverage).

2.2.3. Long-term recordings to study temporal variation (part 2b)

In March 2022, 8–9 day continuous recordings were made simultaneously at 2 high traffic density sites (under bridges) and 2 low traffic density sites (rural area). This was carried out in the cities of Veenendaal (8–16 March 2022) and Amersfoort (22–31 March 2022) (Fig. 1C and D). This resulted in 4 recordings at high traffic density sites and 4 recordings at low traffic density sites.

2.3. Data collection

2.3.1. Underwater recordings

We used the same instruments and settings for the underwater recordings throughout the whole study. We used a Soundtrap 300 STD (Oceaninstruments) hydrophone, suspended between an anchor and a sub-surface buoy (Fig. 2). The Soundtrap was set at a sampling frequency of 96 kHz, high PreAmp gain, and with the high-pass filter turned off. The recording time of each recording in part 1 and 2a was 1 min, the long-term recordings (part 2b) were 8–9 days continuous recordings. During each 1-min recording, any potential recognizable sound source would be noted down in the field (such as rain, ducks landing in the river or passing cars). In the city transect (part 2a) and long-term recordings (part 2b), the hydrophone was placed in the middle of the river, suspended between an anchor and buoy, 30 cm above the river bed (Fig. 2B).

During the cross-section recordings (part 1), we made use of a special pulley system (Fig. 2A) to place the hydrophone in the correct position. In each river cross-section, took 1-min recordings at several width and depth positions (Fig. 2A). At each position, the buoy was suspended just below the water surface. We recorded in 3 cross-sections at each location approximately 3 m apart. If the width and depth of the river was too small, we carried out fewer recordings. The river dimension criteria for the amount of recordings are summarized in supplementary materials, Tables 1 and 2 This yielded a minimum of 3 recordings per sample location ($3 \cdot 1 \cdot 1$) and a maximum of 27 ($3 \cdot 3 \cdot 3$), resulting in a total of 273 1-min recordings.

2.3.2. Hydro-geomorphological & meteorological water quality variables (river characteristics & weather conditions) (part 1b)

At each river cross-section location (Fig. 1B), we measured weather conditions and river characteristics either directly or calculated based on other variables, see supplementary materials, table 3, for a complete overview of variables measured and equipment or formulas used. Variables were always measured before or during each recording session, depending on practicality and whether it could be done without disturbing the sound recordings. Water velocity and all water quality variables were always measured at 50 cm below the water surface. In addition to the variables in supplementary materials, table 3, we collected sediment samples using a Van Veen grab, but decided against using that in the data analysis, since all sites had similar sediment characteristics (sandy with some stones, dead leaves and branches).

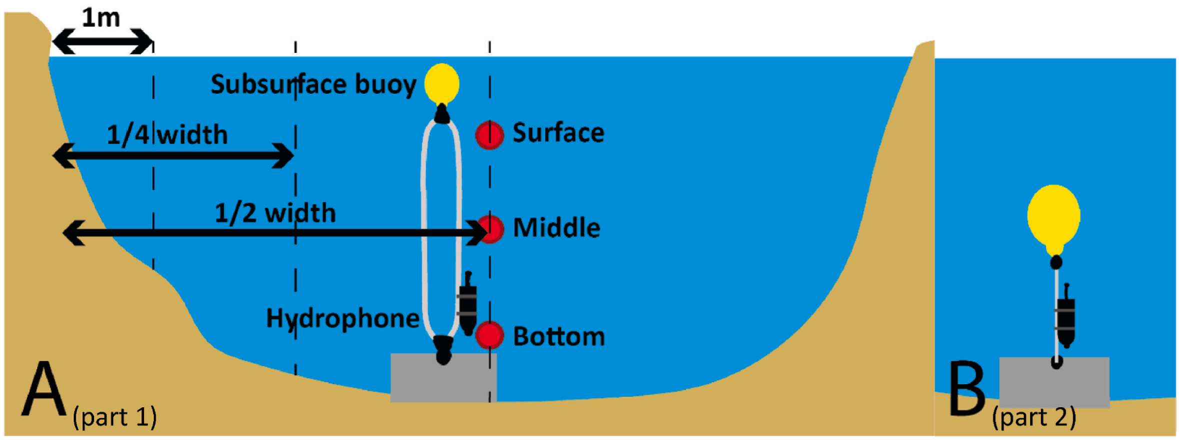

Fig. 2. Both recording setups. A; Soundtrap suspended between an anchor and subsurface buoy, with a trolley system to easily adjust the depth position of the hydrophone. B; Soundtrap suspended between an anchor and subsurface buoy with fixed height.

2.4. Data analysis

For all 1-min sound recordings collected in the river cross-sections (part 1) and city transects (part 2a), we inspected the quality by listening to them, and visual inspection of spectrograms in the audio program Audacity™. Any peculiar sounds in the recordings were noted down in the comments. In some of the city transect recordings, artifacts caused by noise from our nearby boat anchor were cut out of the recordings.

To investigate the spectral differences among river segments (part 1a), we calculated power spectral densities for each 1-min recording, with a fast fourrier-transform in R, using Hann windows with a 50% overlap, and a window length equal to the sampling frequency (96 kHz) in order to achieve a 1 Hz frequency resolution. The median and upper- and lower quartiles were calculated in order to compare groups of recordings, such as river segments, levels of urbanization, and day vs night.

Furthermore, to explore how local river and weather conditions explain the variation in the river cross-section recordings (part 1b), the sound pressure level (SPL) was calculated of 11 full octave bands with center frequencies at 15.625, 31.25, 62.5, 125, 250, 500, 1000, 2000, 4000, 8000 and 16000 Hz. These octave bands were used to carry out two separate Principal Component analyses (PCAs) on stream soundscapes (octave bands) and stream characteristics (c.f. Tonolla et al., 2010). We also applied a Redundancy Analysis (RDA) to test for the effect of river characteristics & weather conditions on the river soundscape (octave bands) (part 1b). Additionally, to investigate the effect of position in the river cross-section on the soundscape (part 1a), we carried out a RDA of position variables on the SPL of octave bands in all cross-section recordings ($n = 276$). To correct for the effect of the size of the river, we also ran a partial RDA with Area of the cross-section as a covariate. To investigate the effect of water velocity on the soundscape, we carried out an RDA of water velocity and position variables on a subset of the 1-min recordings positions at which water velocity was measured ($n = 38$). To investigate the effect of river characteristics and weather conditions on the soundscape, we carried out an RDA of river characteristics and weather conditions on the mean SPL of octave bands at each location ($n = 20$).

To investigate temporal patterns in the river soundscapes (part 2b), the long-term recordings were visualized in the form of spectrograms with a temporal resolution of 1 min, and a frequency resolution of 1 Hz. Any patterns that stood out from the long term spectrogram were inspected further through visual inspection of 2 h spectrograms with a higher temporal resolution in the audio program Audacity™. The window length settings were adjusted to achieve a desired temporal and frequency resolution depending on the situation. Example spectrograms were made of several biophonic sounds we encountered. For illustration purposes, background noise was reduced using the audacity noise reduction tool with the following settings: Noise reduction: 12 dB, Sensitivity: 6.00 and Frequency smoothing: 3. We then applied a band pass filter for the frequency range of the signal of interest and made spectrograms using a custom R script with a window size of 2048 and 99% overlap.

3. Results

3.1. Characterizing and understanding natural river soundscapes (part 1)

Sound pressure levels (SPL) of natural river soundscapes varied among river segments most in the spectrum between 1 and 20,000 Hz (Fig. 3). The Eem river segment (most downstream and largest section), had the highest median SPL over the whole spectrum below 10 kHz. The brooks, Lunterse beek and Barneveldse beek, had the lowest median SPL over most of the spectrum. The river segments in Valleikanaal had a similar spectrum as the brooks, although Valleikanaal downstream had a higher median SPL in the lower frequencies (<20 Hz), while Valleikanaal upstream had higher median SPL in the higher frequencies (>500 Hz). A small peak is visible at 3 kHz, which was caused by self-noise from the recording setup. Most river segments are relatively quiet and are likely close to the lower recording range of the hydrophone.

To investigate the effect of position in the river cross-section on the soundscape (part 1a), we carried out a Redundancy Analysis (RDA) of position variables on the SPL of octave bands in all recordings ($n = 276$) (Fig. 4A). A forward selection yielded a model with Area of cross-section ($p < 0.001$) and Distance from side ($p = 0.036$) as significant variables. The resulting RDA explained 39% of the soundscape variation across all 1-min recordings. The river segments groupings revealed that the Eem had little to no overlap in octave band SPL compared to other rivers (Fig. 4A). Lunterse beek & Barneveldse beek had the most overlap, while Valleikanaal upstream and downstream revealed some dissimilarity in the lower and higher frequencies.

To investigate the effect of water velocity on the soundscape (part 1b), we carried out a RDA of water velocity and position variables on a subset of the 1-min recordings positions at which water velocity was measured ($n = 38$) (Fig. 4B). A forward selection yielded a model with Area of cross-section ($p < 0.001$), Water velocity ($p = 0.025$) and Distance from side ($p = 0.047$) as significant variables. The resulting RDA's adjusted R^2 was 59%, and significant ($p < 0.001$). Together they explained 59.61% of the soundscape variation. Area of cross-section was positively associated with most octave bands, while Water velocity was positively associated with lower frequency octave bands of 250 Hz and below (Fig. 4B).

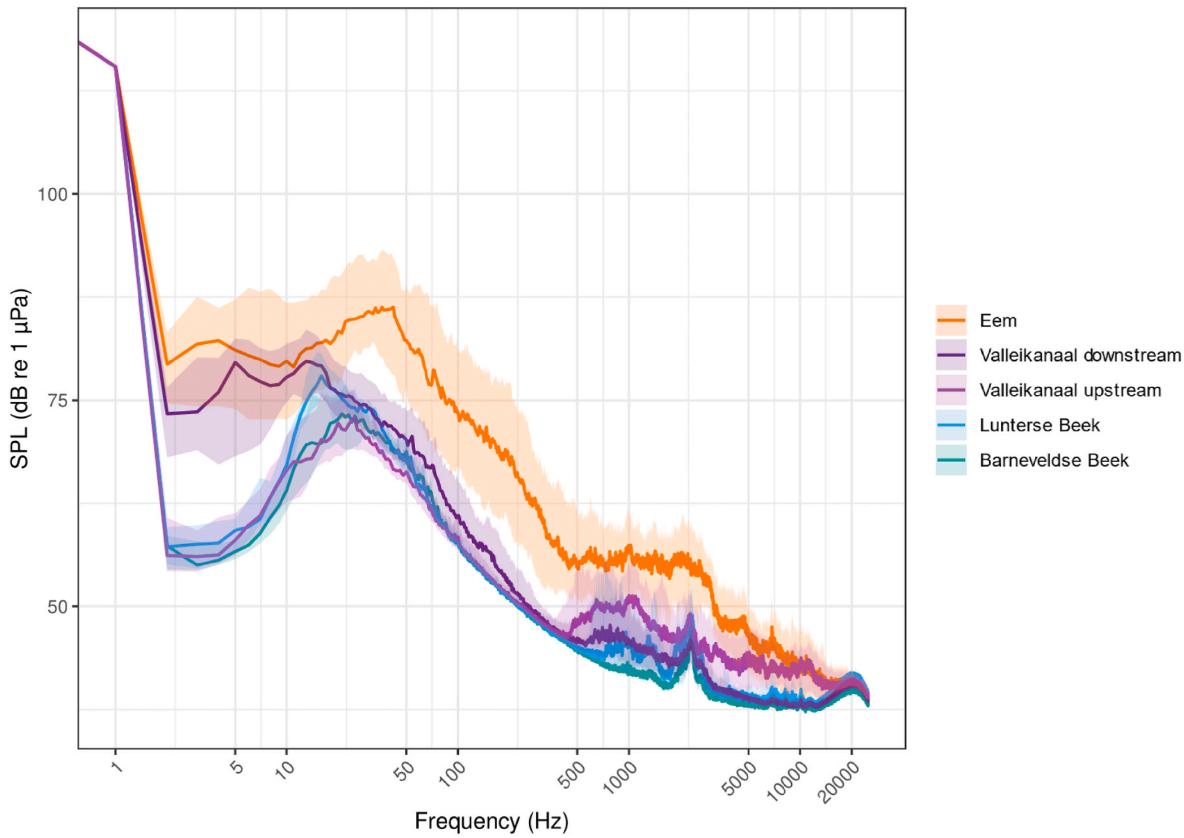

Fig. 3. Power spectral density graph among river segments. The solid line indicates median SPL and the spread indicates upper and lower quartiles. All 1-min recordings (n = 276) in the river segments are included: Eem (n = 76), Valleikanaal upstream (n = 72), Valleikanaal downstream (n = 84), Lunterse Beek (n = 22), Barneveldse Beek (n = 22).

To further investigate the relationship between Distance from side and the soundscape (part 1a), a partial RDA was carried out with Water velocity and Area of cross-section as covariates (Fig. 4C). A forward selection yielded a model with Distance from side as the only significant variable ($p = 0.026$). The resulting RDA's adjusted R^2 is 3.00%, and is significant ($p = 0.03$). Distance from side explained 4.03% of the variation among recordings, while Area of cross-section and Water velocity as covariates explained 55.59% of the variation. Distance from side was negatively associated with the lower octave bands of 500 Hz and below (Fig. 4C). Furthermore, when we corrected for Area of cross-section and Water velocity, all river segments groupings overlapped (Fig. 4C).

To investigate the effect of river characteristics & weather conditions on the soundscape (part 1b), we carried out an RDA of river characteristics and weather conditions on the mean SPL of octave bands at each location (n = 20) (Fig. 4D). A forward selection yielded a model with Area of Cross-section as the only significant variable. The resulting RDA's adjusted R^2 was 59.09%, and significant ($p < 0.001$). Area explained 61.36% of the variance in octave band composition among locations.

3.2. *Anthropogenic noise assessed via spatial and temporal variation (part 2)*

The recordings from the two city transects through Veenendaal and Amersfoort (Fig. 1C) (part 2a) revealed differences in soundscape between rural and more urbanized areas and during day and night (Figs. 5 and 6). The main difference in SPL among urbanization types is in the lower frequencies below 200 Hz. The Suburban and Urban categories had a higher SPL compared to the soundscape in Rural areas. Where Suburban had the highest overall SPL over most of the spectrum. During daytime, the underwater soundscape across all recording sites had a higher SPL compared to night over the whole spectrum (Fig. 6). During nighttime, a peak is visible at 4 kHz, which was caused by chorusing *Sigara striata*, a common species of water boatman.

During the long-term recordings in the cities of Veenendaal and Amersfoort (part 2b), there were clear diurnal cycles in traffic noise from nearby roads and biotic sounds from night-time chorusing *Sigara striata* (Fig. 7). Traffic noise has the strongest contribution to frequencies between 5 and 50 Hz but seemed to commonly affect frequencies up to 3000 Hz. Furthermore, multiple sound events occurred each day that reached frequencies of 20 kHz and higher. Under bridges in cities, traffic noise caused a higher mean SPL and a broader spectrum than the recordings in rural areas. Nonetheless, a diurnal pattern was still visible in all rural areas, likely caused by human activity on the nearby cycle paths or far-away road traffic. In both the rural setting and under bridges, the SPL was lower in weekends than during weekdays, and lowest on Sundays. A rain event on March 31 in Amersfoort mainly affected frequencies above 1 kHz (Fig. 7D). In the river Eem in Amersfoort motorized boats are allowed, which is reflected in occasional broadband sound peaks (Fig. 7C and D).

To illustrate the diversity of biophonic sounds in rivers we highlight some sounds of known (or suspected) species encountered in our recordings (Fig. 8). We have encountered sounds from 4 distinct animal groups: Amphibians such as the Common toad (*Bufo bufo*) (Fig. 8A), insects such as *Sigara striata* (Fig. 8B) and *Callicorixa praeustra*, fish such as of the European perch (*Perca fluviatilis*) (Fig. 8C) and Birds such as the Eurasian chaffinch (*Fringilla coelebs*) (Fig. 8D), Carrion crow (*Corvus corone*) (Fig. 8E) and Common Chiffchaff (*Phylloscopus collybita*).

4. Discussion

Here, we report one of the first descriptions of variation in

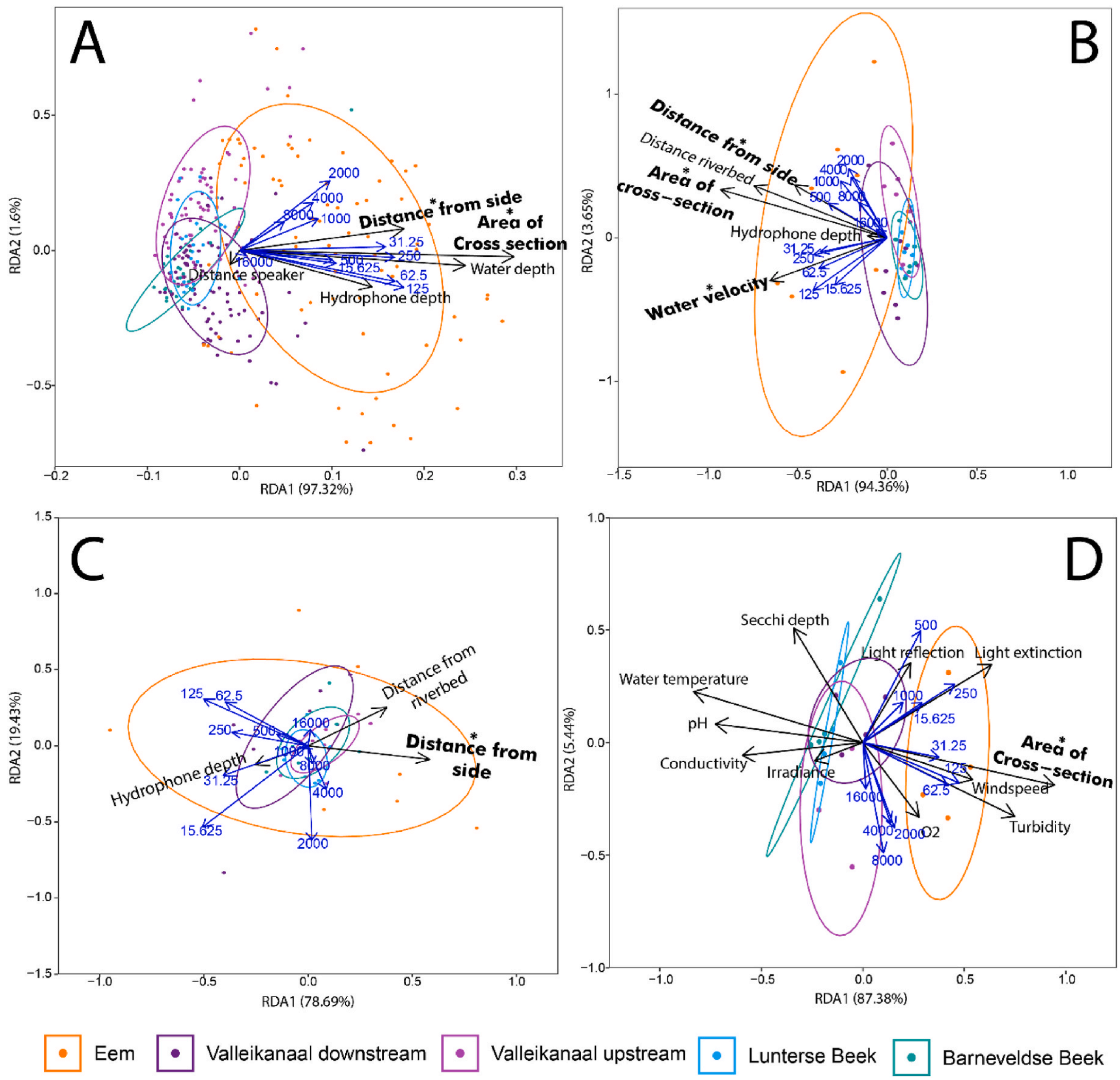

Fig. 4. RDA plots of full octave band SPL of 1-min recordings against local river characteristics and weather conditions cross-section data, colors indicate samples in different river segments, ellipses give the 90% confidence area of the river segments. The different plots are RDAs on different subsets of the data with varying spatial characteristics: A: Octave band SPL of all sample points and their relationship with position in the river cross-section and river size, B: Subset of A, at each position in which water velocity was measured, C: Partial RDA with Area of cross-section and Water velocity as covariates, to explore the relationship between octave band SPL and distance from side, D: Mean octave band SPL at each cross-section location, and their relationship with local river characteristics and weather conditions. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

underwater soundscapes of low-land river habitat. In answer to our first question, we found that 1a) river sound profiles vary with river scale and cross-sectional position, and 1b) that the variation was explained most by area of cross-section, water velocity, and distance to the riverbank. Weather conditions did not have a significant influence on the recordings' days of our data set. We also found evidence of acoustic presence of fish, amphibians, and aquatic invertebrates. In answer to our second question, we found that 2a) human activities appeared audible underwater in almost all recordings. Urban and suburban river parts had elevated sound levels relative to rural river parts. Furthermore, 2b) daytime levels were louder than night time sound levels, and bridges and nearby road traffic were much more prominent with diurnal and weekly patterns of anthropogenic noise in the river soundscapes.

4.1. *Natural soundscapes in Dutch rivers*

Although absolute sound pressure levels were low, we found significant variation in spectral profiles related to the physical features of the slow-flowing rivers. Several acoustic studies in rivers and streams reported significant spatial variation in spectral profiles, which were mostly explained by sediment type, water velocity, depth and width (Wysocki et al., 2007; Tonolla et al., 2010; Geay et al., 2017; Kacem et al., 2020), which is in line with our findings. However, we found that area of cross-section is a better predictor of spectral profiles than depth and width separately. We found that area of cross-section was associated with SPL of all octave bands (15.625–16000 Hz), and water velocity with low-frequency octave bands (15.625–250 Hz). A larger area of cross-section or river depth likely increases SPL in low frequencies due to a higher sound propagation potential caused by the cut-off frequency, but will also increase SPL in all other frequencies simply because there is a larger volume of potential sound sources nearby (Forrest et al., 1993).

Our findings are in slight contrast with Tonolla et al. 2011, who found positive correlations between depth and low-frequency octave bands (31.5–900 Hz), and between water velocity and mid-frequency

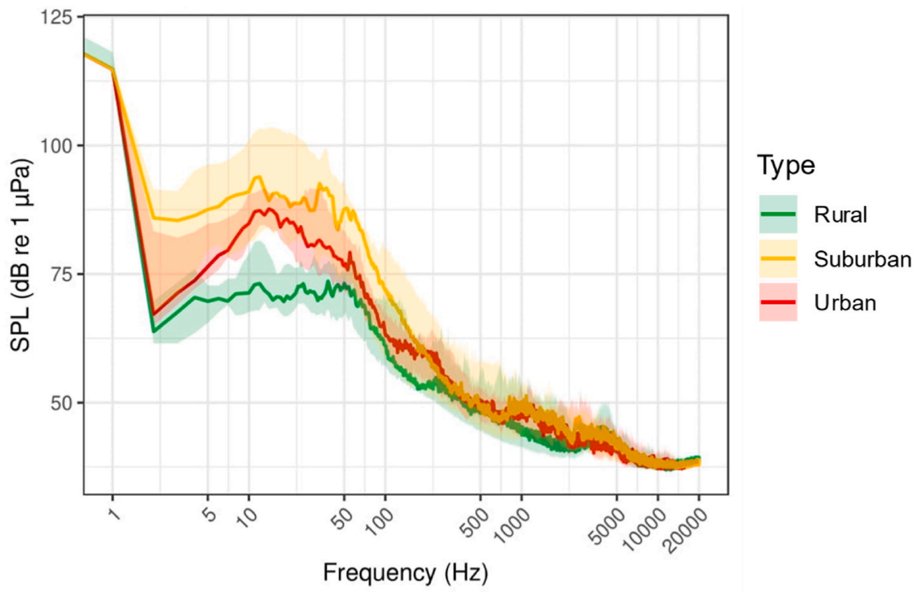

Fig. 5. Power spectral density graph of city transect data at different levels of urbanization: Rural (n = 27), Urban/Rural (n = 14), Urban (n = 23). The solid line indicates median SPL and the spread indicates upper and lower quartiles.

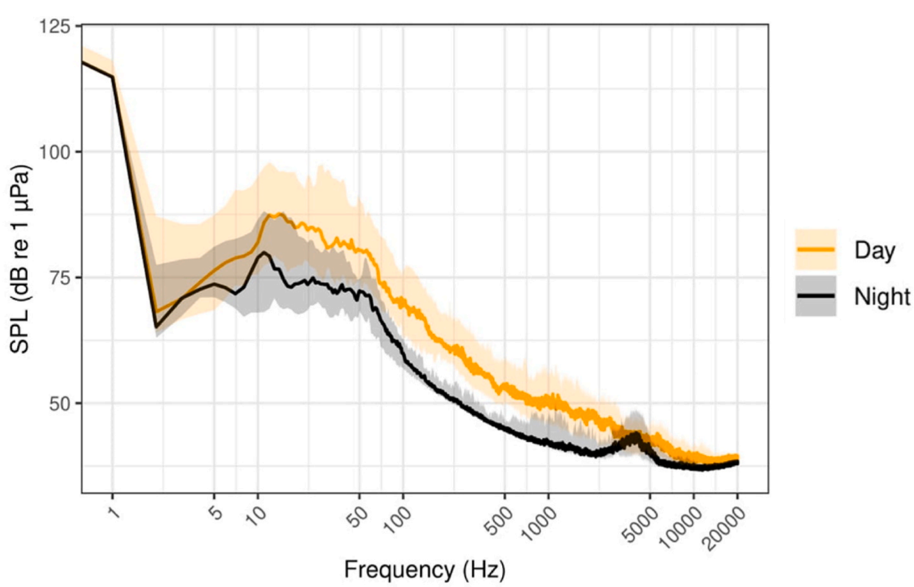

Fig. 6. Power spectral density graph of city transect data at day and night: Day (n = 34), Night (n = 30). The solid line indicates median SPL and the spread indicates upper and lower quartiles.

octave bands (1000–8000 Hz). This discrepancy may be explained by the faster water flow (average of 0.7 m/s), compared to our Dutch lowland rivers (maximum of 0.35 m/s). As water velocity increases, flow related sound sources such as turbulence and sediment transport may start to dominate the soundscape at mid-range frequencies between 1000 and 8000 Hz, masking the effect of area of cross-section in those frequencies (Tonolla et al., 2009). Despite the slow-flow conditions in the Valleikanaal-Eem river system, this is still enough to elicit spatial soundscape variation. Furthermore, we provide evidence of soundscape variation at small spatial scales, within a river cross-section.

Besides abiotic explanatory variables of continuously present sound profiles, we found several distinct sound events from biotic sources of aquatic and terrestrial animal species. We have identified several species of aquatic invertebrates and one suspected fish and one suspected toad species. We encountered many more potentially biotic sound events, but most cannot be attributed to specific species yet. Still, it is clear that soniferous activity of especially aquatic insect and fish species is widespread in freshwater systems (Desjonqueres et al., 2015; Greenhalgh et al., 2020; Rountree et al., 2020; van der Lee et al., 2020). The night-time chorusing of water boatman (*Sigara striata*) in our recordings even made such a significant contribution to the underwater soundscape that it showed up in our relatively large-bin processing of long-term recordings. Other species did not chorus on a consistent spatial and temporal basis, and their more short-term events require small-bin processing techniques to show up in habitat-specific soundscape characterization.

In addition to the aquatic animals, there are more potential sources for the underwater biophony. Terrestrial animals vocalizing in air also contributed to spatial differences in the underwater soundscape, which was illustrated by the chiffchaff, finch and crow songs in our underwater

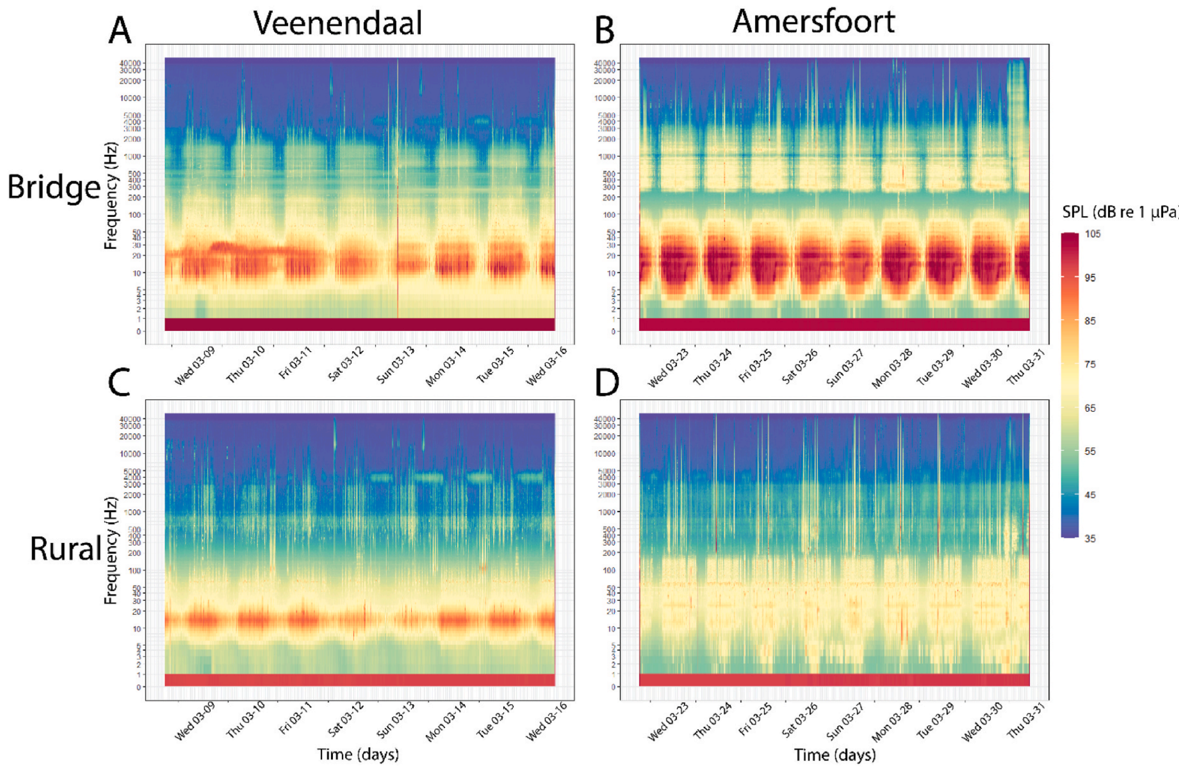

Fig. 7. Four examples of one-week spectrograms, with average SPL at 1-min timesteps at recording locations inside- and outside the cities of Veenendaal and Amersfoort.

recordings. Furthermore, bubbles produced by aquatic plants, through photosynthesis and microorganism respiration, have also been reported to produce short pulses with wide frequency bands (Felisberto et al., 2015; Kratochvil and Pollirer, 2017; Freeman et al., 2018; van der Lee et al., 2020). However, we do not believe they contributed much to our current recording set since most of our recordings were conducted in winter and early spring, which meant there was still very limited aquatic plant cover.

4.2. Potential for fish orientation and navigation

Low levels of distinct sound profiles may provide important cues to local fish species with the most advanced hearing adaptations. Spatial soundscape discrimination within this quiet river system may be challenging to fish species with less sensitive hearing. Still, less common transient sound events not captured in our analysis, may still be above auditory thresholds of most fish, providing them with information about local sound sources. Furthermore, the fish species with the most advanced hearing abilities, in terms of detection thresholds and broad frequency range (up to 5000 Hz), are all of freshwater fish (Fay and Popper, 2000; Putland, Montgomery and Radford, 2019). It has been suggested that hearing specializations have evolved in quiet habitats such as lakes, slow flowing waters, and the deep sea, for the detection of relatively low-amplitude sounds of wide-ranging frequencies in their environment, and not necessarily for communication purposes (Ladich, 1999; Amoser and Ladich, 2005). The resident fish species that inhabit these quiet waters may thus be well adapted to distinguish the subtle, low sound-level variation in habitat-specific soundscapes. Furthermore, the directional nature of particle motion may likely improve perceptual ability of subtle sounds, as well as add significant environmental information (Nedelec et al., 2016; Popper and Hawkins, 2018; Rogers et al., 2021).

Dramatic variation in dynamic range among marine, low-land rivers, and high-elevation torrents may inflict challenging auditory circumstances for migratory fish that pass through all. Diadromous fish such as the Atlantic salmon (*Salmo salar*) and European eel (*Anguilla anguilla*) have relatively high auditory thresholds compared to other fish species (Hawkins and Johnstone, 1978; Jerkø et al., 1989). Atlantic salmon hearing thresholds are thought to be above sound levels of a marine soundscape under quiet weather conditions, but below the sound levels of a turbulent river (Hawkins and Johnstone, 1978). In humans, the sensitivity of the auditory system is highly adaptive to average levels of ambient sound levels (Welch and Fremaux, 2017). This adaptation allows detection and discrimination of acoustic signals and cues over a wide dynamic range. As far as we know, such sensory adaptation has yet to be discovered in migratory fish, although they do have temporary threshold shifts (Amoser and Ladich, 2003; Nissen et al., 2019). These are typically considered as detrimental, but may actually be adaptive under some circumstances such as strong changes in auditory requirements while passing through different habitats (Egner and Mann, 2005; Lechner et al., 2011) or with changing seasons in soniferous fish (Forlano et al., 2015).

4.3. Presence and problems of anthropogenic noise

Anthropogenic noise seemed acoustically omnipresent underwater in the form of traffic noise. All our long-term recordings revealed diurnal acoustic fluctuations that are most likely attributable to land-based traffic noise, even in the rural locations, hundreds of meters up to kilometres away from busy roads. One of our rural recording locations (Fig. 7C) that was situated approximately 300 m from a highway had up to 20 dB higher SPL at 20 Hz compared to the more remote rural recording location (Fig. 7D). Therefore, it seems that land-based traffic noise easily propagates, through air or substrate, over several hundred meters, possibly even up to kilometres. This would mean that most global freshwater soundscapes could be affected by land-based traffic noise. Which is consistent with findings from a widespread freshwater acoustic study in the United States, in which traffic noise had a mean

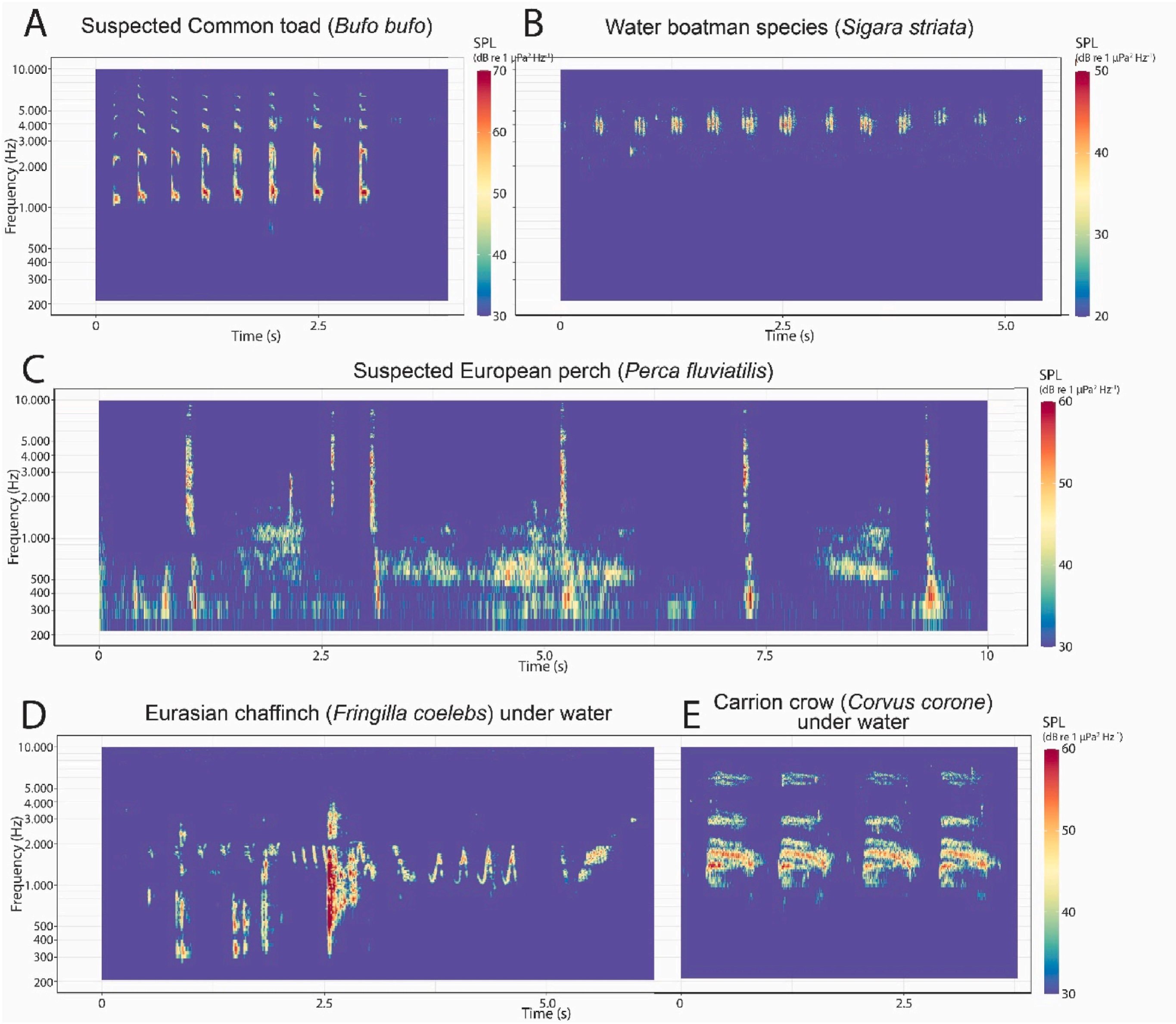

Fig. 8. Example spectrograms of biophonic sounds from different species groups encountered in the recordings. Frequency and time axes are proportional for all spectrograms. Sound Pressure Level (SPL) dB color scale differs among spectrograms. A; Suspected Common toad (*Bufo bufo*) calls with Sigara striata in the background. B; Water boatman species Sigara striata stridulations. C; Suspected European perch (*Perca fluviatilis*) calls under a bridge, with background noise from passing cars. D; Eurasian chaffinch (*Fringilla coelebs*) song, note the presence of another unknown sound source. E; Carrion crow (*Corvus corone*) calls. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

percent time contribution per location of more than 40% (Rountree, Juanes and Bolgan, 2020). This raises serious concerns about the potential impacts of land-based traffic noise on aquatic life, and distance to road traffic may be of particular importance in protecting sensitive aquatic habitat.

Low sound level habitats are likely especially vulnerable to disturbance and masking. The naturally quiet nature of these soundscapes can be considered a quality that allows easier detection of subtle sound sources that carry information, but this may make them especially vulnerable to anthropogenic noise pollution. Habitats with more dominant continuous sound sources such as turbulent rivers may not allow for detection of subtle sound sources such as aquatic plant bubbles or would greatly reduce the range over which communication signals can propagate. If organisms in these soundscapes have evolved to rely on these subtleties in their acoustic environment, then masking could occur already at relatively low levels of anthropogenic noise and at relatively large distances from noisy human activities. We therefore believe that we need more studies, as there still is a general lack of insight into whether and how fish use natural soundscapes and to what extent they are affected by city, bridge or road traffic or boat noise.

5. Conclusions

Our results add another case of distinct habitat-dependent underwater soundscapes from a relatively unexplored water system. The slow-flowing and relatively quiet rivers of Dutch lowlands revealed spectral profiles associated with hydro-morphological features, in particular by area of cross-section, water velocity, and distance to the riverbank. This is similar to other studies in louder marine or fast-flowing river systems, but different in the sense that very faint natural sounds may contribute to habitat-specificity and provide potential cues to aquatic organisms for orientation and navigation in activities that may be critically important to their fitness. Our spatial replication and methodological exploration of hydrophone position indicated habitat-associated soundscapes, but also revealed that it may matter in which part fish swim and where one records the soundscape. Water-flow related acoustic variation suggested flow-associated sound sources, but it may also be worthwhile to explore floating hydrophone systems to exclude potential flow-noise artifacts. Finally, we found a widespread and often prominent presence of anthropogenic noise, and we believe that the relatively quiet nature of these aquatic ecosystems makes them especially vulnerable to disturbance and masking. We therefore need more studies to gain a fundamental understanding of how fish use natural sound to make behavioral decisions and to assess how and to what extent acoustic information loss, as well as other effects of anthropogenic noise such as distraction, stress and avoidance, could lead to population level consequences in fish.

CRediT authorship contribution statement

Kees te Velde: Writing – original draft, Visualization, Software, Resources, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Amy Mairo:** Resources, Methodology, Investigation, Formal analysis, Data curation. **Edwin THM. Peeters:** Writing – review & editing, Supervision, Resources, Formal analysis. **Hendrik V. Winter:** Writing – review & editing, Supervision, Conceptualization. **Christian Tudorache:** Writing – review & editing, Supervision, Conceptualization. **Hans Slabbekoorn:** Writing – review & editing, Supervision, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Acknowledgements

. We also thank water board Vallei & Veluwe, Peter Snelderwaard and Jeroen Hubert for the helpful exchanges during this study. Further thanks to Danielle Crowley, Stefan Slings, Larissa Baan and Vincent van der Tuin for their contributions during the fieldwork. And many thanks for financial support and advice from ARK, WWF, and Sportvisserij Nederland.

SATURN has received funding from the European Union's Horizon 2020 research and innovation programme under grant agreement No. 101006443.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.envpol.2024.124517.

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