ARTICLE

The riverscape meets the soundscape: acoustic cues and habitat use by brook trout in a small stream

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Abstract: Hydromorphological descriptors such as substrate type, water depth, and velocity are commonly used to describe fish habitat, but few studies have focused on how underwater sounds affect habitat use by freshwater fish. We evaluated the influence of the underwater soundscape and other habitat descriptors on the spatial distribution of brook trout (*Salvelinus fontinalis*) in a small stream in eastern Canada. Habitat measurements were made at high spatial resolution (2.5 m intervals). High acoustical heterogeneity of stream habitats (40–150 dB re 1 µPa) was related to differences in water velocity and depth as expected from theory. Brook trout densities were positively related to broadband sound pressure levels (SPL), irrespective of water velocity and depth, but in interaction with habitat type. The positive relationship between brook trout densities and SPL could be related to the high auditory threshold of salmonid fishes. Alternatively, brook trout may use the underwater soundscape to select favourable feeding habitats. Underwater sounds integrate the many environmental dimensions of a stream and may be used by fish as cues for habitat selection.

Résumé : Si des descripteurs hydromorphologiques comme le type de substrat et la profondeur et la vitesse de l'eau sont communément utilisés pour décrire l'habitat des poissons, peu d'études se sont intéressées à l'incidence des sons subaquatiques sur l'utilisation de l'habitat par les poissons d'eau douce. Nous avons évalué l'influence du paysage sonore subaquatique et d'autres descripteurs de l'habitat sur la répartition spatiale des ombles de fontaine (*Salvelinus fontinalis*) dans un petit cours d'eau de l'est du Canada. Les mesures de paramètres de l'habitat ont été prises à haute résolution spatiale (intervalles de 2,5 m). Une forte hétérogénéité acoustique des habitats du cours d'eau (40–150 dB, niveau de référence : 1 µPa) était reliée à des variations de la vitesse et de la profondeur de l'eau, comme permettent de la prédire des considérations théoriques. Les densités d'ombles de fontaine étaient positivement reliées aux niveaux de pression acoustique (NPA) de large bande, indépendamment de la vitesse et de la profondeur de l'eau, mais en interaction avec le type d'habitat. La relation positive entre les densités d'ombles de fontaine et les NPA pourrait être associée au seuil d'audition élevé des salmonidés. Par ailleurs, les ombles de fontaine pourraient utiliser le paysage sonore subaquatique pour sélectionner des habitats d'alimentation favorables. Les sons subaquatiques intègrent les nombreuses dimensions environnementales d'un cours d'eau et pourraient être utilisés par les poissons comme indices pour la sélection d'habitats. [Traduit par la Rédaction]

Introduction

Under natural conditions, underwater habitats that range from quiet shallow lakes to fast-flowing cascades show a rich mosaic of sounds (Amoser and Ladich 2005; Wysocki et al. 2007a). Lotic (flowing water) environments can be particularly noisy (European streams and rivers: Lugli and Fine 2003; Amoser and Ladich 2005, 2010), with underwater sound pressure levels reaching up to 155 dB (re 1 µPa) at high water discharge (447 m³·s⁻¹) and velocity (2.6 m·s⁻¹) (bankfull conditions at a segment of the Flathead River, Montana; Tonolla et al. 2011). Even within a single river, sound spectra differ between habitat types and may vary in intensity and shape over just a few metres (e.g., Tonolla et al. 2010). Water depth, current, and bottom substrate are hydromorphological factors known to influence the propagation of sound in shallow waters (Rogers and Cox 1988; Lugli and Fine 2003; Tonolla et al. 2009; Bradbury and Vehrencamp 2011). Because of the heterogeneity of underwater sound sources and habitat structures, the soundscape

of freshwater lotic systems is particularly patchy. This natural mosaic of underwater sounds, termed "acoustic daylight", creates the background environment against which an acoustic receiver, such as an individual fish, can detect various structures (Buckingham 1999).

The notion that the structure of the soundscape should select for organisms with specific acoustic adaptations is termed the "eco-acoustic constraint hypothesis" (ECH; Ladich 2014). An early synthesis of the behavioural audiogram of 46 fish species found partial support to the ECH (Schellart and Popper 1992). Although preliminary observations were correlative, fish species with a higher sensitivity to sounds at best hearing frequency tend to inhabit shallow fresh waters and to feed at the base of the food chain (Schellart and Popper 1992). On the experimental side, fish acoustic habitat selection has been studied in a limited number of cases. Common sole (*Solea solea*) followed by telemetry in outdoor experimental enclosures sought quieter areas during rainstorm

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Table 1. Hydromorphology of different habitat types in Gregoire Stream.

Habitat type (% of total)	Water depth (cm)	Water velocity (cm·s⁻¹)	Stream width (cm)	Primary substrate (%)	Secondary substrate (%)
Pool (14)	42 (22–100)	0 (0–24)	420 (225–810)	Bedrock (39)	Small boulder (20)
Glide (30)	19 (8–37)	0 (0–9.3)	260 (150–540)	Small boulder (30)	Large cobble (27)
Run (2)	23 (19–33)	18 (1.5–29)	240 (155–510)	Large cobble (45)	Small cobble (36)
Riffle (40)	15 (7–29)	15 (0–43)	250 (110–515)	Small boulder (41)	Large cobble (35)
Cascade (13)	13 (6–30)	12 (0–37)	300 (110–530)	Small boulder (62)	Large cobble (42)
Waterfall base (1)	52 (12–68)	7.5 (0.9–33)	300 (95–480)	Bedrock (75)	Large boulder (25)

Note: The percentage of samples relative to the total number of samples ($N = 593$) is shown for each habitat type. Median values and percentiles (5%–95%) are reported for water depth, water velocity, and stream width. The percent prevalence of primary and secondary substrates is reported for each habitat type.

episodes (Lagardère et al. 1994). Marine juvenile fish tested in laboratory and outdoor sound-addition experiments were disproportionately attracted by reef habitat sounds (Radford et al. 2011; Huijbers et al. 2012). All of the 32 species of marine fish (spanning 18 families) followed by Radford et al. (2011) in a sound-addition experiment were attracted by the reef fringing sounds, whereas only 15 of these species were observed on the "silent" control sites. In another field experiment conducted in a small river, four cyprinid species (*Nocomis micropogon*, *Luxilus coccogenis*, *Notropis rubricroceus*, *Campostoma oligolepis*) were found to be more attracted to rock-shuffling sounds associated with food supply than to white noise playbacks (Holt and Johnston 2011). Indirect evidence of acoustic habitat selection also exists for yellow perch (*Perca flavescens*), which feed more actively on noisy days than on quiet days under the ice sheet of a large fluvial lake (Roca et al. 2020). A first step towards testing the ECH in natural lotic systems is thus to demonstrate that fish select habitats on the basis of acoustic cues, irrespective of other confounding factors.

Approximately 66% of the 12 000 known freshwater fish species on Earth bear specialized hearing adaptations (Nakatani et al. 2011). By the end of the Permian, the otophysic connection between the swim bladder and internal ear evolved in a common marine ancestor, which radiated into thousands of modern freshwater fish species (Betancur-R et al. 2013). However, increased hearing sensitivity in fish may not always be beneficial, especially in noisy waters (Schellart and Popper 1992). In their synthesis of behavioural audiograms, Schellart and Popper (1992) predicted that fish living in quiet environments would have a better sensitivity to sounds at best hearing frequency, but that the reverse would be true for fish living in waters with strong current. For example, Chinook salmon (*Oncorhynchus tshawytscha*), which ascends fast-flowing rivers to spawn, has a poorer hearing sensitivity (hearing threshold around 110 dB over 100–300 Hz frequency mode) than most cyprinid, catfish, and perch species (Ladich and Fay 2013), which are found in more quiet waters. The patchy mosaic of underwater ambient sounds in rivers thus provides a unique setup for studying acoustic selection in fish adapted to such systems.

The objective of this study was to investigate fish habitat use along two main environmental dimensions of the lotic environment: hydromorphological and acoustical habitats. First, we evaluated the overlap between hydromorphological and acoustical habitat features at high spatial resolution within a stream. We then explored whether fish population density responded to variation in acoustical habitat features after accounting for hydromorphology. Our study considered resident brook trout (*Salvelinus fontinalis*) in a stream reach. Brook trout represents a suitable model species for our purposes because it is adapted to stream environments, is often found without competitor fish species, and has known preferences for specific hydromorphological habitats (Chapman and Bjornn 1969; Gibson 1973; Rodríguez 1995; Young 1996; Deschênes and Rodriguez 2007).

Methods

Study site

The study was conducted from 29 June to 17 September 2017 in Gregoire Stream, a second-order stream in southern Quebec, Canada (46°05′40″N, 71°25′58″W). The area has a rain–snow regime characterized by peak water flows in spring and low flows in summer. We delineated a reach of 1150 m in length that comprised an upstream stretch (stream distance = 0–430 m) and a downstream stretch (stream distance = 430–1150 m), which differed in slope and riparian vegetation and were separated by a road crossing. The upstream stretch had a shallow slope, a predominance of riffles and glides, and mostly shrub cover. The downstream stretch had a steeper slope, more fast-flow habitats (cascades and waterfalls), and forest cover. We placed markers along the riverbank to divide the reach into 460 adjacent sections, each 2.5 m in length.

Hydromorphological measurements and habitat classification

Between 31 July and 14 August, we visited the reach on four occasions on days with low or no precipitation and measured the following hydromorphological habitat descriptors: water velocity (cm·s⁻¹), water depth, stream width (cm), and primary and secondary substrate dominance. On each occasion, we measured these variables in fifty 2.5 m sections. The sections were randomly selected without replacement from a uniform distribution over the section identifiers. We also measured the same set of variables in the sections where fish were caught (see section on Fish counts below). We measured water depth at the center of the section and stream width across the wet streambed. In each section, we measured mean water velocity (Global Water Flow Probe model FP111, Texas, USA) by slowly moving the probe up and down the water column continuously for 40 s. We assessed the dominant and subdominant wet substrates using the Wentworth granulometric scale (Wentworth 1922). Assignment to substrate size categories was based on particle diameter (range in mm): clay (0–0.0039), silt (0.0039–0.0625), fine sand (0.0625–0.5), coarse sand (0.5–2), fine gravel (2–8), coarse gravel (8–16), small pebble (16–32), large pebble (32–64), small cobble (64–128), large cobble (128–256), small boulder (256–1024), large boulder (1024–4096), bedrock (>4096). In addition to the hydromorphological measurements of habitat features, we further characterized habitats by partitioning the stream into 185 discrete habitat units, each of which was assigned to one of six habitat types: pool, glide, run, riffle, cascade, and waterfall base, following the habitat classification in Meehan (1991). We distinguished between glides and runs based primarily on the slower flows in the former (Table 1). We measured the length of each habitat unit along the reach to the nearest 0.5 m.

Fish counts

We conducted two electrofishing surveys: the first from 29 June to 14 July and the second from 13 to 17 September. We found one fish species (brook trout) and one crayfish species (*Cambarus*

bartonii) in the study reach. Fish were caught by two operators using a backpack electrofisher (Smith-Root 15-C, Washington, USA) and dipnets, moving along an upstream trajectory. We recorded the number of fish caught and their position along the reach to the nearest 2.5 m. We held fish in an instream flow-through enclosure until they recovered. We considered only individuals above 65 mm total length, for which reliable estimates of density could be obtained by electrofishing. All applicable institutional and (or) national guidelines for the care and use of animals were followed: permits 2017-06-07-076-04-S-P from the Ministère des Forêts, de la Faune et des Parcs, and 2016-M.A.R.5 from the Animal Care Committee, UQTR.

Underwater sound recording

We recorded underwater sounds along the stream reach using a H1 hydrophone powered by a PA4 amplifier (Aquarian Scientific, Anacortes, Washington, USA) and connected to a digital recorder (H2n Recorder, Zoom, Tokyo, Japan). We recorded a total of 593 10-second audio clips (16-bit WAV format at a sampling rate of 44.1 kHz) at a depth of 5 cm below the water surface. The position of the hydrophone below the surface was constrained by the shallow water found in a few sections of the reach (Table 1), which also affects the propagation of underwater sounds (see Discussion). We listened to each audio clip with earphones to ensure that the hydrophone was not rubbing on hard surfaces while recording. The recording system has a maximum input of 10 V (root-mean-square, rms) and a rated sensitivity of –190 dB re 1 V·μPa^{-1} over the flat frequency-response range 10–3000 Hz. We used the above specifications to obtain referenced sound pressure level (SPL: dB re 1 μPa) with the PAMGuide functions (Merchant et al. 2015). For each audio clip, we used PAMGuide to compute the frequency spectrum averaged through time (Hann window, 50% overlap) and obtained referenced rms SPL values in 1 Hz frequency bands over the 0.1–10 kHz range.

We recorded one 10-second underwater audio clip in each 2.5 m stream section immediately after we had collected hydromorphological measurements (water velocity, water depth, stream width, substrate type). By this procedure we ensured a close correspondence between the acoustical and the hydromorphological variables in time and space. As we could not record sounds while conducting the fishing surveys, we did a complete acoustic mapping of the reach on 20–21 July, at a spatial resolution of 2.5 m sections that matched fish density observations. Using the procedure described above, we also calculated broadband rms SPL values (SLP$_{broad}$) between 100 and 300 Hz in each 2.5 m section. These values are to be used in our habitat use models because salmonids are most sensitive to sounds within this band (Ladich and Fay 2013).

Data analysis

We evaluated the degree of association between the stream hydromorphological variables (water velocity, water depth, stream width, substrate type) and underwater acoustic variables (SPL values across frequency modes) in a total of 593 2.5 m sections. The acoustic profile of a 10-second audio clip comprises a discrete series of SPL values over a frequency range. However, these values are not independent because adjacent frequencies along the spectrum tend to have similar SPL values. Therefore, to compare the acoustic profiles of different sections along the stream reach, it is convenient to interpret the profiles as functions of SPL values across frequencies. Functional data analysis (FDA) is especially useful to deal with such functions (Ramsay and Silverman 2005; Illian et al. 2009; Embling et al. 2012). We fitted smooth functions (cubic b-splines) to the acoustic profiles using the FDA package (Ramsay et al. 2017) in the R statistical environment (R Core Team 2018). We used a roughness penalty approach based on a generalized cross-validation measure to determine the optimal degree of smoothing (Ramsay et al. 2009). We then per-

formed a functional principal component analysis (FPCA) to explore the variation among acoustic profiles. The first few principal components of a FPCA provide a compact representation of the variation in function profiles across a set of samples, thereby facilitating interpretation (Ramsay and Silverman 2005). We used redundancy analysis (RDA; Wollenberg 1977) to examine the relationship between the hydromorphological variables and the first two principal components of the FPCA.

To evaluate the role of sounds in habitat use by brook trout, we interpolated both the SPL$_{broad}$ (100–300 Hz) values and the hydromorphological measurement at a common spatial resolution (0.5 m). We performed the interpolation by means of generalized additive models (GAM) using thin-plate spline functions. We fitted the GAM models using the mgcv package (Wood et al. 2016) in R.

For each of the 185 habitat units along the stream reach, we averaged the interpolated values for water velocity, water depth, and SPL$_{broad}$. We then summed the number of brook trout individuals detected in each habitat unit, for each of the two fishing surveys. Run and waterfall habitats were not included in analyses of fish density because very few samples were collected from these habitats (Table 1). To examine the effect of the SPL$_{broad}$ on fish density, we fitted a series of negative-binomial regression models with fish counts as the dependent variable and different combinations of hydromorphological variables, habitat types, and SPL$_{broad}$ as covariates. All models included the length of habitat units as an offset term to focus on linear density (fish counts per metre) rather than absolute counts. The baseline model included the stream distance (i.e., the metre mark of the habitat unit along the watercourse), as well as a binary indicator variable coding for the electrofishing survey (first or second), to account for spatial (longitudinal) or temporal (change between surveys) trends in fish densities. Habitat type (cascade, riffle, pool, and glide), SPL$_{broad}$, and their interaction were successively added to the baseline model. For comparison purposes, hydromorphological variables (water velocity and depth) and SPL$_{broad}$ were also successively added to the baseline model. We compared all models with the Akaike information criterion (AIC). Model fits were performed using the glm.nb function of the MASS package (Venables and Ripley 2002) in R.

Results

Acoustic profile of habitats

Six habitat types were observed in the study reach (Table 1). The riverbed comprised mostly coarse substrates of varying size (bedrock, large and small boulders, cobbles). Substantial spatial heterogeneity in physical structure was apparent both within and among habitats (Fig. 1; Table 1). Ambient noise across the stream reach showed a general increase of SPL when going downstream but with considerable local variation (Fig. 1). The first two principal components from the FPCA (FPC1 and FPC2) accounted for 94% of the variation in acoustic profiles. Although the scores from the FPCA do not have a direct ecological interpretation, their relationship with habitat types and hydromorphological features can be examined graphically and by means of multivariate analyses (see below). Habitats were discriminated to varying degrees along the first FPCA axis (Fig. 2). The second FPCA axis helped to discriminate pools from riffles.

Links between hydromorphological and acoustic variables

An RDA relating the acoustic profiles derived from the FDA (FPC1 and FPC2) to the hydromorphological variables (Fig. 3) showed that the first component was most strongly related to water velocity, whereas the second component was associated with water depth. Site scores derived from the FPCA were used to compare the acoustic profiles of extreme sites (±2 SD) with the mean acoustic profile (Ramsay et al. 2009). Sites with high scores along FPC1 had greater SPLs than sites with low scores, with

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Fig. 1. Spatial and temporal variation of the broadband sound pressure level (root-mean-square (rms) SPL; dB re 1 μPa) for six different habitat types in Gregoire Stream (Quebec, Canada). The dotted line represents the elevation profile of the stream, starting at the confluence of Gregoire Stream and the Bagot River.
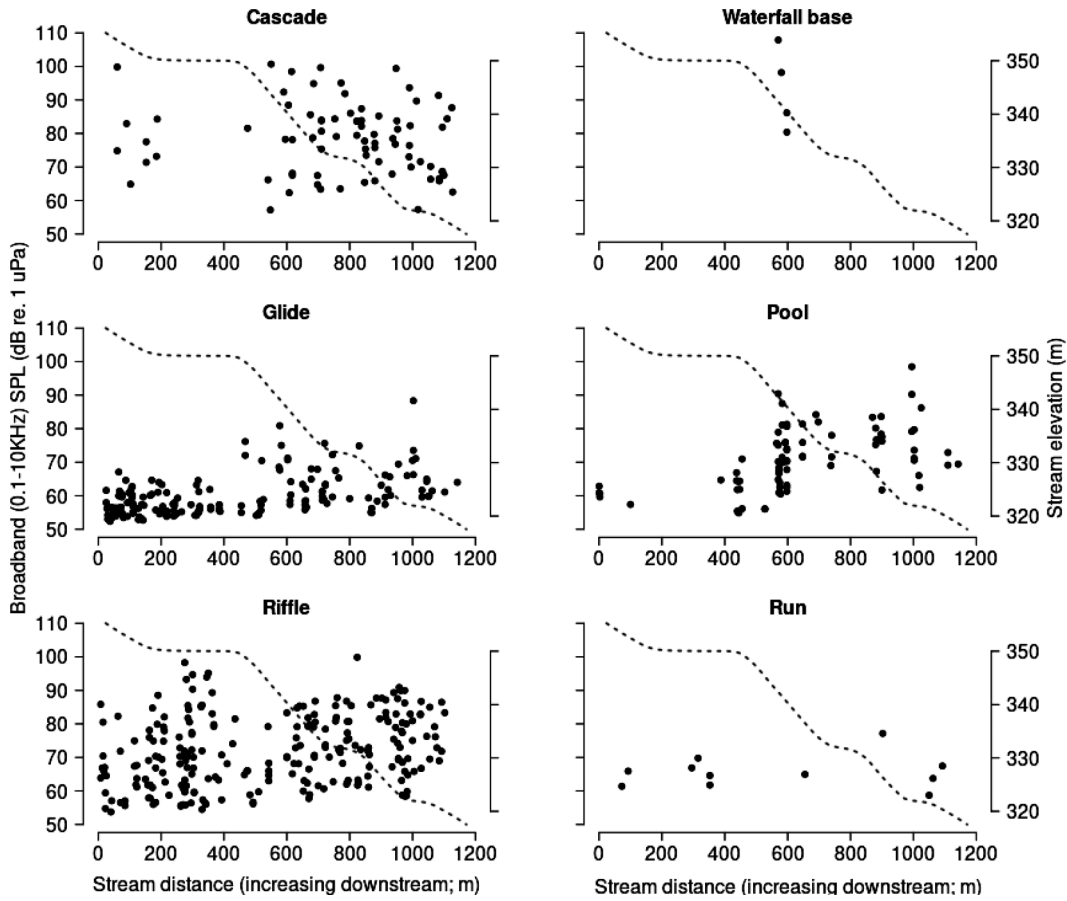

Fig. 2. Functional principal component analysis ordination showing 50% confidence ellipses for each habitat type. Stream sites (dots) are also shown. [Colour online.]
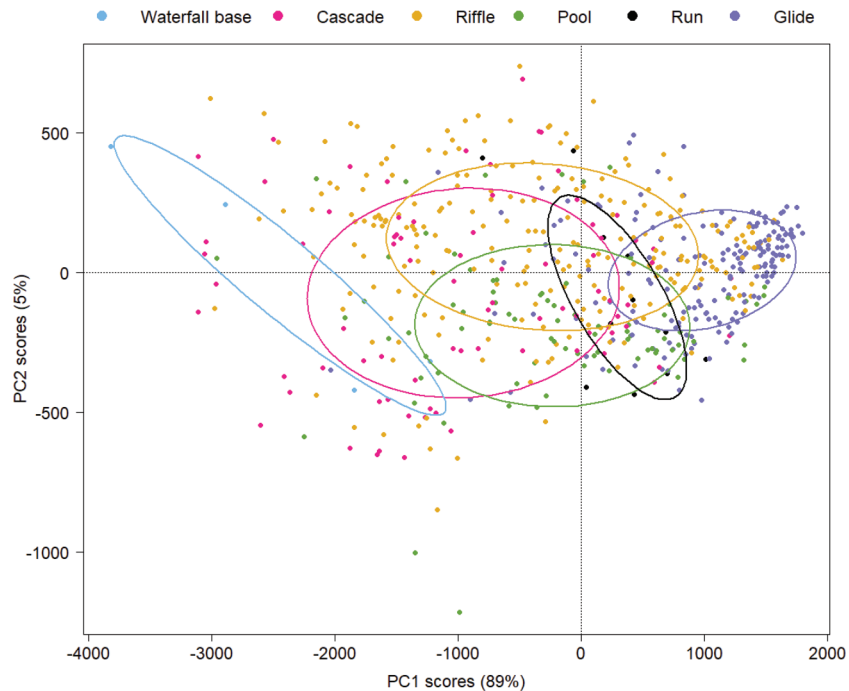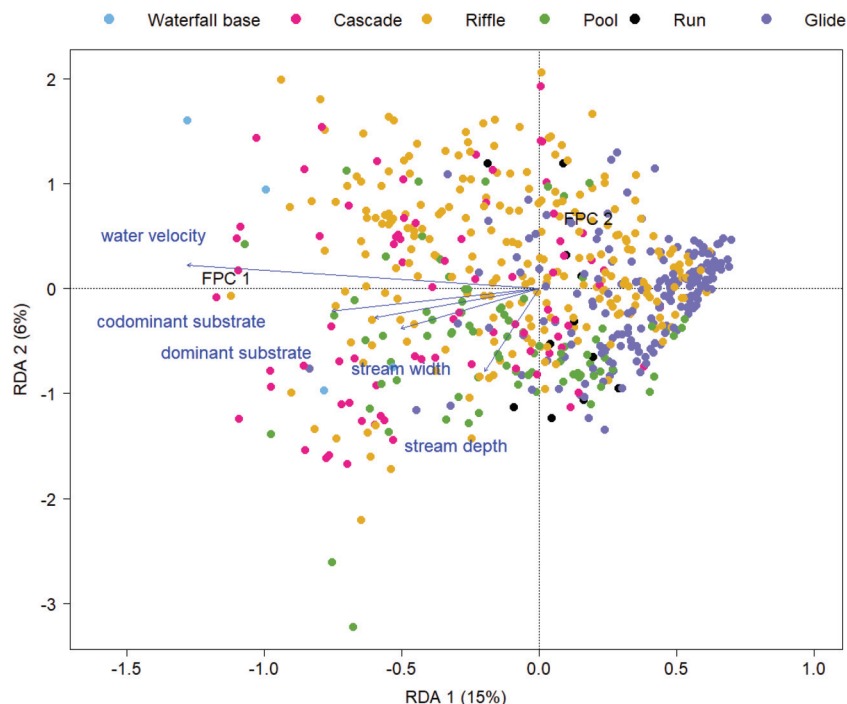
Fig. 3. Redundancy analysis ordination triplot showing the relationships between hydromorphological variables (stream width, water velocity, water depth, dominant and codominant substrates) and the first two principal components of the functional principal component analysis. [Colour online.]

differences in SPLs distributed more or less uniformly across the acoustic profile (Fig. 4). Sites with high scores along FPC2 had greater SPL than sites with low scores for frequencies greater than ~2 kHz, but this pattern was reversed for frequencies below 2 kHz (Fig. 4B). Water velocity was positively correlated with FPC1 (Fig. 3), and thus high FPC1 scores (red curve (refer to online version); Fig. 4A) corresponded to high water velocity values. Water depth was negatively correlated with the FPC2 (Fig. 3) and thus low FPC2 scores (blue curve; Fig. 4B) corresponded to greater water depth. Mean (±1 SD) water depth of representative shallow and deep sites (Fig. 4B) was 14 cm (±7 cm) and 25 cm (±14 cm), respectively. Shallow and deepwater sites on FPC2 presented similar acoustic profiles below 400 Hz and above 4 kHz, but converged in the interval. As a result, the acoustic profiles for shallow and deepwater sites cross around 2 kHz.

Habitat use by brook trout

Although more brook trout were captured in the first survey (318 individuals) than in the second survey (210 individuals), the spatial distribution of counts was comparable in the two surveys (Spearman rank correlation of 0.5 at the scale of habitat units).

The best-performing model of fish density included habitat type, SPL_{broad}, and their interaction as covariates (M3; Table 2). A likelihood-ratio test also favoured M3 over its nearest competitor, M2 (likelihood-ratio statistic = 9.53; df = 4; $P = 0.05$). Model M3 was retained because coefficient estimates for the interaction between habitat type and SLP_{broad} were interpretable from an ecological standpoint (Table 3). In particular, brook trout density was greatest in pools relative to other habitat types, whereas fish density increased with increasing SPL_{broad} in both riffles and pools, but not in glides and cascades (Fig. 5).

Discussion

The use of hydromorphological variables to assess habitat quality in lotic systems has a long tradition in fish ecology (Fausch et al. 1988). Our results show that the spatial and temporal distribution of acoustic habitats in a small stream is influenced by water velocity, water depth, and habitat type (e.g., pool, riffle, glide, cascade; Figs. 3, 4) Variation in acoustic features was related to variation in fish density. Brook trout densities in pools and riffles increased with increasing SPL values within their best hearing frequency range (100–300 Hz) after controlling for the spatial and temporal structure of data. We did not observe comparable density responses in other habitat types. These findings suggest that brook trout may select habitats using acoustic cues, although the causal mechanisms behind the relationship remain so far untested. We hereafter discuss possible explanations to this relationship.

Stream ambient noise

The underwater acoustic profile of shallow lotic systems is affected by both sound sources and sound propagation. The effect of water velocity and depth on SPL can be conceptualized using the Froude number, which is a dimensionless ratio of gravitational and inertial forces (Tonolla et al. 2009). The Froude number increases in proportion to water velocity and the reciprocal of the square root of water depth ($depth^{-1/2}$) ranging from deep slow-flow (Froude ≪ 1) to fast shallow-water flow (Froude > 1). Water velocity and depth, as well as substrate roughness, correlate strongly to underwater SPL in both experimental and natural rivers (Tonolla et al. 2009, 2010). Other studies have shown that underwater SPL in lotic systems varies substantially as the hydrological regime changes in time and space (Lugli and Fine 2003; Amoser and Ladich 2010). The above studies show that the SLP of low-frequency sounds (<1000 Hz) tends to increase with increasing water velocity, discharge, substrate roughness, as well as the size and depth of the water body. Complex interactions among the above factors also influence the shape of the sound spectrum beyond variation in broadband SPL values. Results reported here at a finer spatial and temporal resolution agree with general theoretical predictions and previous empirical observations. The first two axes of the RDA were strongly correlated to water velocity and depth, respectively, and together explained 21% of the variation in acoustic profiles in our stream reach. The broadband SPL of adja-

Fig. 4. Variation in acoustic profiles along the first (A) and second (B) components of the functional principal component analysis. Black solid lines represent the mean acoustic profile. Acoustic profiles for sites with scores 2 SD above (+) or below (–) the mean are also represented. [Colour online.]
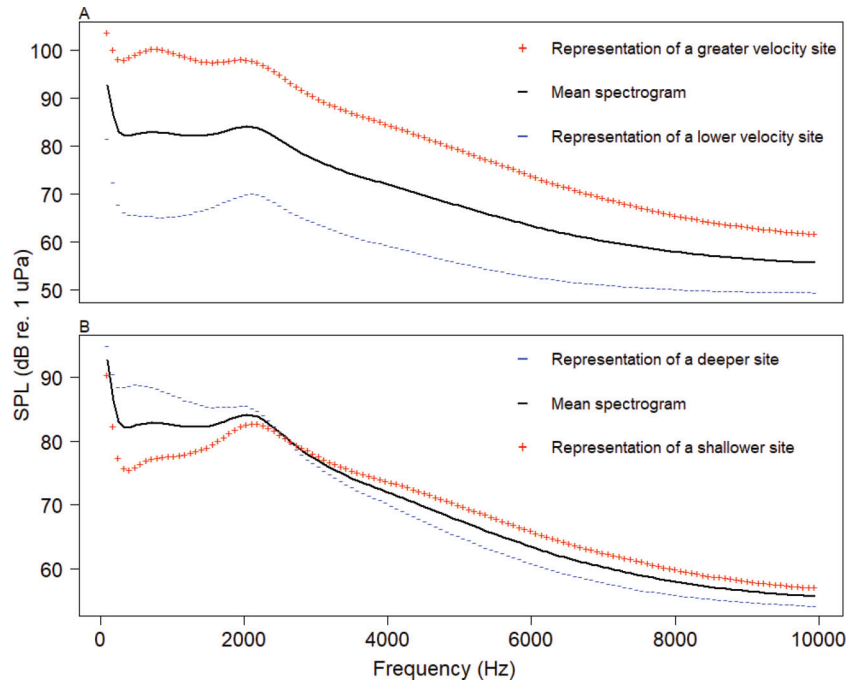

Table 2. Comparison of negative binomial regression models for fish density based on AIC scores.

Model	Covariates	AIC	ΔAIC
M0	Stream distance + fishing survey + offset (unit length)	1119.9	34.8
M1	Stream distance + fishing survey + offset (unit length) + SPL_{broad}	1111.8	26.7
M2	Stream distance + fishing survey + offset (unit length) + habitat type	1085.1	1.5
M3	Stream distance + fishing survey + offset (unit length) + SPL_{broad} + habitat type + SPL_{broad} × habitat type	1083.6	0
M4	Stream distance + fishing survey + offset (unit length) + SPL_{broad} + water velocity + water depth	1112.5	28.9
M5	Stream distance + fishing survey + offset (unit length) + water velocity + water depth	1117.7	34.1

Note: The baseline model (M0) included the position of habitat units along the watercourse (stream distance; m), the fishing survey (first or second survey), and an offset accounting for differences in the length of habitat units (unit length). More complex models (M1 to M5) additionally include various combinations of habitat type (cascade, glide, riffle, pool), broadband underwater sound pressure level (SPL_{broad}; dB), and their interaction (M1 to M3) or combinations of hydromorphological variables (water velocity and depth) and SPL_{broad} (M4 and M5).

Table 3. Coefficient estimate, standard error (SE), and P value for the terms in the fish density model with the lowest AIC score (model M3; Table 2).

Model term	Estimate	SE	P
Intercept	–1.35	0.09	<0.01
Mean sound pressure (SPL_{broad})	0.16	0.08	0.06
Cascade	–0.27	0.15	0.07
Glide	–0.19	0.13	0.16
Riffle	–0.37	0.12	<0.01
Pool	0.82	0.20	<0.01
Stream distance	0.23	0.08	<0.01
First fishing survey	0.20	0.07	<0.01
SPL_{broad}: cascade	–0.35	0.15	0.02
SPL_{broad}: glide	–0.14	0.12	0.25
SPL_{broad}: riffle	0.23	0.15	0.10
SPL_{broad}: pool	0.24	0.12	0.05

cent glide and cascade habitats differed on average by >20 dB, whereas sounds recorded within the same riffle unit at different times could vary from 60 to 90 dB (Fig. 1). Moreover, water velocity alone explained a large proportion of the variation in the SPL of acoustic profiles, irrespective of the frequency mode.

Water depth and substrate type also affect the propagation of underwater sounds across frequency modes. Sounds in shallow

waters do not propagate well under the cutoff frequency determined by both depth and substrate type as represented by the following equation (Rogers and Cox 1988):

$$f_{cutoff} = c_w \left/ \left[4H_c \sqrt{1 - \frac{c_w^2}{c_s^2}} \right] \right.$$

where H_c is the height of the water column (m), c_w the speed of sound in water (m·s⁻¹), and c_s the speed of sound in substrate (m·s⁻¹). For instance, applying this equation to a stream section of 1 m water depth flowing over the bedrock (using a substrate sound speed of 4266 m·s⁻¹; Yasar and Erdogan 2004) would predict a cutoff frequency of 400 Hz. Applying the equation to a stream section of 0.2 m depth (the median of the present study) flowing over the same bedrock type would this time predict a cutoff of 2 kHz. This phenomenon increases the patchiness of acoustic habitats in shallow lotic systems because sounds under the cutoff frequency do not propagate over large distances (Forrest et al. 1993). In the present study, the acoustic profiles of shallow and deepwater sites diverged at low frequencies (<2 kHz), indicating that sounds below 2 kHz attenuate more rapidly in shallow sites. Thus, the statistical framework developed here could be used to identify cutoff frequencies and estimate the specific acoustic im-

Fig. 5. Predicted relationships between brook trout density and broadband (100–300 Hz) sound pressure level (SPL_{broad}; dB re 1 μPa) for different habitat types. Coefficient estimates and standard errors are presented in Table 3. [Colour online.]
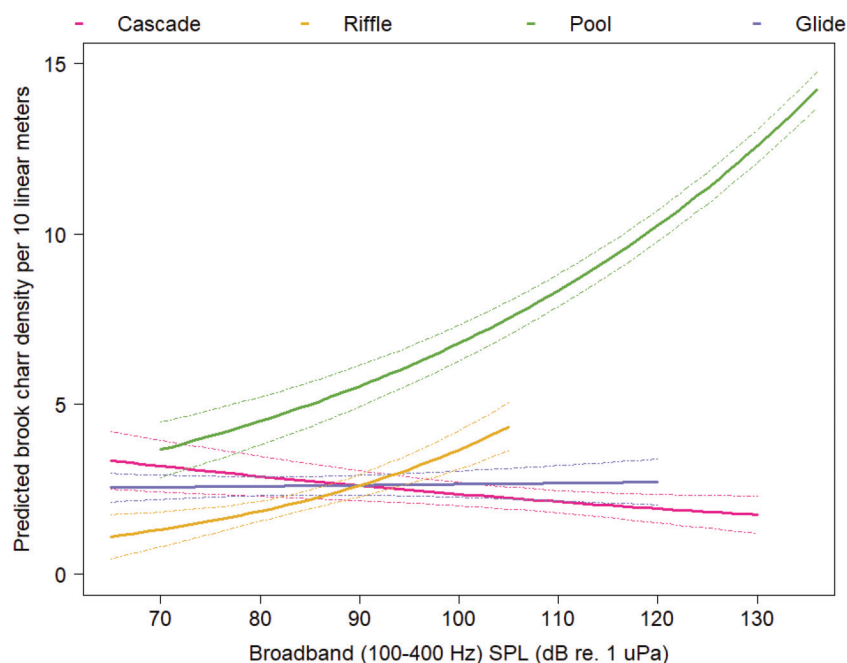
pedance of the substrate in a stream reach. Indeed, the above equation links mathematically the cutoff frequency to substrate impedance and water depth. If one can estimate empirically the cutoff frequency of river sections of known water depth, it is technically possible to solve for the specific acoustic impedance of the substrate. However, the development of this method will require specifically designed experiments with calibrated sound sources.

Influence of ambient noise on brook trout populations

Our statistical models of habitat use showed that habitat type was a better predictor of brook trout density than water velocity and depth. Inclusion of velocity and depth barely improved over the baseline model, whereas the best model included habitat type, SPL_{broad} and their interaction (Table 2). These results were somewhat expected since brook trout is known to have specific habitat preferences (Gibson 1973; Rodriguez 1995; Deschênes and Rodriguez 2007), which may be better represented by categories rather than instantaneous measurements of hydromorphological variables such as water velocity and depth. In the present study, brook trout densities were higher in pools than in the other habitats, as has been found in many previous studies (summarized in Bélanger and Rodríguez 2002).

Brook trout densities increased with increasing SPL in pools and riffles, but not in other habitat types. Brook trout in pools showed a threefold increase in density over the range of SPL values. Several mechanisms could explain this result. First, SPL may be indicative of other potential predictors of habitat quality, such as food availability. In streams, carnivorous fish such as brook trout feed from the benthos or the drift (Chapman 1966; Fausch 1984). Thus, pools with elevated SPL could be indicative of a water inflow associated with food supply by drift (Müller 1953; Nilsson 1957; Chapman 1966). Salmonids tend to seek profitable feeding positions in fast-flowing waters, a strategy that optimizes the ratio of energy gain over food acquisition costs (Chapman 1966; Metcalfe et al. 1997). Hence, fish selecting habitats close to a high water velocity inflow (i.e., noisier pools) could maximize their net energy gain by adopting a sit-and-wait strategy (reviewed in Chapman 1966). It remains to be tested whether brook trout select favourable habitats using acoustic cues or food supply is

the proximate driver behind the relationship. Experimentally, one could playback riffle or cascade sounds in an otherwise quiet pool to evaluate whether brook trout are attracted by those sounds. In a similar experiment, Holt and Johnston (2011) found that cyprinid fish are more attracted by playbacks of rock shuffling sounds, but that the effect did not last, probably because of the lack of corresponding food items.

Another explanation to the observed relationship between SPL values and brook trout densities relates to the ECH, which states that animals are acoustically adapted to natural sounds in their environment (Ladich 2014). This hypothesis proposes that animals found in noisy environments should have a poorer hearing sensitivity than those in generally quiet environments (Schellart and Popper 1992). The rationale behind this proposal is that fish inhabiting fast-flowing waters, like many salmonid species, must be able to endure the loud sounds encountered under natural conditions in streams and rivers. To our knowledge, the hearing sensitivity of brook trout has not been measured yet, but the hearing threshold of other salmonid species is ~110 dB at their best hearing frequency mode around 100–300 Hz (Ladich and Fay 2013), which falls in the upper range among fish. According to the data assembled by Ladich and Fay (2013), the average (min.; max.) hearing threshold of 119 fish species is 92 dB (55; 158) in the 100–300 Hz frequency mode. If one acknowledges that salmonid species have a rather poor hearing sensitivity compared with other fish evaluated using the same general approach, the observed positive relationship between SPL_{broad} (100–300 Hz) and brook trout densities in pool and riffle habitats is compatible with the ECH. We use the term "compatible" here to emphasize that the observed association is correlational.

A negative relationship between SPL_{broad} and brook trout densities would have pointed towards the avoidance of background noise in a species that belongs to a family that lacks specialized hearing adaptations. Our results did not suggest such a noise avoidance effect, in line with previous experiments that investigated the influence of different noise sources on other salmonid species. In particular, the behavioural and growth response of rainbow trout (*Oncorhynchus mykiss*) exposed to anthropogenic sounds was tested in mesocosm experiments. Two cohorts of rain-

bow trout were monitored in aquaculture tanks exposed to three broadband SPL noise treatments (115, 130, or 150 dB re 1 μPa). Noise did not affect the hearing sensitivity, growth, or mortality of this species (Wysocki et al. 2007b). Furthermore, the influence of hydroturbine sounds on rainbow trout swimming behaviour was investigated using an ultrasonic tracking system and four broadband SPL noise treatments: 90, 110, 120, or 130 dB re 1 μPa. Results from the latter study showed not only that rainbow trout did not avoid turbine sounds, but that the proportion of fish detected close to the speaker even slightly increased at 120 dB (Schramm et al. 2017).

SPL values measured with a hydrophone tell us only half of the story about sound perception by fish. Perception of acoustic signals by organisms with inner ears requires that potential energy, in the form of a pressure wave, be transformed into kinetic energy through tympanic structures. In brook trout, this kinetic energy may come indirectly from the vibration of the swim bladder responding to the pressure wave and directly from the motion of particles in the sound field (see Popper and Hawkins 2018). Therefore, neurological influxes in the brain depend not only on the incoming acoustic signals, but also on the distance from the sound source (e.g., near field versus far field), body size, and tissue density, as well as the shape of the tympanic and inner ear structures (Schellart and Popper 1992). We do not know how brook trout perceive underwater sounds, especially when considering that other structures, like the lateral line and external sensory cells, are also sensitive to particle motion. Furthermore, we know that particle motion cannot be easily estimated from broadband SPL values in shallow-water systems. One study measured both the potential and kinetic energy of pile-driving sounds in shallow waters and found a strong and linear correlation (Pearson's $r > 0.85$) between SPL and particle motion values (Ceraulo et al. 2016). Hence, we believe the main finding of our study should prevail irrespective of the sound measurement units used, that is (i) water velocity and depth are the key drivers of underwater sounds in the absence of anthropogenic activities, (ii) habitat types are characterized by different underwater soundscapes, with sharp transitions in space and time, and (iii) pool habitats associated with high SPL values show a higher density of brook trout fish than pools with low SPL values.

Fish in a shallow lotic system, such as the Gregoire Stream, experience rapid transitions in the broadband SPL and the shape of the acoustic profile. This variation in the soundscape bears information on water velocity and depth, but also on distant sound sources associated with water inflow. Acoustic variation could be used by brook trout as proxy for selecting suitable foraging habitats or as a navigating cue. An alternative hypothesis is that brook trout in lotic systems select acoustic habitats that are within their comfort hearing range. This hypothesis implies that lake-dwelling fish would present a better hearing sensitivity (lower threshold) than river-dwelling individuals of the same species. We are not aware of any studies that compare the hearing sensitivity of natural populations in different acoustic environments.

The importance of hearing to freshwater fish is still unclear because we do not know what component of their fitness relates to their ability to discriminate sounds. We do know that fish have evolved a rich diversity of acoustic adaptations (Popper and Coombs 1982; Ladich and Schulz-Mirbach 2016), and yet few studies have investigated acoustic habitat selection in fish populations. In sharp contrast, the number of papers studying the effect of anthropogenic noise on fish is on a steep increasing trend (Radford et al. 2014; Kunc et al. 2014, 2016; Hawkins and Popper 2017). The diversity and intensity of underwater sounds has been increasing in freshwater ecosystems due to the development of anthropogenic activities (e.g., pile-driving, dragging, and dredging) and increased traffic of motorized boats (Myrberg 1990; Andrew et al. 2002; Amoser et al. 2004; Wysocki et al. 2006; Holt

and Johnston 2015). There is growing concern about anthropogenic noise, but knowledge of how fish experience and use the underwater soundscape is limited. A research agenda on acoustic habitat selection by fish was advocated by Fay (2009), but still lags behind in the fields of eco-acoustics and soundscape ecology. Our work reveals the patchiness of the underwater soundscape in a small stream and how it may influence fish densities. Generalization of our results suggests that climate change (e.g., altered precipitation and flow regimes) and the presence of flow control structures (e.g., channel dredging, linearization, damming) have the potential to impact fish distribution in lotic systems.

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