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Comprehensive synthesis of the diversity of hearing abilities and sound production mechanisms of freshwater fish species found in northeastern North America

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Abstract

Fish are sensitive to underwater acoustics, with some species actively producing sounds for communication. It is hypothesized that the evolution of hearing and sound production traits in fish has not progressed in parallel, instead responding to distinct pressures, such as the level of ambient noise or the presence of specialized mechanisms related to hearing and sound production. However, evidence supporting these hypotheses has been restricted to isolated case studies, thus lacking a broader perspective, especially for freshwater fish. In this study, we i) provide the first comprehensive synthesis of hearing and sound production mechanisms in 149 freshwater fish species found in northeastern North America, and ii) examine the relationship between species' hearing sensitivity, ecological descriptors, and habitat characteristics influencing sound levels and propagation. Our analysis highlights the scarcity of data on freshwater fish but identifies three "acoustic groups" based on the match/mismatch between hearing and sound production mechanisms. Additionally, our findings suggest that hearing sensitivity correlates with the ambient sound levels of the species' noisiest habitats, nesting behavior, and substrate type of their growing habitat. We emphasize the urgent need for baseline acoustic data in both resident and migratory freshwater fish species to better understand the biological and ecological roles of hearing and sound production, and to develop predictive models for their responses to changing soundscapes.

Keywords: freshwater fish, bioacoustics, hearing threshold, sound production, ecoacoustical constraint hypothesis.

1. Introduction

The acoustic dimension is an essential feature of aquatic habitats. Sound travels fast and over long distances in aquatic environments. As a result, many aquatic species have evolved to detect sounds and communicate using acoustic signals (Erbe et al. 2022). Furthermore, this ability to hear and produce acoustic signals is particularly advantageous in environmental conditions that impair other senses, such as sight; e.g., under ice or in turbid water (Bradbury and Vehrencamp 2011).

Fish have evolved a great variety of inner ear and accessory hearing structures that allow them to detect sounds. All fish species are sensitive to the particle motion component of sound through their inner ear. It is estimated that more than one third of all teleost species have evolved mechanisms for detecting sound pressure (Ladich and Schulz-Mirbach 2016). Examples of accessory hearing structures include the Weberian apparatus, large swim bladders, anterior bladder protrusions that extend close to the inner ear, and air-filled cavities directly connected to the inner ear (Ladich and Schulz-Mirbach 2016). Fish hearing acuity is typically assessed by measuring the hearing thresholds (HT) of individual fish. The HT represents the lowest sound intensity (measured in decibels, dB) at which a fish can detect or respond to sounds at a particular frequency and typically measured in units of pressure level (dB re 1 µPa) or particle motion (dB re 1m s^{-2}). The best hearing frequency (BHF) is defined as the frequency at which the lowest HT is observed. Both HT and BHF can be determined using behavioural or conditioning methods (e.g., Behrend and Bitterman 1962; Popper 1970), electrophysiological methods (e.g., Fay and Popper 1974) or auditory evoked potentials (AEP), also known as auditory brainstem response (ABR). The latter method is more widely used and involves attaching cutaneous electrodes externally to the head of the fish (Corwin et al. 1982).

We still know relatively little about the fish species that produce active sounds (i.e., sounds with functional or social significance produced voluntarily through specialized structures). It is estimated that fish families comprising soniferous species account for approximately two-thirds of all actinopterygian fish species (Rice et al. 2022). Broad categories of sound production mechanisms can be defined based on morphological specializations. A first category involves the vibration of the swim bladder. This vibration is initiated by intrinsic or extrinsic sonic (drumming) muscles attached directly to the swim bladder, or by flat tendons surrounding the swim bladder dorsally or ventrally (Fine and Parmentier 2015). Stridulation is another category encompassing a variety of mechanisms. It generally involves the rubbing of bony elements, such as pharyngeal teeth or fin rays, against each other or the pectoral girdle (e.g., Ballantyne and Colgan 1978; Rigley and Muir 1979). Other observed mechanisms include tendon plucking by the pectoral fins (Kratochvil 1978), pectoral girdle vibration by sonic muscles (e.g., Ladich and Kratochvil 1989; Zeyl et al. 2016), and the movement of air through the fish's pneumatic duct and guts (e.g., Wilson et al. 2004; Kuznetsov 2009). Sound production has been observed in a variety of behavioural contexts including reproduction (courtship, spawning), social interactions (group cohesion), food-source or territory defense, and predator avoidance (Amorim 2006; Fine and Parmentier 2015; van Oosterom et al. 2016). Nevertheless, evidence of the functional significance of sound communication in fish remains relatively scarce, especially in freshwater ecosystems. While identifying a sound produced in a behavioural context may suggest a functional role, it does not confirm it.

Accessory hearing structures and sound production mechanisms have often evolved independently in different fish taxa (Ladich and Schulz-Mirbach 2016; Rice et al. 2022). The sense of hearing is believed to be more primitive than sound production, and its evolution is thought to be driven by selective pressures that enhance fish adaptation to their natural habitat, rather than by the need to optimize acoustic communication between conspecifics (Ladich 2000). The ‘ecoacoustical constraint hypothesis’ postulates that the hearing sensitivity of a fish is adapted to the ambient noise of its habitat (Amoser and Ladich 2005; Ladich 2014). In particular, the ambient noise level (<1kHz) of underwater microhabitats is positively related to water velocity (e.g., Wysocki et al. 2007; Tonolla et al. 2009; Speares et al. 2011; Kacem et al. 2020). Spares et al. (2011) recorded an average sound pressure difference of ~ 40 dB between riffle (~ 100 dB re 1µPa) and pool (~ 57 dB re 1µPa) habitats, while Kacem et al. (2020) related the spatial heterogeneity in sound pressure levels to changes in water velocity and depth (40 to 150 dB re 1µPa). However, to date, evidence supporting the ecoacoustical constraint hypothesis has been limited to specific case studies, thus lacking a broader perspective (e.g., Lugli et al. 2003; Amoser and Ladich 2005; Picciulin et al. 2010; Niemiller et al. 2013). For instance, Niemiller and collaborators (2013) found that two species of cavefish in the family Amblyopsidae have lost part of their hearing range, which coincided with the frequency range of ambient underwater noise. In contrast, the great diversity of sound production mechanisms in fish, along with the paradox that fish primarily hear and produce low-frequency sounds (<0.5kHz), have led to the suggestion that the evolution of call patterns may be constrained by sound production mechanisms or hearing frequency limitations, rather than by habitat acoustics (but seeFay and Popper 2000; Ladich 2004; Lugli 2015). For example, Amorim et al. (2018) showed that the spectral characteristics of the sounds produced by two goby species where in tune with their auditory abilities. In addition, they suggested that sound production and hearing in these species may have coevolved in response to the local acoustic environment.

Noise pollution in the oceans is raising global concerns (e.g., Duarte et al. 2021), and its pervasiveness extends to freshwater ecosystems as well. For example, about 8,000 merchant vessels, with different noise profiles, operate on the St. Lawrence River (Canada) annually, one of the world's most important commercial waterways (Slack et al. 2023). However, the effects of anthropogenic sound and its potential synergies with other stressors are poorly documented in freshwater fauna, and the underlying mechanisms are not understood (but see Barbeau et al. 2024). To better guide research efforts on the effects of noise pollution on freshwater fish and enforce effective conservation objectives, it is essential to establish baseline bioacoustical data of both resident and migratory fish species, and to gain a deeper understanding of the biological and ecological functions of hearing and sound production.

In this study, we i) present the first comprehensive synthesis of the most recent information on the diversity of hearing and sound production mechanisms of freshwater fish species found in northeastern North America, and ii) assess the relationship between species' hearing sensitivity, ecological descriptors, and habitat characteristics influencing sound levels and propagation. Firstly, we hypothesized that species inhabiting fast-moving waters (riffles, rapids, or shore waves) would have higher HTs compared to those in moderate (runs, estuaries, shorelines) and calm waters (pools, ponds, backwaters), in accordance with the ecoacoustical constraint hypothesis. We also hypothesized that species that build nests during reproduction should exhibit overall lower HTs, as selection would favor mechanisms that increase fish awareness of their surrounding environment to facilitate territorial defense or anti-predator strategies. This is particularly true in aquatic environments with reduced visibility, where early detection of predators may rely more on acoustic signals than on visual or chemical cues (Ladich 2022). Secondly, we expected the BHFs of species to be related to water depth and substrate type in their natural habitat. We hypothesized that the BHF of species inhabiting shallower water would be higher, since the propagation of low-frequency sounds is limited by depth (e.g., Schellart and Popper 1992; Ladich and Popper 2004).

Additionally, due to the sound attenuation properties of the substrate (Rogers and Cox 1988; Ballard and Lee 2017), we predicted that BHFs would be higher in species associated with vegetated, fine-grained or muddy sediments (slow bottoms) and lower in species associated with coarse-grained or sandy sediments (fast bottoms).

2. Material and Methods

2.1. Data collection

We included in our study all native or introduced fish species, resident or migrant, that have been identified so far in the northeastern North America's freshwaters (North America - north of the 41st parallel, east of the 92nd meridian; Fig. 1), for a total of 149 species. We screened the scientific literature (Mingelbier et al. 2016 and 2019), official technical reports from the Ministère de l'Environnement, de la lutte contre les changements climatiques, de la Faune et des Parcs (MELCCFP, Québec, Canada), published fish guides (Bernatchez and Giroux 2012; L'Hérault 2021) and expert's knowledge to construct the list of species.

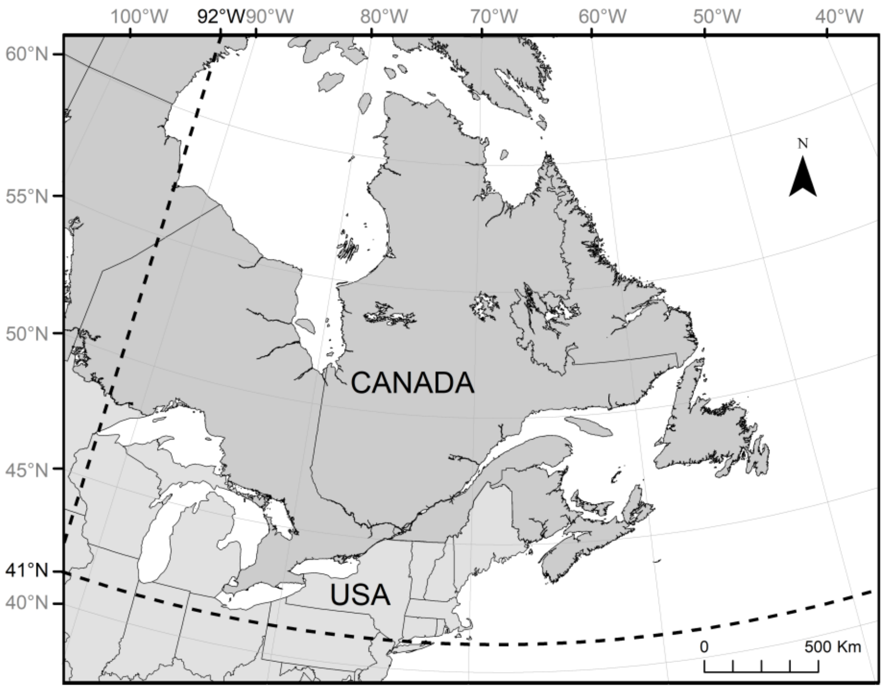

Fig. 1 Map of the region of study. The study comprised migrant and resident fish species found in northeastern North America's freshwaters; north of the 41st parallel and east of the 92nd meridian.

We conducted an extensive literature search in Scopus and Google Scholar databases for books, technical reports, theses, dissertations, and journal articles containing information on species-specific hearing and sound production mechanisms. We standardized the search terms, only varying the species name: TITLE-ABS-KEY ("*Species scientific name*" OR "*Species common English name*") AND ALL (hearing OR auditory OR audiogram OR bioacoustics OR sound OR vocal OR sonic OR soniferous). We extracted information on the inner ear morphology of the species, presence or absence of accessory hearing structures, hearing thresholds, hearing frequency ranges, recordings of active sound production, call types, call spectral and temporal patterns, and sound production mechanisms (see SM Table 1 and 2 for a detailed list and description of all variables extracted). We used the FishSounds web page (Looby et al. 2022) and the Fish Ecology

Library (www.fishecology.org/soniferous/Misc_sounds/Misc_sounds.htm) to access and evaluate recordings of fish species' vocalizations.

To extract variables characterizing the biology and ecology of fish species, we consulted FishBase (Froese and Pauly 2022), textbooks (e.g., Scott and Crossman 1974; Bernatchez and Giroux 2012; L'Hérault 2021), as well as technical reports from governmental agencies, independent advisory panels and international commissions (i.e., Fisheries and Oceans Canada, Committee on the Status of Endangered Wildlife in Canada –COSEWIC, and Atlantic States Marine Fisheries Commission). We considered habitat suitability information for growing and reproduction habitats independently. We assigned each species to one habitat category of water velocity (calm, moderate, or rapid) and to one category of dominant substrate type (fine, coarse, mixed, or vegetation). We classified the growing habitat depth of each species as shallow, intermediate, or deep, while the reproduction habitat depth as < 1m, < 3m, < 6m or ≥ 10m. We also classified species into four groups based on their nest-building behaviour: no nest, open nest, sheltered nest, or cavity nest (see SM Table 1 for a detailed description of the variables). Every line in the database corresponded to a single species. Multiple entries could refer to the same species if multiple measurements for the same variable (e.g., HTs, BHFs, or call types) were reported across different literature sources. The relevant variables were averaged and aggregated, resulting in one observation per species.

2.2. Statistical analysis

Two linear mixed-effects models were used to assess the relationship between fish HT or BHF and biological factors and habitat descriptors. Only species with HT and BHF records were considered for the models (n=33). We further restricted the statistical analysis to species for which HT was measured as sound pressure (n=29), as the number of particle motion measures was too small to support robust predictions. Out of the 29 species, only five had HTs based on measurements obtained through behavioural or physiological audiograms. For the remaining species, HTs were measured using AEP audiograms (SM Table 1). A log transformation of the dependent variables was applied to meet the normality assumption of least squares regression residuals. The first model included the log-transformed HT (dB re 1μPa) as the dependent variable, with growing habitat water velocity, reproduction habitat water velocity, and nest-building behaviour as independent variables. The second model included the log-transformed BHF (Hz) as the dependent variable, growing habitat depth, reproduction habitat depth and dominant substrate type as independent variables. The presence or absence of different types of accessory hearing structure was included as a random effect in all models. Inclusion of this term allowed us to control for phylogenetic relatedness and for the effect of auditory specializations on HTs (e.g., Amoser and Ladich 2005). Models were fitted using the 'lmer' function from the 'lme4' package (Bates et al. 2014) in R (R Core Team 2023, v. 4.2.3). Maximum likelihood estimation was used to calculate model parameters, and p-values (<0.05) were used to evaluate the statistical importance of model terms. Model fit was evaluated through visual verification of assumptions (normality of residuals, normality of random effects, linear relationship, homogeneity of variance and multicollinearity) using the 'check_model' function from the 'performance' package (Lüdecke et al. 2021). Additionally, explained variance (conditional and marginal r-squared) was assessed to quantify model fit.

3. Results

3.1. Paucity of baseline bioacoustical data

A total of 149 resident and migrant freshwater fish species found in northeastern North America were included in this work. They belong to 26 different families and 19 orders (Fig. 2). We found quantitative records of HT and BHF for 33 of those species (22%; 13 orders and 16 families) and reports of sound production for 48 species (32%; 11 orders,16 families). Of the 48 fish species identified as producing active sounds in the literature, 31 had their spectral and temporal repertoires described. The sound production mechanism could be determined for 26 of the 48 species (Fig. 2, SM Table 2). Hearing and sound production mechanisms were both assessed for 12 species (SM Table 1). Out of the 149 species, 30 currently have a status under the Canadian Species at Risk Act (COSEWIC 2022), 16 of which are classified as threatened or endangered. The HT of one threatened species (*Acipenser fulvescens*) was published, whereas active sound production was reported in four species with a precarious status, including *A. fluvescens* and *A. oxyrinchus* (SM Tables 1,2). Overall, we identified publicly accessible recordings of sounds produced by 16 species (SM Table 2).

In our species pool, we found representatives of the main hearing mechanisms reported in fish, including: i) species with Weberian apparatus, ii) species with anterior bladder extensions or air-filled cavities directly attached to the inner ear, iii) species with no connection between the swim bladder and the inner ear, and iv) species without swim bladder (see Fig. 2 for examples). We also retained three main sound production mechanisms: i) stridulations associated with pectoral spines or pharyngeal teeth (also jaw teeth and other bony structures attached to mouth pieces and gills), ii) girdle's vibrations induced by muscles connecting the cranium with the pectoral gridle, iii) swim bladder vibrations associated with either the percussion of sonic (drumming) muscles or body contractions (Fig. 2). Air movement was also reported in the literature as another means for active sound production in a few freshwater species; however, no clear or specific mechanism was identified, nor the acoustic function confirmed.

One main caveat of acoustic communication is that the sound produced should be tuned to the hearing abilities of conspecifics (Fay and Popper 2000; Ladich 2004; Lugli 2015). We were not able to statistically assess the relationship between the dominant frequency of the produced sounds and the species' BHF, due to insufficient statistical power (n=13). Nevertheless, we observed that the dominant frequency matched the BHF in species producing sounds via swim bladder or the pectoral girdle vibrations (median dominant frequencies of the sounds: 108Hz and 180Hz respectively). In contrast, sounds generated through stridulation or air movement typically exhibited higher dominant frequencies (median dominant frequencies of the sounds: 1568Hz and 2410Hz respectively) (SM Fig. 1).

3.2.Acoustic groups

Our compilation of the presence or type of accessory hearing structures, sound production mechanisms, and evidence of active sound production for 149 freshwater fish species found in northeastern North America suggests the existence of three acoustic groups. The "specialist group" comprises species with specialized hearing mechanisms (e.g., Weber apparatus, or swim bladders with appendages or extensions towards the inner ear) and sound production mechanisms (i.e., drumming muscles or stridulatory structures). This group includes representatives from the Ictaluridae (e.g., *Ameiurus nebulosus*), Catostomidae (e.g., *Catostomus commersonii*), Cyprinidae (e.g., *Pimephales notatus*) and Sciaenidae families. Although there is no data on the accessory hearing structure of *Aplodinotus grunniens,* other sciaenid species exhibit specializations such as anterior extensions of the swim bladder (Fig. 2). In contrast, the "generalist group" includes species that lack specialized hearing structures and show minimal evidence of active sound production. Representative of this group may present sound production structures that serve other functions (e.g., pharyngeal teeth). Members of the generalist group include species from the Ascipenseridae (e.g., *Acipenser oxyrinchus*), Centrarchidae (e.g., *Lepomis gibbosus*), Lepisosteidae (e.g., *Lepisosteus osseus*), Luciopercinae (e.g., *Sander vitreus*), Esocidae (e.g., *Esox lucius*), Gasterosteidae (e.g., *Apeltes quadracus*) and Salmonidae (e.g., *Salvelinus alpinus*) families. Finally, the “mismatch group” consists of species that show a clear discrepancy between hearing and sound production mechanisms. At one end of the spectrum are species known to possess hearing adaptations but limited evidence of active sounds or production mechanisms (i.e., air movement or no record), such as members of the Hiodontidae (e.g., *Hiodon alosoides*) and Clupeidae (e.g., *Dorosoma cepedianum*) families. At the other end of the mismatch spectrum are species with clearly identified sounds or production mechanisms (e.g., girdle vibrations associated to cranioclavicular muscles), yet poor hearing abilities due to the absence of a swim bladder. This includes sculpins (Cottidae; e.g., *Cottus bairdii*), gobies (Gobiidae; e.g., *Neogobius melanostomus*), and darters (Etheostomatinae; e.g., *Etheostoma flabellare*) (Fig. 2).

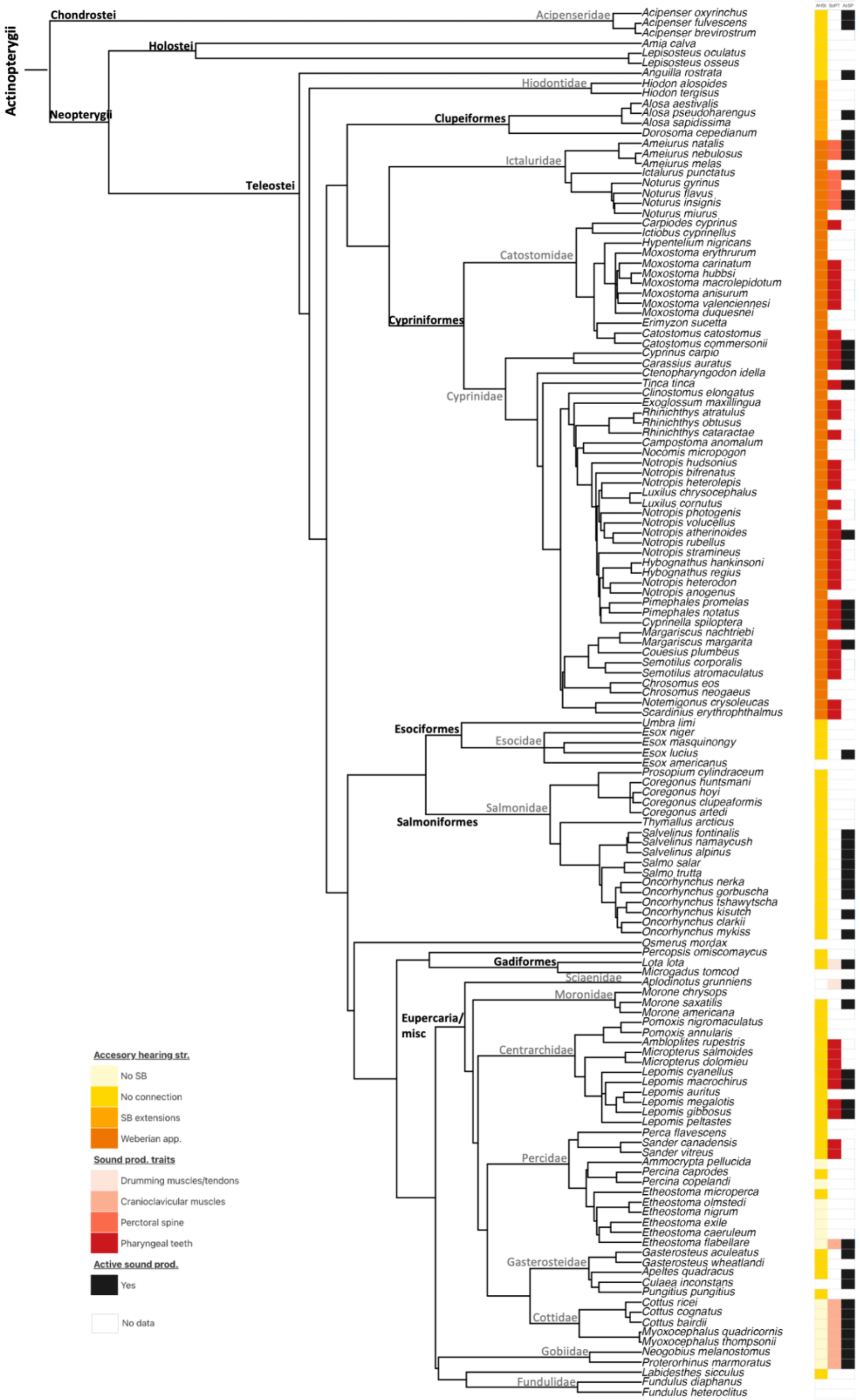

Fig. 2 Phylogenetic tree, pruned from Rabosky et al. (2018), for 144 freshwater fish species found in northeastern North America. Petromyzontidae species (5) were omitted here. The presence/absence and type of accessory hearing

structures, sound production mechanisms and evidence of active sound production are presented for the adult form of every species for which records were available in the literature.

3.3. Hearing threshold and best hearing frequency

We tested the relationships between fish HT or BHF and biological factors and habitat descriptors. Mixed-effect regression models fitted the data well (HT model: conditional R^2= 0.56 and marginal R^2= 0.37; BHF model: conditional R^2= 0.59 and marginal R^2= 0.35). Water velocity in reproduction habitats, along with nest-building behaviour, had a statistically positive effect on HT (Fig. 3), regardless of the presence, absence, or type of accessory hearing structure. Compared to calm conditions, moderate and rapid water flows in reproduction habitats were associated with an average increase in HT of 20% and 36%, respectively. Additionally, species building nests, whether open, sheltered or in cavities, had higher HTs on average (by 20%, 37% and 30% respectively) than those without nest-building behaviours. In contrast, water velocity in the growing habitat showed no effect on species HTs.

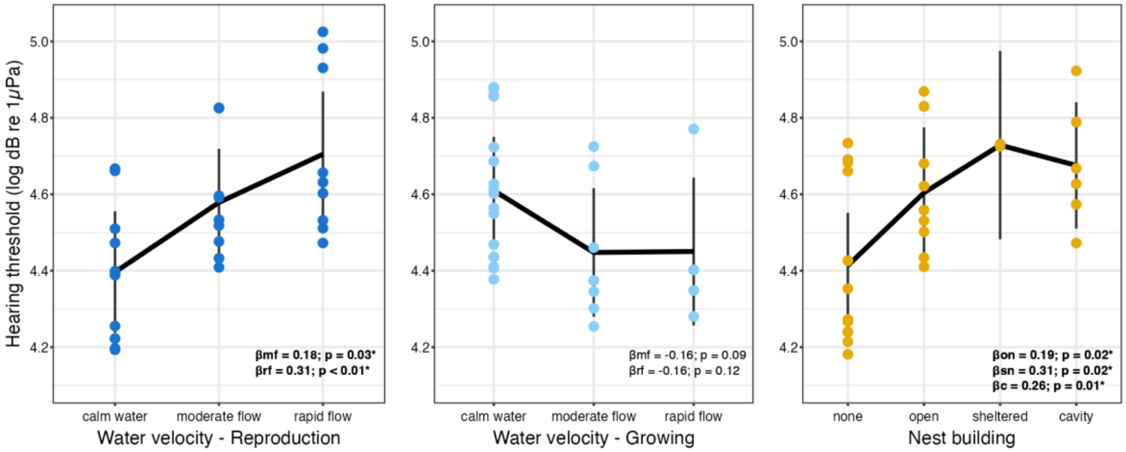

Fig. 3 Partial residual plots from the regression model showing the effect of the independent variables on species hearing threshold (HT). The black lines represent the average predicted effect of the explanatory variables on HTs, with the vertical lines indicating the 95% confidence intervals. The coloured dots represent the partial residuals for

each variable, i.e. the residuals after subtracting the contribution of all the other explanatory variables. Beta values denote the coefficients of the explanatory variables in the model, and the asterisks (*) indicate significant (< 0.05) "p-values".

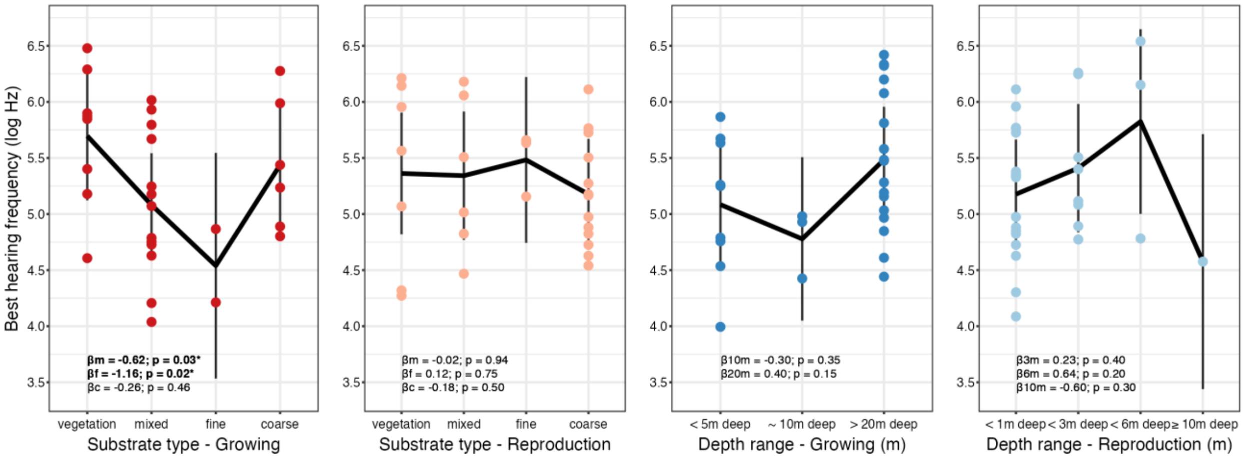

Fig. 4 Partial residual plots from the regression model showing the effect of the independent variables on species best hearing frequency (see legend in figure 2 for an explanation of the variables and model parameters).

Results showed that some variables associated to the physical structure of the growing habitat were significantly related to species BHFs (Fig. 4). Species inhabiting growing habitats with dense vegetation had higher BHFs on average than those associated with other substrate types (Fig. 4). The lowest average BHF was found in species associated with fine-grained or muddy sediments; however, this result needs a careful interpretation because there were only two species in the group. The relationship between BHF and substrate type in the reproduction habitat was not significant. Depth range categories did not show a statistically significant effect on BHF in either growing or reproduction habitats.

4. Discussion

Our synthesis provides the first comprehensive portrait on the hearing adaptations and sound production mechanisms of the freshwater fish found in northeastern North America. This portrait allowed us to underline the paucity of data on fish hearing and sound production traits, to identify three acoustic groups, and to assess the relationship between species hearing sensitivity and habitat descriptors. Our results highlight the constraints imposed by ambient sounds on fish hearing abilities and provide a roadmap to better understand the ecology of freshwater soundscapes.

4.1. Paucity of baseline bioacoustical data

We observed a general lack of, and inconsistency in, the bioacoustical data on freshwater fish species found in northeastern North America. On one hand, the auditory acuity of most species is unknown or has been assessed only once using a single protocol. On the other hand, sound production remains anecdotal in most cases, the "active" nature of its production is rarely verified, and it is unclear whether some species are truly silent or simply understudied. These knowledge gaps undermine our capacity to generalize the bio- and eco-acoustical principles driving sound detection and acoustic communication in fish. For example, robust data on the spectral patterns of actively produced sounds could provide a more complete understanding of the effect of anthropogenic noise on acoustic masking. Additionally, it could improve our comprehension of the importance of low amplitude signalling in fish communication (Reichard and Anderson 2015). There is an urgent need to assess fish hearing acuity and active sound production in a standardised and systematic way. This assessment should include not only repeated measurements of HT and BHF to deepen our understanding of intraspecific variation, but also an in-depth description of the vocal repertoire, including sound pressure level at the source.

We found that few of the fish sounds ("call types") reported in the literature were well understood in terms of production mechanisms and functionality. For the 13 sounds for which we were able to gather complete information, we observed that dominant frequencies were close to the species' BHF in those producing sounds through swim bladder or the pectoral girdle vibrations. In contrast, stridulatory and air movement sounds typically exhibited higher dominant frequencies. The mechanisms involved in the production of stridulatory sounds are relatively well understood and are associated to gill movements, the rubbing or clapping of pharyngeal or jaw teeth, or to the abduction and adduction of the pectoral fins within the pectoral girdle (Fine and Parmentier 2015). Some stridulatory sounds have been documented during aggressive interactions and predator-prey encounters and are postulated to function as distress calls (e.g., Ballantyne and Colgan 1978; Fine et al. 1997; Bosher et al. 2006). Air movement related sounds have primarily been observed in physostomous fish, such as salmons and herrings, and are attributed to the resonant vibration of air bubbles displaced through the ductus pneumaticus or released into the water. Some of these sounds have also been associated with fish in distress (e.g., Rountree et al. 2018) and have been suggested to play role in fish schooling behavior (e.g., Kuznetsov 2009). However, their ecological significance has not yet been clearly or consistently established. In this context, we stress the importance of assessing the functionality of sounds produced by fish in general, particularly the functional role of sounds produced through stridulations and air movement mechanisms.

4.2. Acoustic groups

We identified three main acoustic groups from our species pool by combining the available knowledge on fish hearing and sound production mechanisms: specialists, generalists and mismatched. These groups have no fixed boundaries and should not detract from the need for fundamental research on the bioacoustics of freshwater fish species. Nevertheless, they provide a framework for understanding the ecology of hearing and sound production in fish. One question arising from our categorization is whether common factors (e.g. feeding strategy, spawning mode, habitat depth) constrain the relationship between hearing and sound production in fish. For example, the "mismatch group" includes species with very contrasted feeding strategies. Mooneyes and clupeids have mainly an open-water pelagic lifestyle, while sculpins, gobies and darters are predominantly bottom dwelling-species inhabiting small rivers. In addition, acoustic groups could assist regulators in making informed decisions regarding environmental noise. Current action plans aimed at regulating underwater noise levels are mainly based on anthropogenic levels at the sources. New regulations could also take into account the development stage, life history and hearing acuity of fish (e.g., Popper et al. 2014). Yet, active sound production (e.g., the spectral patterns or types of sounds produced) is never considered because we know little about the biology of sound production, the ecological relevance of these sounds and how they affect the response of fish to anthropogenic noise. The acoustic groups could provide a novel and more comprehensive perspective on the relationship between underwater noise and fish bioacoustics and serve as a guide to identify or re-evaluate conservation targets.

4.3. Hearing threshold and best hearing frequency

We found that fish hearing threshold (HT) was positively related with the water velocity categories (used here as proxy for ambient sound levels) of their reproduction habitat, with rapid flows associated with the highest HTs, regardless of the presence or type of accessory hearing structures. This result suggests that the hearing sensitivity of freshwater species found in the northeastern North America may be adapted to the ambient sound levels of their habitat, providing preliminary support for the ecoacoustical constraint hypothesis. Moreover, it implies that species' HTs are more influenced by the ambient sound levels of their reproduction habitats than by those of their growing habitats. Indeed, within our species pool, fish species that grow in slow-moving waters use either calm, moderate or rapid waters for reproduction. However, no species that grow in fast or moderate flowing water use calm waters for reproduction. For example, *Catostomus catostomus* and *Pimephales promelas*, are two cyprinid species with Weberian apparatuses. *C. catostomus* breeds in fast-flowing water and has a slightly higher HT (82 dB) than *P. promelas* (76 dB), which spawns in calm water. In comparison, *Acipenser fulvescens* and *Esox lucius* do not have specialized hearing structures. *A. fulvescens* spawns in fast-flowing waters and exhibits a higher HT (118 dB) than *E. lucius* (92 dB), which prefers calm waters for reproduction. These findings suggest that species' HTs are adapted to the noisiest conditions of their natural habitats. However, water velocity is only one factor influencing the local ambient sound level. Other factors that could affect the ambient sound level of underwater habitats include rainfall, wind, and position in the water column (e.g., Wenz 1962; Ma et al. 2005).

The average HT of species building nests (open, sheltered or in cavities) was higher than the HT of species without a nest-building strategy. This contradicts our initial hypothesis, which predicted greater sensitivity to sounds among species that show some level of parental care. It also raises the question about the relative importance of acoustic, visual, and chemical signals in the early detection of predators in nest-building species during reproduction. Unexpectedly, species that build nests during reproduction and exhibit some level of territorial defense, including acoustic signaling, were the same species that showed higher HTs (e.g., *Lepomis macrochirus*, *Lepomis megalotis*, *Pimephales notatus*, *Etheostoma flabellare*, *Neogobius melanostomus*). In the case of sculpins, gobies, and darters, it is already documented that the acoustic properties of their nests, in combination with a "quiet window" in the ambient sound level, may compensate for their lower hearing acuity (Zeyl et al. 2016). Further studies on soniferous nest-building species, such as some cyprinids and percids, should provide a better understanding of the external and internal factors that influence their hearing acuity, as well as the role of acoustic signals in their reproductive success.

We found a significant effect of the substrate type on BHF, independently of the presence or types of accessory hearing structure. In line with our hypothesis, BHF was higher in species whose growing habitat was characterized by vegetated substrates. These species are typically found in habitats with calm slow-flowing waters, independently of water depth. For instance, *Lepomis macrochirus* and *Ctenopharyngodon idella* are species associated with vegetated substrates and show relatively high BHFs (400 and 300 Hz, respectively) compared to species associated with gravelly and rocky substrates, such as *Cottus ricei* or *Etheostoma flabellare* (200 and 100 Hz, respectively). However, *L. macrochirus* prefers shallow areas (< 5m), while *C. idella* inhabits larger water bodies and a wider depth range (0-30 m). Lower frequencies do not propagate over long distances in shallow water, and submerged vegetation accentuates sound propagation losses (e.g., Rogers and Cox 1988; Lee et al. 2019). Species inhabiting vegetated and calm habitats with heterogeneous water depths may benefit from developing sensitivity to higher frequencies, thus extending their detection range. Indeed, densely vegetated areas may also be associated with low visibility, making reliance on acoustic cues a useful evolutionary strategy.

We did not observe an effect of water depth (for either growth or reproduction habitats) on the BHF of the species. This result aligns with the idea that depth may not be a strong environmental filter on species' hearing frequency. A possible explanation is that fish typically communicate over short distances, making water depth less relevant (Ladich and Schulz-Mirbach 2016). Alternatively, environmental filtering based on water depth may have been strong on species' ancestors (see Ladich and Popper 2004) but may have subsided over time due to the increasing importance of other factors such as the physical structure of the habitat or the development of acoustic communication. However, our understanding of the intraspecific variation in BHF remains limited due to the paucity of records and variability in the results.

5. Conclusion

The freshwater ichthyological fauna of northeastern North America covered the main categories of hearing specializations and sound producing mechanisms reported in the literature. We highlight the general lack of baseline bioacoustical data for freshwater species and provide a comprehensive overview on the relationship between species' HTs and BHFs and habitat descriptors. Our results suggest that variation in species hearing acuity may be determined by the ambient noise level of the noisiest habitat, the nesting strategy, and the substrate of growing habitats. Describing the hearing and sound production mechanisms of fish species is a cornerstone of soundscape ecology. A predictive understanding of species' responses to changes in the soundscape can only be achieved by assessing both sound sources and propagation properties, as well as modes of sound production and detection. This comprehensive synthesis makes a valuable contribution to advancing research on fish bioacoustics, particularly for freshwater species found in northeastern North America.

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Figure legends

Fig. 1 Map of the region of study. The study comprised migrant and resident fish species found in northeastern North America's freshwaters; north of the 41st parallel and east of the 92nd meridian.

Fig. 2 Phylogenetic tree, pruned from Rabosky et al. (2018), for 144 freshwater fish species found in northeastern North America. Petromyzontidae species (5) were omitted here. The presence/absence and type of accessory hearing structures, sound production mechanisms and evidence of active sound production are presented for the adult form of every species for which records were available in the literature.

Fig. 3 Partial residual plots from the regression model showing the effect of the independent variables on species hearing threshold (HT). The black lines represent the average predicted effect of the explanatory variables on HTs, with the vertical lines indicating the 95% confidence intervals. The coloured dots represent the partial residuals for each variable, i.e. the residuals after subtracting the contribution of all the other explanatory variables. Beta values denote the coefficients of the explanatory variables in the model, and the asterisks (*) indicate significant (< 0.05) "p-values".

Fig. 4 Partial residual plots from the regression model showing the effect of the independent variables on species best hearing frequency (see legend in figure 2 for an explanation of the variables and model parameters).

Statements and Declarations

Conflict of interest The authors declare no conflict of interest.

Availability of data Data are available in SM tables 1 and 2.

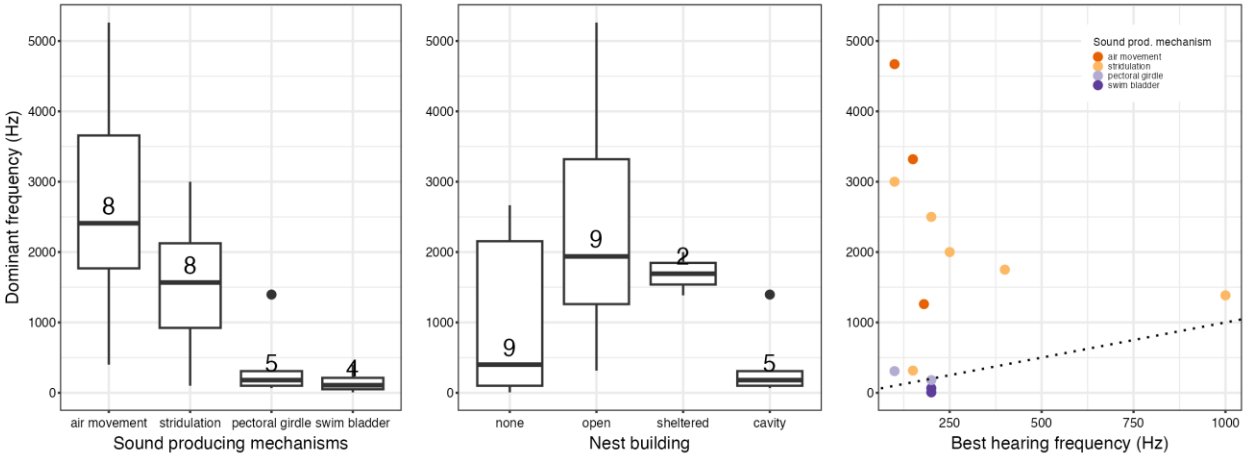
Authors contributions All authors contributed to the study conception and design. Material preparation, data collection and analysis were performed by [Irene T. Roca]. The first draft of the manuscript was written by [Irene T. Roca] and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Supplementary material

SM Table 1 Table containing synthesised information on the ecology and auditory sensitivity data available for 149 species of freshwater fish in northeastern North America.

SM Table 2 Table containing summarised information on the sound production of the 149 freshwater fish species of northeastern North America.

SM Fig. 1



SM Fig. 1 Dominant frequency of the fish produced sounds as a function of sound producing mechanisms, nest building behaviour and the species' BHF. Boxplots shows the median and the number of samples per category. Error bars depict 95% confidence intervals. The dashed line represents a 1:1 line.