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EVALUATING HYDROPHONES FOR DETECTING UNDERWATER-CALLING FROGS

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Abstract.—**Amphibians are declining and disappearing worldwide at an alarming rate, emphasizing the need for accurate surveys to document the distribution and abundance of this imperiled taxon. Automated recorders are a powerful tool for surveyors to continuously monitor for calling amphibians. We are discovering, however, that many species of frogs call when submerged underwater, making it challenging if not impossible for terrestrial observers to use microphones to detect them. Here, we conducted two field experiments to assess the efficacy of hydrophones for detecting underwater frog calls. We designed the first to directly compare detection probability of underwater frog calls by hydrophones, microphones, and human observers. We designed the second to evaluate the wetland characteristics that most influenced the detection distance of hydrophones. We found that hydrophones were 30 times more likely to detect underwater calls relative to microphones and 8.5 times more likely relative to human observers. Hydrophones detected underwater frog calls emitted 65 m away and performed best when water was deep (> 50 cm) and there were few submerged obstacles (i.e., logs) present. Hydrophones may be an important tool for herpetologists to survey for a suite of frog species known to vocalize underwater and, as more practitioners use hydrophones, the list of underwater-calling frogs is certain to grow.**

Key Words.—bioacoustics; detection probability; passive acoustic monitoring

INTRODUCTION

Amphibians are declining and disappearing worldwide (Alford and Richards 1999; Voyles et al. 2009). Efforts to accurately document the distribution and abundance of amphibians are critical to understanding the extent of these declines and to aid in the implementation of conservation actions. Fortunately, most frogs and toads vocalize during the breeding season to find or attract mates. These advertisement calls are usually species-specific and if the calls have previously been described, anuran species can be identified by their vocalizations; thus, acoustic surveys (either with human observers or recording instruments) are commonly used to survey for anurans (e.g., De Solla et al. 2006). Surveys in which observers make repeated visits to sites during predefined seasons or times and record the species and numbers of individuals they hear calling are referred to as manual calling surveys (MCS), and have been used for over a century (e.g., Gibbs and Breisch 2001). If sites are repeatedly sampled over time using the same methods, estimates of detection probability and occupancy (i.e., presence or absence of a species) can be generated, providing much-needed data for the conservation of frogs and toads (Gibbs and Breisch 2001; Marsh and Trenham 2008). Both of the largest standardized amphibian monitoring protocols that are widely used in the U.S., the Amphibian Research and Monitoring Initiative (ARMI; Muths et al. 2005) and the recently retired North American Amphibian Monitoring Program (NAAMP; Weir and Mossman 2005) rely on MCS. Despite their use and ease of implementation, MCS have inherent limitations and researchers have rapidly adopted automated acoustic approaches (Sugai et al. 2019).

Automated recording devices (consisting of one or more microphones and a recording unit) and passive acoustic monitoring approaches allow researchers to continuously record calling behavior at a given site, which remedies the short-term nature of most MCS and avoids the disturbance associated with researchers being present. Automated recorders may be preferable to MCS for species that have very short or unpredictable breeding seasons, when 3–10 min of human observation at a location is insufficient for detection (Williams et al. 2013). Automated recording devices are particularly useful for intensive monitoring of anuran populations over long-term deployments (Blumstein et al. 2011). Additionally, recorder costs have decreased significantly and technical capabilities have increased in recent years, enabling increased use at large temporal and spatial monitoring scales.

For frogs that call underwater, however, both terrestrially focused MCS and automated recording approaches may be insufficient to accurately assess their occurrence, and anuran surveys rarely use recorders equipped with hydrophones for their surveys (but see Nelson et al. 2017). Some species of frogs, many of which are imperiled, frequently call underwater, such as the Gopher Frog (*Lithobates capito*) and Dusky Gopher Frog *(L. sevosa;* Jensen et al. 1995), Chiricahua Leopard Frog (*L. chiricahuensis*; Platz 1993; Degenhardt et al. 1996), Northern Red-legged Frog (*Rana aurora*; Licht 1969), Spotted Frog (*R. pretiosa*; Morris and Tanner 1969), Foothill Yellow-legged Frog (*R. boylii*; MacTague and Northen 1993), and European Common Spadefoot Toad (*Pelobates fuscus*; Frommolt et al. 2008). This behavior is also widespread throughout Pipidae (Ringeis et al. 2017), a family of frogs with members that are invasive on four continents (Lobos et al. 2014). Additionally, because underwater-calling frogs are rarely detected via airborne surveys, many of these species are also data deficient. Thus, accurate surveys to document their distribution and abundance are critically important. Because the air-water interface limits the transmission of underwater sounds into the air (Godin 2008), underwater frog calls may be inaudible to human observers listening from the terrestrial environment (Frommolt et al. 2008; Brunetti et al. 2017; Zheng 2019) or only audible over short distances (< 10 m; Jensen et al. 1995). Therefore, it is unlikely that traditional MCS or automated recorders using in-air microphones are effective options for surveying underwater-calling species. Researchers focused on surveying such species must rely on different methodologies to overcome the limitations of MCS and in-air microphones.

Acoustic recorders equipped with hydrophones in place of, or in addition to in-air microphones have become a staple of marine mammal research (e.g., Best et al. 1998) and are widely used to study marine and freshwater fishes (Luczkovich et al. 2008; Rountree et al. 2019). Several researchers have used hydrophones to record underwater-calling frogs in both the field (MacTague and Northern 1993; Dutilleux and Curé 2020) and laboratory (Hannigan and Kelley 1986). It is unclear, however, how effectively this technology can be adopted to conduct surveys for underwater-calling frogs in variable field conditions and how well hydrophones would perform relative to traditional methods. The detection range of hydrophones likely varies based on the acoustic characteristics of the emitted vocalization and environmental variables such as water depth, turbidity, temperature, bottom substrate, and presence of barriers to sound propagation (e.g., submerged vegetation; Forrest et al. 1993). The utility of hydrophones, however, for recording frogs and understanding the influence of how environmental conditions impact detection probability and detection range of calling animals on hydrophones in shallow water systems has not yet been investigated to the same extent as in marine systems. Here, our objectives were twofold: to compare the effectiveness of human observers, in-air microphones, and submerged hydrophones for detecting frog calls generated underwater; and to quantify the effects of environmental variables on the detection probability of underwater-generated frog calls in shallow freshwater wetlands.

MATERIALS AND METHODS

We conducted two field experiments to assess the efficacy of hydrophones for detecting underwater frog calls. We designed the first to directly compare detection probability of underwater frog calls by hydrophones, in-air microphones, and human observers. We designed the second to evaluate the wetland characteristics that most influenced the detection distance of hydrophones. We conducted both experiments during October 2017 at the Cornell Lab of Ornithology in the Sapsucker Woods Preserve Ithaca, New York, USA (42.48°N, 47.45°W). We chose this location because of the availability of wetlands of varying sizes and characteristics, and at this time of year, no frogs were vocalizing to interfere with our broadcast frog calls.

Equipment.—Our series of playback experiments (described below) used a combination of underwater speakers for broadcasting sounds, and a dip hydrophone system for recording. We played underwater sounds using an underwater speaker (AQ339, Lubell Labs, Inc., Whitehall, Ohio, USA; frequency response 20 Hz to 17 kHz), connected to a portable amplifier powered by a 12 V marine battery, and connected to a laptop computer playing sounds. We recorded sounds with an Aquarian H2a omnidirectional hydrophone (Aquarian Audio & Scientific, Anacortes, Washington, USA; frequency sensitivity: -180 dB re: 1V/µPa; frequency loss = 10 Hz to 100 kHz) connected to a two-channel hand-held audio recorder (Olympus LS-10, Olympus Corp., Center Valley, Pennsylvania, USA). Because the audio recorder had a variable gain (auto-gain control), we calibrated the signal chain of the system by comparison (sensu Bobber 1970), using a SoundTrap ST300 STD (Ocean Instruments, Auckland, New Zealand), with an end-to-end calibrated sensitivity of -176 dB re: 1V/µPa. Through this calibration by comparison, the end-to-end sensitivity of the Olympus LS-10 recorder with the Aquarian Hydrophone was -156.1 dB re: 1 V/µPa. We estimated source levels of the playback sounds using the passive sonar equation (Source Level = Receive Level + Transmission Loss) with cylindrical spreading transmission loss (Urick 1983). To quantify in-air detection of underwater sounds during human listening trials, we used a shotgun microphone (MKH 60-1, frequency loss = 50 Hz to 20 kHz; Sennheiser Electronic GmbH & Co., Old Lyme, Connecticut, USA) connected to the audio recorder.

Experiment 1: comparison of three survey methods.—To compare the effectiveness of hydrophones, in-air microphones, and human observers at detecting underwater-generated frog calls, we conducted an experiment that tested all three methods simultaneously at a single wetland. We broadcast pre-recorded Gopher Frog and Chiricahua Leopard Frog calls from underwater speakers while a human observer stood near a shotgun in-air microphone and a hydrophone. We compared the number of emitted calls that we detected by each method.

To make comparisons, we first created a 3 min and 45 s playback sequence consisting of 16 alternating Gopher Frog and Chiricahua Leopard Frog calls. We played half of the call sequences at a high amplitude (source level: 118 dB RMS re: 1 µPa) and half at a low amplitude (source level: 113 dB RMS re: 1 µPa). We obtained representative calls from a reference collection (Davidson 1996). Because both species emit broadband calls (Gopher Frog frequency range: 300–9,000 Hz, peak frequency: 1055 Hz; Chiricahua Leopard Frog frequency range: 450–11,000 Hz, peak frequency: 800 Hz), we anticipated frequency-dependent signal attenuation in shallow water (e.g., Forrest et al. 1993).

In a series of 16 trials, we placed two underwater speakers at pre-selected locations within the wetland. We placed one speaker at a distance of either 4 or 8 m from the recording devices and human observer, and we placed the other at 12 or 16 m. We changed speaker locations between trials. We attached each speaker to a stake to control its depth and to ensure that it did not move during the course of a trial. We placed dummy stakes at various locations in the wetland to prevent human observers from knowing where each of the speakers was deployed during their trial. During playback, we played only one call sequence at a time (i.e., speakers at different distances did not broadcast simultaneously).

We recruited eight volunteers from the Cornell Lab of Ornithology to participate in the trials. Each human observer participated in two trials and we moved the speakers between trials. We gave volunteers several minutes to listen to and learn the calls of the two focal frog species. Then, one at a time (volunteers did not observe other trials), observers stood at the margin of the wetland beside the in-air microphone and hydrophone, and listened for the duration of the approximately 3 min 45 s survey. Each time the volunteer detected a frog call, they raised their hand to indicate a detection, and one of the authors recorded it and matched it to the call currently being emitted.

We positioned observers next to a tripod holding the recorder. We attached one channel via coaxial cable to a hydrophone and the other to an in-air microphone. We placed the microphone at the edge of the wetland on a tripod approximately 1.5 m high, and we placed the hydrophone just within the margin of the wetland in approximately 0.5 m-deep water. The observer, in-air microphone, and hydrophone were all < 1 m from each other.

After we completed all trials, we used Kaleidoscope Pro (Wildlife Acoustics, Inc., Maynard, Massachusetts, USA) to label each individual frog call emitted during trials as detected or not detected by the hydrophone and microphone. We used a combination of listening and visual inspection of waveforms and spectrograms to determine whether each call emitted during a survey was detected by each method. If a call could be heard on the recording by either of the authors reviewing the data (BAD and PJW), we marked it as detected. Alternatively, if the waveform or spectrogram was distinct enough to indicate the presence of a frog call, we also marked it as detected. We chose this method as it likely reflects how the typical practitioner attempting to detect the presence of an underwater-calling species would approach the data. We marked each call as detected or not detected by human observers based upon whether or not they raised their hand while that call was emitted.

For analyses, we treated each emitted call as an independent unit. Thus, during each trial there were 16 unique calls emitted (half Gopher Frog and half Chiricahua Leopard Frog). We used a binomial mixed model (Proc GLIMMIX in SAS 9.4; SAS Institute Inc., Cary, North Carolina, USA) with a response variable of detected (1) or not detected (0). We evaluated the fixed factors of species (Gopher Frog or Chiricahua Leopard Frog), distance (4, 8, 12, or 16 m), and amplitude (low or high) for their influence on detection. We used observer identity as a random factor to account for observer bias and potential background noises occurring during each trial. We describe the likelihood of detection by each method by using odds ratios (OR).

Experiment 2: frog call attenuation in shallow wetlands.—To evaluate the influence of wetland characteristics on the detection of underwater-generated frog calls by hydrophones, we conducted playback trials in a series of diverse wetlands and measured underwater sound propagation. Wetlands ranged in size from 100–1,300 m^2 (measured via satellite imagery) and covered a spectrum of habitat features, from completely non-vegetated, shallow, and ephemeral depressions, to heavily-vegetated, deep ponds with complex underwater structures such as logs, rocks, and debris. We considered shallow wetlands to be those with a maximum depth of

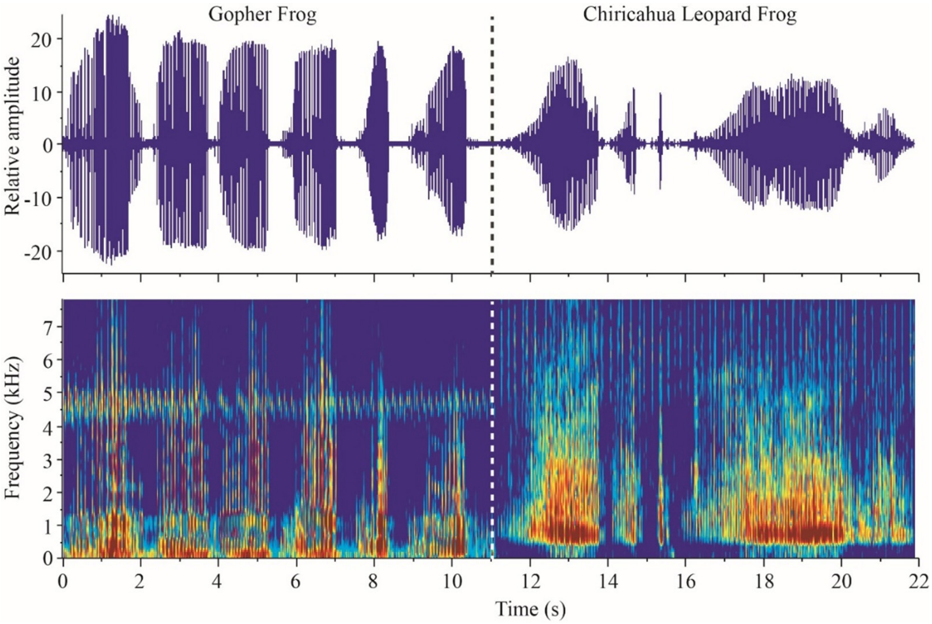

Figure 1. Representative playback sounds with waveform (top) and spectrogram (bottom) of the playback sequence used for experiments comparing hydrophones, in-air microphones, and human observers displayed in RavenPro 1.4 (Cornell Lab of Ornithology, Ithaca, New York, USA). Spectrogram is shown with fast fourier transform (FFT) = 512 points, and a relative color scale, with warmer colors representing higher sound levels. The playback sequence used in field trials contained 16 alternating call sequences of Gopher Frog (*Lithobates capito*) and Chiricahua Leopard Frog (*L. chiracahuensis*). The first call sequence of each species is shown here.

< 1 m whereas deep wetlands consisted of ponds > 2 m in depth.

In five wetlands, we established a total of eight transects 10–70 m in length that crossed a range of habitat features. One large wetland had four, non-overlapping transects and four smaller wetlands had one transect each. At one end of each transect, an underwater speaker was attached to a stake to ensure that it did not move during a given trial. The speaker was connected via coaxial cable to an amplifier and laptop computer located on the shore and controlled by an author (ANR). We set the speaker to play a truncated version of the playback sequence used in Experiment 1 that consisted of a call sequence of Gopher Frog, followed by a call sequence of Chiricahua Leopard Frog (Gopher Frog playback source level: 118 dB re: 1 μPa @ 1 m; Chiricahua Leopard Frog playback source level: 119 dB re: 1 μPa @1 m; Fig. 1). For each trial, one author (BAD) stood 1 m in front of the speaker, holding the audio recorder attached to a hydrophone and headphones. We submerged the hydrophone so it was suspended at the mid-point of the water column, approximately 0.5–1 m. After waiting for the water around the hydrophone to settle (no audible noise on the headphones), we initiated the playback sequence and repeated individual trials with the speaker positioned just under the surface of the water, in the middle of the water column, and at the bottom. After playback was completed at all three speaker depths, we moved the hydrophone back to a distance of 5 m from the speaker, and repeated playback from all three depths. At two transects, we used only one speaker depth (middle of the water column) because the water was very shallow. This process continued until the playback sequence was played at 5 m increments moving away from the speaker (except for the initial 1 m distance) for the length of the transect. The number of sequences played at a transect ranged from six to 90 (median = 24).

We measured the following habitat variables at every location the hydrophone was submerged: water depth (range = 14–91 cm), turbidity (range = 6–240 nephelometric turbidity units; NTU), substrate depth (range = 0–42 cm), and number of submerged obstacles (logs or woody debris > 8 cm diameter) between the speaker and hydrophone (range = 0–12 obstacles; Appendix Figs. 1–5). We measured water depth and substrate depth with a meter stick. We measured turbidity using a standard turbidity tube and converted to NTU (Anderson and Davic 2004). We measured water temperature at the wetland level, but because of low variability among wetlands (range = 15.6–17.2° C), we excluded this variable from the analyses.

After we completed all trials, we processed the resulting acoustic data to label each frog call as detected or not detected by the hydrophone using the same methodology as in Experiment 1. To evaluate the influence of environmental covariates on detection by the hydrophone, we created Generalized Linear Mixed Models with a binomial response variable of detected (1) or not detected (0) and used a logit link function.

We used function glmer in package lme4 (Bates et al. 2015) in Program R v. 3.6.1 (R Core Team 2019). We evaluated the following fixed variables for their influence on detection: distance to speaker, water depth, turbidity, substrate depth, number of obstacles, speaker depth (near-surface, mid-water column, or bottom), and species of call emitted (Gopher Frog or Chiricahua Leopard Frog). We standardized continuous variables by subtracting the mean from each observed value and dividing by the standard deviation of that variable. Substrate depth and number of obstacles were significantly correlated ($t = 9.43$, df = 250, $P < 0.001$, $r = 0.51$) and were thus not included in the same model. We included wetland identity as a random block effect. We ranked 27 candidate models based on Akaike's Information Criterion (AIC; Burnham and Anderson 2002) to determine the relative influence of wetland characteristics on detection by the hydrophone. We considered models with a ΔAICc < 2 to be competitive.

Results

Experiment 1: Comparison of three survey methods.—During the course of 16 trials by eight observers, 256 underwater frog calls were emitted. Overall, survey method had a significant effect on the number of underwater calls detected ($F_{2,582} = 59.88$, $P < 0.001$). Hydrophones detected 79% of calls, human observers detected 50%, and in-air microphones detected only 16% of calls (Fig. 2). Hydrophones were 30 times more likely to detect underwater calls relative to microphones ($t = -10.67$, df = 582, $P = 0.001$, $\beta = 3.42$, OR = 30.57) and 8.5 times more likely relative to human observers ($t = -7.48$, df = 582, $P = 0.001$, $\beta = 2.14$, OR = 8.49). The amplitude at which a speaker emitted calls also had a significant effect on the likelihood of detection ($F_{1,583} = 35.07$, $P < 0.001$), with louder calls more frequently detected than quieter ones ($t = 5.92$, df = 583, $P = 0.001$, $\beta = 1.02$, OR = 2.77). The species of frog emitted also had a significant effect on detection ($F_{1,583} = 15.81$, $P < 0.001$) with Gopher Frogs more frequently detected than leopard frogs ($t = 3.98$, df = 583, $P < 0.001$, $\beta = 0.673$, OR = 1.95). Surprisingly, the distance of the speaker to the recording unit and observer did not influence detection probability ($F_{1,561} = 0.12$, $P = 0.724$).

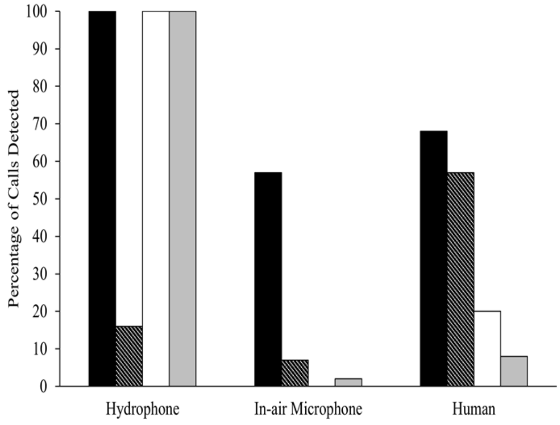

Figure 2. Percentage of broadcast Gopher Frog (*Lithobates capito*) and Chiricahua Leopard Frog (*L. chiricahuensis*) calls detected by a hydrophone, in-air microphone, and human observers in Experiment 1. Bars indicate calls broadcast at a high amplitude (source level: 118 dB RMS re: 1 μPa) for Gopher Frog (solid black), low amplitude (source level: 113 dB RMS re: 1 μPa) for Gopher Frog (dark hatched), high amplitude for Chiricahua Leopard Frog (solid white), and low amplitude for Chiricahua Leopard Frog (gray).

Experiment 2: Evaluation of wetland characteristics.—A total of 252 underwater frog call sequences were emitted at eight transects across five wetlands, 54% of which were detected by the hydrophone. There was substantial variation in detection across wetlands; for example, the hydrophone detected frog calls up to 65 m away in one transect, but failed to detect calls from only 1 m away in another. The top-ranked model (AICc weight = 0.84) indicated the number of submerged obstacles and water depth had the greatest influences on detection by the hydrophone (Fig. 3; Table 1). No other model was competitive (ΔAICc < 2) and this model substantially outperformed the intercept-only model (ΔAICc = 133.13). Detection increased as the number of submerged obstacles between the speaker and hydrophone decreased ($\beta = -8.71$, standard error [SE] = 1.40, $P < 0.001$; Fig. 3A). No calls were detected when greater than two submerged obstacles were between the speaker and hydrophone. Detection increased with increasing water depth ($\beta = 0.62$, SE = 0.16, $P < 0.001$; Fig. 3B). Detection decreased as the hydrophone was placed farther from the speaker ($\beta = -0.88$, SE = 0.16, $P < 0.001$). Lastly, detection was related positively to turbidity ($\beta = 1.39$, SE = 0.50, $P < 0.011$) and substrate depth ($\beta = 0.57$, SE = 0.24, $P = 0.020$).

Table 1. Ranking of Generalized Linear Mixed Models evaluating the influence of wetland characteristics on detection of frog calls by a hydrophone (Experiment 2), based on Akaike's Information Criterion corrected for small sample size (AICc). The acronym ΔAICc = AICc for a given model minus AICc for the top model. Variables are K = number of model parameters, wi = Akaike weight, and LL = log-likelihood. No model was competitive (ΔAICc < 2) with the top model. The top model, next closest model, and intercept-only model are presented; all other models had a ΔAICc > 31.

Model	ΔAICc	wi	K	LL
Number of submerged obstacles + water depth	0	0.84	4	-82.87
Number of submerged obstacles + turbidity	3.27	0.16	4	-84.50
Intercept only	133.1	0	2	-151.5

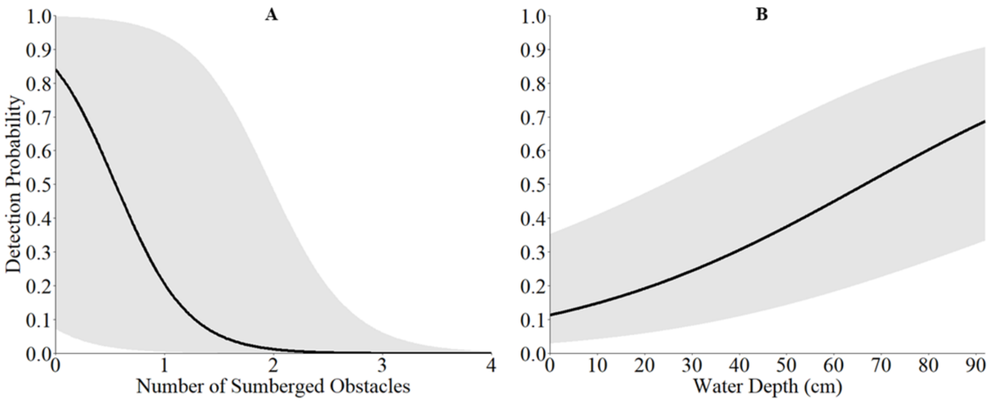

Figure 3. Effect of the number of submerged obstacles (A) and water depth (B) on detection probability of underwater Gopher Frog (*Lithobates capito*) and Chiricahua Leopard Frog (*L. chiricahuensis*) calls by a hydrophone. Black line = model-predicted estimate; gray shading = 95% confidence interval.

Discussion

Our results show that underwater frog calls were more reliably detected by observers using hydrophones than in-air microphones or traditional aural surveys and that wetland characteristics, primarily submerged obstacles and water depth, influenced the range at which hydrophones detected underwater frog calls. Several researchers have described the difficulty of detecting underwater frog calls when listening terrestrially with some observers indicating that frogs are inaudible (Razzetti et al. 2006; Frommolt et al. 2008) and others stating that frogs are audible from only 10 m away (Jensen et al. 1995). These observations and our results suggest that traditional auditory methods may simply be unsuitable to survey for the growing number of species that are known to call underwater.

It is currently unclear how widely applicable anuran surveys using hydrophones will be because we do not yet have a firm understanding of which species call underwater and how frequently they do so. To date, underwater calling behavior has been detected for a small handful of frog species in North America, South America, Africa, and Europe (e.g., MacTague and Northen 1993; Frommolt et al. 2008; Brunetti et al. 2017; Zheng 2019). Many of the species known to call underwater are of conservation concern, which indicates two things: first, surveys for these species are important and needed to understand their distribution and population status, and second, these species have probably received more research attention because of their conservation status, indicating that many common species likely call underwater but the behavior has not yet been documented. Surveys for these imperiled and cryptic species would likely benefit from using hydrophones instead of or in conjunction with traditional methods (MCS and in-air microphone arrays). A possible outcome of more widespread use of hydrophones may be finding that some of these species are more widely distributed than currently thought if hydrophones improve our ability to find them. Similarly, the African Clawed Frog (*Xenopus laevis*) is considered invasive on four continents and researchers would benefit from enhanced detection methods. The increasing use of hydrophones in anuran surveys and studies will almost certainly identify underwater calling behavior in additional species as well as elucidate many aspects of this behavior.

The use of hydrophone surveys for underwater-calling species will primarily depend on two aspects of their ecology: how frequently they call underwater versus in the air and what habitat they breed in. Beyond anecdotal observations, little is known about the frequency with which these species call below the water relative to above the water. Given (2005) showed that Pickerel Frogs (*Rana palustris*) switch to underwater calling when they are disturbed by humans. Future experiments with hydrophones will provide more information about the frequency of this behavior and what factors influence the decision to call underwater.

Our results show that the aquatic environment will have a large influence on the ability of hydrophones to detect underwater-calling frogs, with calls in some wetlands detected upwards of 65 m while others could not be detected from only 1 m away (in a single highly vegetated wetland). Our results indicate that underwater frog calls are best detected by hydrophones in deeper water with few underwater obstacles. Licht (1969) described a situation in which Spotted Frogs vocalized in water only a couple of cm deep while Northern Red-legged Frogs vocalized completely submerged in over 0.6 m of water in the same wetland. It is likely that hydrophones in this wetland would be more effective at detecting the calls of the Northern Red-legged Frog than the Spotted Frog. Similarly, the European Common Spadefoot calls from relatively deep underwater where it can rarely be seen or heard from shore (Frommolt et al.

2008; Dutilleux and Curé 2020) but makes an excellent candidate for hydrophone monitoring. Likewise, the Lake Titicaca Frog (*Telmatobius coleus*) calls while submerged in 2–3 m of lake water while clinging to vegetation and also presents an ideal situation for underwater recording (Brunetti et al. 2017). Other underwater-calling frogs, such as the Gopher Frog, can inhabit diverse wetlands ranging from ephemeral Carolina bays to semi-permanent wetlands with complex structure (Palis 1998). Extensive suspended particulate matter in the water column (i.e., high turbidity) may absorb sound energy and decrease propagation distance, but we found the opposite to be true in our study, likely due to the propensity for sound to travel better through a dense medium than a less-dense one (Bobber 1970). The application of hydrophone surveys will be context dependent, driven largely by wetland characteristics and the behavior of the focal frog species. When conditions are suitable, however, our results indicate that hydrophones are a promising technology for surveying underwater-calling frogs.

Recent advances in availability and decreased costs of hydrophones and recorders make it more likely that practitioners will have ready access to the needed equipment. Automated recording devices have become a ubiquitous research tool for anuran biologists (e.g., Dorcas et al. 2009) with numerous commercial products readily available and advancements in software programs making data analysis more user-friendly (Knight et al. 2017). Many acoustic recorders have multiple channel inputs that would allow practitioners to use in-air microphones and hydrophones simultaneously to maximize detection probability of both aerial and underwater frog calls. We should note that our demonstration used an omnidirectional hydrophone and a directional in-air microphone. Because our validation experiment placed speakers in only one direction from the recorders (-30° to 30°), our directional microphone was essentially serving as omnidirectional in regards to all possible speaker placements. Practitioners deploying both approaches in the field simultaneously will need to make informed choices regarding omnidirectional or directional microphones based on the placement of recorders within wetlands and the desired area of coverage. Marine mammologists and fish biologists have been the first to monitor their focal organisms via hydrophone (e.g., Klinck et al. 2010; Tricas and Boyle 2015) and now anuran biologists can also make use of this technology. Our results suggest that hydrophones are a promising technique for herpetologists surveying for underwater-calling frogs and that this technique will provide answers to many questions about the distribution, behavior, and ecology of a handful of imperiled and poorly understood species.

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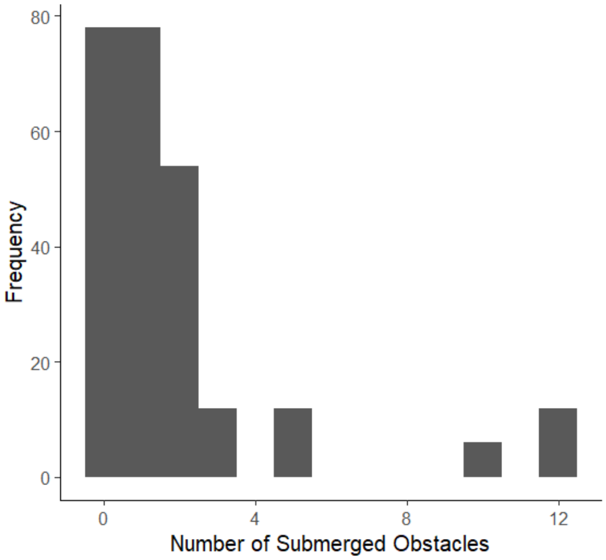
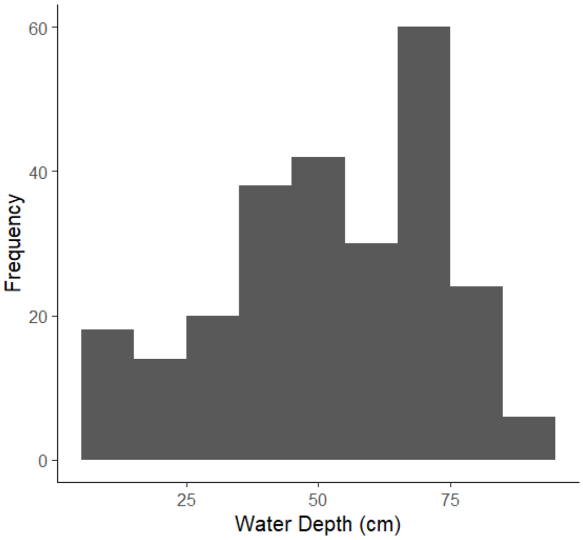
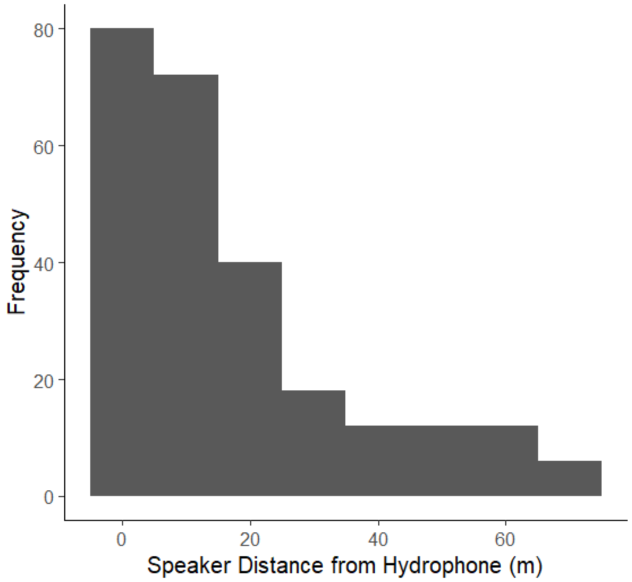
APPENDIX



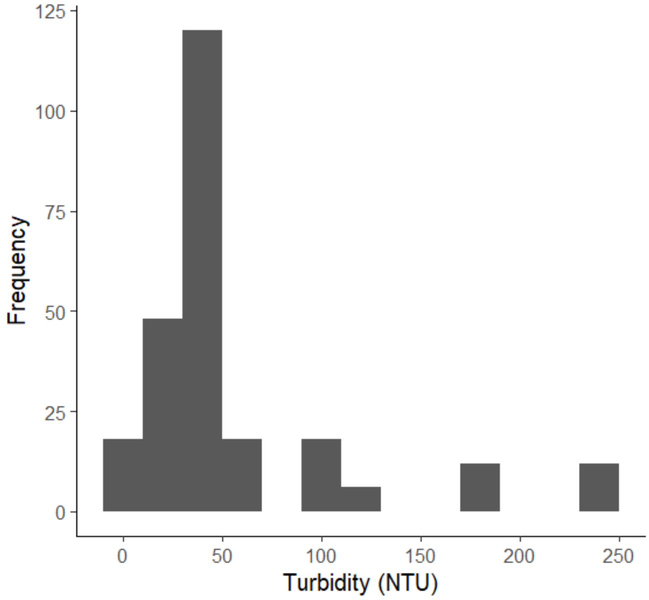
APPENDIX FIGURE 1. Frequency histogram showing distribution of number of submerged obstacles in wetlands located at Sapsucker Woods, Cornell Lab of Ornithology, Ithaca, New York, USA, where the sound propagation of underwater frog calls was evaluated.



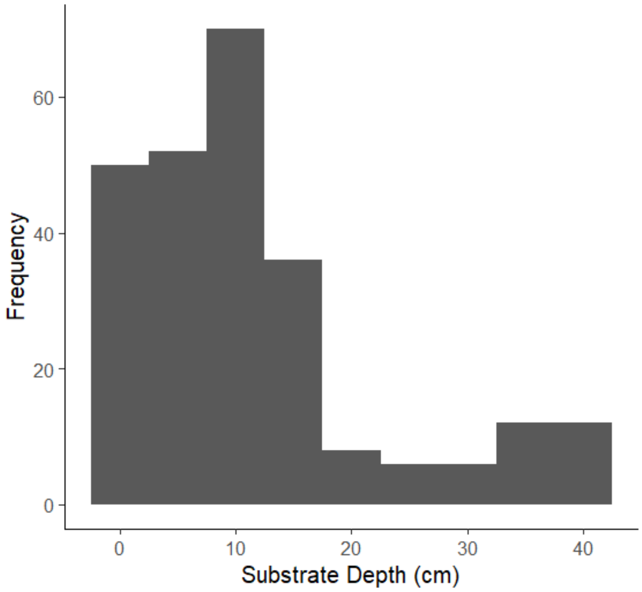
APPENDIX FIGURE 2. Frequency histogram showing distribution of water depth in wetlands located at Sapsucker Woods, Cornell Lab of Ornithology, Ithaca, New York, USA, where the sound propagation of underwater frog calls was evaluated.



Appendix Figure 3. Frequency histogram showing distribution of distance between speaker and hydrophones during trials conducted in wetlands located at Sapsucker Woods, Cornell Lab of Ornithology, Ithaca, New York, USA, to study the sound propagation of underwater frog calls.



Appendix Figure 4. Frequency histogram showing distribution of water turbidity in wetlands located at Sapsucker Woods, Cornell Lab of Ornithology, Ithaca, New York, USA, where the sound propagation of underwater frog calls was evaluated.



Appendix Figure 5. Frequency histogram showing distribution of substrate depth in wetlands located at Sapsucker Woods, Cornell Lab of Ornithology, Ithaca, New York, USA, where the sound propagation of underwater frog calls was evaluated.