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Evidence of sound production by spawning lake trout (*Salvelinus namaycush*) in lakes Huron and Champlain

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Abbreviation: digital spectrogram long-term acoustic recorders (DSG)

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Abstract

Two sounds associated with spawning lake trout (*Salvelinus namaycush*) in lakes Huron and Champlain were characterized by comparing sound recordings to behavioral data collected using acoustic telemetry and video. These sounds were named growls and snaps, and were heard on lake trout spawning reefs, but not on a non-spawning reef, and were more common at night than during the day. Growls also occurred more often during the spawning period than the pre-spawning period, while the trend for snaps was reversed. In a laboratory flume, sounds occurred when male lake trout were displaying spawning behaviors; growls when males were quivering and parallel swimming, and snaps when males moved their jaw. Combining our results with the observation of possible sound production by spawning splake (*Salvelinus fontinalis* × *Salvelinus namaycush* hybrid), provides rare evidence for spawning-related sound production by a salmonid, or any other fish in the superorder Protacanthopterygii. Further characterization of these sounds could be useful for lake trout assessment, restoration, and control.

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Introduction

Lake trout (*Salvelinus namaycush*) interest biologists and fishery managers worldwide because of their extraordinary diversity (Muir et al. 2015), recreational and commercial importance (Muir et al. 2013), and invasiveness (Crossman 1995; Ruzyski et al. 2003; Hansen et al. 2016). In the Laurentian Great Lakes, lake trout were historically the predominant top predator and an important commercial fish species (Baldwin et al. 2009; Muir et al. 2013). However, sea lamprey predation and overfishing led to near extirpation of lake trout in the early 1950s (Eschmeyer 1957; Muir et al. 2013). An extensive stocking program currently maintains lake trout populations in many areas of the Great Lakes, because natural recruitment remains low (Muir et al. 2013). In some large lakes of western North America such as Yellowstone and Flathead, lake trout are a damaging invasive species (Koel et al. 2005). Describing cues involved in reproduction could be beneficial by inspiring new management actions either to enhance reproduction where populations are valued or tactics that increase removal where populations are invasive (Zimmerman and Krueger 2009).

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Many fishes possess adaptations related to the production and detection of acoustic stimuli, and use acoustic stimuli to communicate, especially during reproduction (reviewed by Zelick et al. 1999; Kasumyan 2009). All fishes whose auditory sensitivities have been evaluated are able to detect low frequency sounds (up to 600 Hz; Popper 2003), with many species possessing specialized adaptations to detect much higher frequencies (Mann et al. 2001; Popper 2003; Popper & Fay 2011). Further, many teleost fishes can produce sounds via direct contact between bones, rapid contraction of specialized muscles near the swim bladder and pectoral girdle, and plucking of tendons (Kaatz 2002; Ladich 2004; Amorim 2006; Ladich et al. 2006; Kasumyan 2008). Eavesdropping on spawning fishes – termed passive acoustic sampling –

therefore can be a powerful approach to quantify spawning intensity, periodicity, and habitats for a range of teleost species (Luczkovich et al. 2008).

A role of acoustic communication in reproduction has been hypothesized for lake trout (Zimmerman and Krueger 2009), but has not been investigated. Lake trout spawn primarily at night (Muir et al. 2012), which indicates that spawning behaviors may be guided by nonvisual cues. Closely-related salmonids (*Coregonus lavaretus*, *C. nasus*, and *Salmo salar*) whose auditory sensitivities have been evaluated detect low frequency sounds with relatively low sensitivity compared to other species (Hawkins and Johnstone 1978; Amoser et al. 2004; Mann et al. 2007). Closely-related species can have substantially different acoustic sensitivities (Mann et al. 2001), so making comparisons among taxa is difficult. If lake trout also have low auditory sensitivity, acoustic communication could still be effective because spawning activity in lake trout may be associated with calm, likely low-noise, weather after storm events (Royce 1951; Muir et al. 2012; Callaghan et al. 2016). Lake trout also spawn in aggregations, possibly making even low sensitivity adequate for acoustic communication. Lake trout and brook trout (*S. fontinalis*) hybrids (splake) have been reported to produce sounds during spawning, either as active acoustic emissions or as a result of physical disturbance of substrate during spawning (Berst et al. 1981; Esteve et al. 2008).

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Our objective was to characterize sounds associated with lake trout spawning, given the hypothesis that sounds are produced by spawning lake trout to coordinate reproduction. We evaluated the predictions that follow as an initial test of this hypothesis: sounds associated with lake trout spawning should (1) be present during the spawning period on spawning reefs at night (when lake trout spawn; Muir et al., 2012), but not on non-spawning reefs, (2) be most common when spawning behaviors are directly observed on spawning reefs, and (3) be detected in a laboratory flume when spawning behaviors are observed. Prediction 1 was tested by deploying autonomous acoustic recorders in northern Lake Huron in the Drummond Island Lake Trout Refuge on well-characterized spawning and non-spawning reefs during the pre-spawning and spawning season (Binder et al. 2015, 2016). Prediction 2 was tested by deploying a time-synchronized acoustic recorder and video camera in Lake Champlain at a well-known spawning reef and correlating the presence of lake trout and their reproductive behaviors to specific sounds. Prediction 3 was tested by deploying a time-synchronized acoustic recorder and video camera in a laboratory flume where lake trout were actively displaying spawning behaviors.

Methods

Prediction 1: Sounds associated with lake trout spawning should be present during the spawning period on spawning reefs at night, but not at nearby non-spawning reefs.

Hydrophone deployment

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Four digital spectrogram long-term acoustic recorders (DSG; Loggerhead Instruments Inc., Sarasota, FL) were deployed in the Drummond Island Lake Trout Refuge between 16 Oct 2014 and 14 Nov 2014; two were deployed at locations where lake trout are known to spawn annually and two were deployed at locations with similar substrate that are known not to be used by lake trout for spawning (Fig. 1; Binder, personal observation). Evidence of spawning was based on the presence of eggs. The DSGs were secured to concrete blocks using cable ties and the hydrophone component of the DSG was positioned parallel to the bottom. To control for environmental noise such as rain and waves, all sites were less than 3.5 m deep, had rocky substrate, and were equally susceptible to wave action (large waves typically come from the south and east at these sites). Based on egg surveys (S. Farha, personal observation), and fine-scale positional acoustic telemetry tracking of 101 tagged lake trout detected during the 2014 spawning season (see Binder et al. 2016 for full methodological details), lake trout spawning peaked between 27 October and 01 November, but trout were present on the reef starting in early October and until at least mid-November when the hydrophones were removed (Binder et al. 2016).

Data subsampling

Limitations on data storage precluded continuous recording during the deployment period, so the DSGs recorded three minutes out of every ten. For example, data were recorded from 0800 to 0803, not recorded from 0803 to 0810, recorded again from 0810 to 0813, and so on during the deployment period. DSG 1202 failed shortly after deployment, so data were only available from one spawning reef. Analyzing all the sound files was not possible given the staffing available, so the data were subsampled such that there were sufficient data on which contrasts between location (spawning versus non-spawning), spawning period (pre-spawning versus spawning), and time of day (night versus day) could be evaluated (Table 1).

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Data processing

Individual sounds were discriminated and analyzed directly from the field recordings. The software package Goldwave (http://www.goldwave.com/features.php, Goldwave Inc., St. John’s, Newfoundland) was used to visualize and archive sounds of interest. Before quantifying the occurrence of specific sounds, random sections of data from different DSGs and times were scanned to determine how many different types of sounds were present. For each type of sound that showed repeatability in the data files, we archived representative examples and gave the sound anthropomorphic descriptions such as growl, snap, or click.

After the initial qualitative survey to determine what sound types were present, the number of occurrences of each sound type was quantified in 3-min intervals during specific dates and times (Table 1**).** A single person reviewed and characterized sounds to reduce observer bias between sampling periods.

Data analysis

For each type of sound classified, we manually evaluated whether the frequency of occurrence of that sound, defined as the number of times each sound occurred during each 3 min clip subsampled from each time period, varied with hydrophone deployment site (spawning or non-spawning), period (pre-spawning or spawning), and time of day (night or day) using general linear models. Specifically, to determine if a sound was more frequently observed at the spawning site versus the non-spawning site during the spawning period at night, data IDs 2 (spawning) and 4+5 (non-spawning) as presented in Table 1 were contrasted. To determine if a sound at the spawning site during the spawning period was more frequently observed at night than during day, data IDs 2 and 3 were contrasted. To determine if a sound at the spawning site at night was more common during the spawning season than during the non-spawning season, data IDs 1 and 2 were contrasted. Model assumptions of residual heteroscedasticity were evaluated and, if needed, data were square-root transformed (in this case growls and snaps needed transformation).

Prediction 2: Sounds associated with lake trout spawning will be most common when lake trout and their spawning behaviors are observed.

Hydrophone and camera deployment

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Time-synchronized sound and video data were collected at a known lake trout spawning site in Lake Champlain (Gordon Landing breakwall) to link specific sounds to the presence of lake trout and their spawning behaviors. This was also done to investigate if other fishes such as lake whitefish (*Coregonus clupeaformis*) and burbot (*Lota lota*) co-occur with spawning lake trout at this site and could be the source of the sounds. The Gordon Landing breakwall is a small spawning reef (570 m^2) in 0.3-4.0 m of water with substrates consisting of angular rubble and cobble (Ellrott and Marsden, 2004). A DSG and underwater camera (960H 170° Ultra-Wide Angle Color Bullet Camera with 2.2mm lens, Speco Technologies, North Lindenhurst, New York) connected to a shore-side DVR (Compact 4 Channel H.264 Mobile SD Card DVR Recorder, Super Circuits, Austin, Texas) and monitor (Foldable TFT-LCD Color Monitor, E-Best) were deployed from 31 Oct 2015 to 10 Nov 2015 at the outer end of the breakwall. This site was chosen because it allowed us to tend and power the video equipment from land, which allowed for longer video recording times. To obtain video images at night, 2 LED flood lights (Laguna Power Glo, Laguna Ponds, Mansfield, MA) with red filter lenses (Laguna Color Lens, Laguna Ponds, Mansfield, MA) were used to illuminate the reef without apparent disruption to lake trout behavior. Divers deployed and retrieved the gear and did not observe lake trout eggs when the equipment was deployed, but observed eggs when it was retrieved. The camera was able to monitor approximately 25% of the reef, but the hydrophone likely detected all sounds produced in association with spawning at that reef, although no range tests were conducted. As such, sounds detected on the hydrophone could have been produced by lake trout that were not visible on the camera, making correlation of specific sounds to specific behaviors tenuous.

Data subsampling and analysis

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Poor video quality due to turbidity and condensation on the camera lens precluded analysis of the complete video record. Sound data were also compromised at times by environmental and anthropogenic noise (waves and boat traffic). Despite these challenges, high quality video and sound data were obtained during most of the time between 08 Nov and 10 Nov, so we subsampled time-synchronized video and hydrophone data during the 1-hr period after each of the following times: 2000 on 08 Nov 2016, at 0000, 0600, 0800, 1200, and 1600 on 09 Nov 2016, and 0400 and 0900 on 10 Nov 2016, such that each 1-hr period was sampled once between 08 Nov 2016 and 10 Nov 2016; by doing so, we were able to contrast sound and behavior data though time across these three dates. The data from these hours were subsampled in the same way as described for prediction one; three minutes out of every ten were sampled where 0800 to 0803 was sampled and 0803 to 0810 was not sampled. We referenced previous reports (Esteve et al. 2008; Muir et al. 2012; Binder et al. 2015) to define specific behaviors to quantify: (1) follow: a lake trout swimming in the same direction within close proximity to another swimming lake trout; (2) parallel swim: two lake trout swimming side by side, usually very close to or touching one another, while keeping the same speed and directional movements; (3) quiver: two or more lake trout position themselves near bottom, cease swimming, and one fish initiates low-amplitude lateral vibratory movements, triggering quivering in the other fish that may continue for two to three seconds; (4) bubble release: release of bubbles through the gills or mouth; (5) nudge: one lake trout, with mouth closed, butts, snout hitting against the side of another fish, which can be a gentle or aggressive behavior; (6) nip: one lake trout opens mouth and closes jaws against a part of the body of another fish; (7) jockey: two or more males attempt to occupy closest position to a single female while swimming just above the bottom; (8) mouth snapping: a lake trout opens mouth and quickly closes jaws. A single observer reviewed and

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characterized sounds (same person as prediction 1). A second observer estimated fish abundance and the frequency of occurrence of individual behaviors. Using the underwater lights as reference points, we only recorded fish and their behaviors if they were within 5 m of the camera because that was the extent of our night viewing capabilities.

To determine if sounds heard on the hydrophones were related to specific spawning behaviors, the number of specific sound types heard during each 3-min period (response variable) was correlated with the number of lake trout and their display of spawning behaviors (explanatory variables) during that same 3-min period using general linear models. Correlation among explanatory variables (fish and their behavior) seemed likely, so Pearson rank correlation analyses were conducted prior to developing a full model including all possible predictors. If predictors were highly correlated, individual models contrasting the occurrence of a sound with a single explanatory variable (e.g., fish, following behavior) were constructed. Candidate models were evaluated using Akaike information criteria (AIC; Burnham and Anderson, 2002), where weighted Akaike information criteria (wiAIC) were used to determine which explanatory variable best explained variability in the response, where $wiAIC = -2\ln(L) + 2k$ (Wagenmakers and Farrell 2004). Model assumptions of residual heteroscedasticity and normality were met without transforming the response variables (snaps and growls).

Prediction 3: Sounds associated with lake trout spawning will be detected in a lab when spawning behaviors are observed.

Experimental flume and lake trout

Laboratory experiments were conducted in the flume bioassay described in Buchinger et al. (2015) during the nights of 13 Dec 16, 14 Dec 16, and 15 Dec 16 with sexually mature male Seneca Strain lake trout obtained from United States Fish and Wildlife Service, Sullivan Creek

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National Fish Hatchery and sexually mature female lake trout obtained directly from northern Lake Huron via angling. Sex and reproductive state were determined by expression of gametes. Briefly, the flume was 2.5 m × 1.85 m × 0.6 m, and had a water velocity of 0.014 m·s−1, and was supplied with Lake Huron water at 4° C that originated from a deep-water intake (25 m). To provide spawning substrate, reefs were constructed (1.5 m × 0.85 m × 0.13 m) at the upstream end of the flume using rock 10-20 cm in diameter. Each night, three males (680 mm – 835 mm) and one female (660 mm - 710 mm) were placed into the flume from sunset to about 5 hours after sunset. Lake trout behavior was observed using infrared lights (IRLamp6; www.batmanagement.com) and overhead night-vision video (Axis Q1604). Sounds were observed using a hydrophone (HTI-96-MIN; Sensitivity = 165dB/re 1µPa; High Tech Inc. Long Beach MS, USA) and recorder (Tascam, Linear PCM Recorder, DR-05) that was time synched with the video camera to the nearest second. The hydrophone was suspended 5 cm below the water surface in the center of the experimental raceway.

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Data analysis

The frequency of specific sound types and their association with specific lake trout spawning behaviors were summarized. First, all sound data collected were reviewed using Goldwave as described in the methods for predications 1 and 2. Then, an observer reviewed lake trout behavior 2.5 sec before and after each specific sound, noting spawning behaviors (following, parallel swim, quiver…etc) as described in the methods for prediction 2.

Results

Prediction 1: Sounds associated with lake trout spawning should be present during the spawning period on spawning reefs at night, but not at nearby non-spawning reefs.

Nine distinct sounds were classified (knock, rock, growl, thump, click, snap, scrape, burp, and gulp), of which snaps, growls, and gulps were heard exclusively at the Drummond Island spawning reef, so only those three sounds were of interest as lake trout spawning sounds (Table 2). Gulps, while being exclusively detected at the spawning reef, were relatively rare, were likely environmental noise, and were not heard at the Lake Champlain site (see prediction 2). However, snaps and growls were recorded frequently at both locations and were regular in acoustic structure and therefore were further characterized. Snaps and growls were similar in duration (approximately 1.5 s; Fig. 2), but snaps had a stable frequency distribution up to approximately 170 Hz without a clear dominant frequency within that range (Fig. 2D). Growls were of lower frequency, with peak frequencies at 20 and 50 Hz and little energy above 100 Hz (Fig. 2B).

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During the spawning period on the Drummond Island reef, growls and snaps were heard at higher rates at night than during the day (growls: $t = 7.32$, $p < 0.001$; snaps: $t = 3.57$, $p < 0.001$), whereas gulp rates did not vary with time (Table 2; gulps: $t = 0.17$, $p = 0.867$). The frequency of growls was higher during the spawning period at night than during the pre-spawning period at night (growls: $t = 7.38$, $p < 0.001$), but the frequency of snaps was higher during the pre-spawning period than the spawning period ($t = 2.64$, $p = 0.009$). The frequency of gulps did not differ between pre-spawning and spawning periods (gulps: $t = 0.32$, $p = 0.746$).

Prediction 2: Sounds associated with lake trout spawning will be most common when lake trout and their spawning behaviors are observed.

As in Lake Huron, snaps and growls were also heard at the lake trout spawning site in Lake Champlain during the spawning season and were most common at night (Fig. 3;

Supplemental sound files S1 and S2; Supplemental video 1). No other fish species were observed on our camera except for a few schools of yellow perch (*Perca flavescens*) during the day; American eels (*Anguilla rostrata*) were also observed at the site on a different camera. Gulps were not heard and were thus dismissed as an artifact of the sampling location at the Drummond Island spawning reef. Lake trout were observed on the camera at all times of day, but were much more abundant during the night (Fig. 3). Of all the lake trout spawning behaviors quantified, only following, parallel swimming, and jockeying were observed frequently (roughly between 5-40 individual behaviors each 3 min). An inability to consistently observe other spawning behaviors was likely a function of the high density of lake trout present at night and the limited viewing distance of the camera (lake trout courting and spawning can occur over tens of meters; Supplemental video 1).

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The number of fish, follows, parallel swims, and jockeying observed during each 3-min period were positively correlated (Pearson correlation coefficient greater than 0.42 and p-value <0.001 for all contrasts; Fig. 4), so AIC was used to determine which individual response variable best explained variability in snaps and growls. For both snaps and growls, number of lake trout observed best explained variability (Table 3). Of the other explanatory variables evaluated, parallel swimming ranked second for explaining the number of snaps and jockeying ranked second for explaining the number of growls.

Prediction 3: Sounds associated with lake trout spawning will be detected in a lab when spawning behaviors are observed.

Snaps and growls were observed in a laboratory flume containing lake trout displaying spawning behaviors (Table 4). Most sounds were observed when lake trout were moving (~70 – 80%) and most of the movement was attributed to the males (~60-80%; Table 4) rather than the female. While specific sounds were not always associated with specific spawning behaviors, about 50% of the snaps were associated with nudging and jaw movements (nips and snaps; supplemental video 2) and about 70% of the growls were associated with quivering and parallel swimming (Fig. 5; Supplemental video 3).

While reviewing the sound data, a third sound, herein named thump, was often heard (Table 4). Thumps sounded similar to growls, with the primary difference being that thumps were singular and growls resembled drawn-out drumming. Thumps were characterized as sounds of approximately 0.1-0.15 s duration with peak frequency of 60-70 Hz and a rapid fall-off of acoustic energy with increasing frequency above 100 Hz (Fig 6). Thumps were generally not associated with a specific behavior and were heard when lake trout were following, parallel swimming, nudging, moving their jaws, and quivering (Supplemental video 4). Although the lake trout displayed mating behaviors in the flume, no eggs were deposited during these experiments.

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Discussion

Our results provided evidence for sound production by lake trout during reproduction. Two sounds, snaps and growls, were recorded from populations of lake trout in northern Lake Huron and Lake Champlain. Snaps and growls were observed exclusively at lake trout spawning reefs, were more common at night, and were directly correlated with lake trout spawning behaviors. Furthermore, snaps, growls, and thumps were heard in a laboratory flume at specific times when lake trout displayed mating behaviors. Combining our results with the observation of possible sound production by spawning splake (*Salvelinus fontinalis* × *Salvelinus namaycush* hybrid; Berst et al. 1981), provided rare evidence for sound production by a salmonid, or any other fish in the superorder Protacanthopterygii (Neproshin et al. 1974; Fine and Parmentier 2015).

The sounds recorded suggested sound-producing mechanisms other than simple physical contact between lake trout and the substrate, or among conspecifics. Berst et al. (1981) documented three sound types when observing spawning splake: (1) 'clicks', a sound between 500 and 1200 Hz with a duration of about 0.10 s and suspected to be produced by the jaw closing, (2) 'thumps', a sound between 100 and 3000 Hz with a duration of 0.10-0.35 sec and suspected of being produced by the swim bladder, and (3) a sound between 50 and 500 Hz and a duration of 1.5 sec. The snaps and growls described in our study were much longer in duration and lower in frequency than 'clicks' and 'thumps' described in Berst et al. (1981), and most closely resemble sound (3) above. However, sound-generating mechanisms were not investigated by Berst et al. (1981) nor in our study, and remain unknown. Nonetheless, the "growls" presented here are similar in structure to sounds recorded from other species that use swim bladder vibrations to produce sounds (Saucier and Balz, 1993; Connaughton and Taylor, 1995; Ramcharitar et al. 2006). Indeed, growls occurred at times in the lab when male lake trout were parallel swimming, indicating that physical contact between two fish or fish and the substrate may not be required to produce growls. The snap sounds were higher in frequency than typical swim bladder sounds, but sounds produced by other fish species have often been reported at these frequencies (reviewed in Ladich 2004; Kasumyan 2008). Snaps were also observed in the lab when lake trout moved their jaws, but also when lake trout were nudging and when lake trout were displaying no specific spawning behaviors. Both sounds recorded at the lake trout spawning areas were also recorded frequently in the lab and were regular in acoustic structure, suggesting that some of them were volitional sounds. The "thunps" recorded in our lab study are

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of the same duration as sound (3) in Berst et al. al. (1981) and may represent the same sound type. While burbot, another known sound-producing species, co-occur with lake trout, their sounds are much different than the sounds recorded here and occur during the February spawning period (Cott et al. 2014), so given these differences and the lack of burbot in our video observations, we are confident that the sounds collected were not from burbot.

Communication associated with mating generally serves to find or select mates. Many species use visual, olfactory, or auditory cues to attract or aggregate potential mates (Atema et al. 1988; Sargent et al. 1998). Lake trout may form spawning aggregations simply based on mutual attraction to substrate that will support egg incubation (i.e., visual or hydrological cues, Marsden and Krueger 1991); smell has been hypothesized to also play a role in attracting lake trout to spawning sites (Foster 1985, Buchinger et al. 2015). However, sound likely transmits further in water than visual cues of substrate, and could serve to aggregate lake trout at a spawning site. Lake trout do not spawn en masse; females spawn with one to several males who have accompanied them in pre-spawning movements (Muir et al. 2012). Behavioral theory suggests that females of species that have a high investment in their gametes or offspring should be picky about choosing mates (Clutton-Brock and Vincent 1991; Barbosa and Magurran 2006), but how mate selection occurs in lake trout is unknown. Therefore, a second possible function of sound production in lake trout may be an element of courtship signaling by males.

The seasonal and diel patterns of sound production, and spawning behaviors associated with snaps and growls in the lab and field, hint at their source and behavioral relevance. At Drummond Island Reef, snaps were more common during the pre-spawning period than the spawning period despite similar numbers of lake trout being present (Fig. 1). We speculate that snaps may be produced primarily by males, who aggregate at spawning locations several weeks

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prior to spawning and the arrival of females (Muir et al. 2012); snaps may signal to females the presence of spawning substrate, availability of a number of potential mates, and may also be an aggressive signal among males. Indeed, our laboratory analysis found that snaps occur when males close their jaw, often during male-to-male conflicts, but can also occur when males nudge each other. Growls were relatively uncommon during the pre-spawning period, but very common at night during the spawning period, and may be produced by either sex during courtship or spawning. As such, they may be intentional signals that serve to attract mates or repel competitors, or may simply be produced incidentally while expressing gametes; for example, Pacific salmon gape widely during spawning (Esteve 2005), though any associated sounds have not been recorded. Our laboratory experiments show that growls were most common when quivering, but also occurred when male trout were parallel swimming (limited physical contact). Interestingly, snaps and growls were predominantly detected at night, but telemetry and video data from both populations show that lake trout were still present on the spawning reefs during the day. Therefore, the presence of lake trout alone does not explain our recordings of snaps and growls on spawning reefs; instead, sounds were associated with lake trout that were actively spawning. While our results allow speculation on the behavioral function of sounds produced by spawning lake trout, many questions remain regarding the mechanism and context of sound production, and the detection and response to sounds produced by conspecifics.

The quantity of snaps and growls detected at the Gordon Landing breakwall was 10 – 20 times greater than that detected at Drummond Island spawning reef, which may have been due to a higher density of spawning lake trout at Gordon Landing. However, we do not know the actual number of lake trout that used each reef, and so cannot accurately calculate lake trout density.

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Regardless, we observed over 100 trout per minute within 5 m of our camera during the night at Gordon Landing, so many lake trout were present. The exceptionally high density of lake trout at the Gordon Landing breakwall in Lake Champlain resulted in lake trout obscuring the behaviors of other individuals behind them. This, and the limited observational viewing distance of the camera likely explained why we observed few spawning events at the Gordon Landing breakwall like those described by Muir et al. (2012) and Binder et al. (2015)

Understanding the acoustic biology of lake trout may have direct implications for lake trout managers and ecologists. In the broadest sense, describing cues used during reproduction will offer insights into variables that drive recruitment and genetic diversity (Zimmerman and Krueger 2009). In field applications, passive hydrophones could be used to survey locations and timing of spawning, determine if spawning is correlated with environmental variables (changes in temperature, wind, or waves), or gather species-specific and sometimes individual-specific behavioral data (Rountree et al. 2006, references therein). Accurate and cost-effective assessment data are needed to monitor lake trout restoration efforts in the Great Lakes and control efforts in western North America. Passive acoustic monitoring seems especially viable given that snaps and growls were associated with lake trout spawning behaviors (not just the presence of non-spawning lake trout), and the sounds were observed in a diel pattern consistent with lake trout spawning activity. Acoustic stimuli could also be used to increase use of artificial or restored spawning habitats, as has been suggested for putative olfactory stimuli (Buchinger et al. 2015) or concentrating trout in areas where they are being fished for control in western North American lakes (Hansen et al. 2016). Combinations of olfactory and auditory stimuli could elicit stronger behavioral responses (Kasurak et al. 2012). An understanding of the acoustic biology of lake trout may also be relevant for policy makers. Anthropogenic noises often interfere with

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acoustic communication in fishes (*e.g.,* shipping, offshore windmills, energy exploration; Popper 2003) and the same could be true for lake trout if they use sound to coordinate reproduction.

In summary, we provide evidence that sounds are produced by spawning lake trout and these sounds could be an important aspect of their reproductive ecology. The mechanisms by which these sounds are produced, the ability of conspecifics to hear the sounds produced, and the ecological role of sound communication remain unclear. Continued research in the lab and field will reveal whether monitoring or manipulating sounds may be useful for lake trout assessment, restoration, and control, and provide insights into sound communication by taxa believed to rely more on visual and chemical signals during reproduction.

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Table 1. Subsampling scheme for data obtained from digital spectrogram long-term acoustic recorders deployed in Lake Huron at Drummond Island Lake Trout Refuge during 2014. Acoustic recorders were deployed on lake trout spawning and non-spawning reefs (Location), and data were contrasted before and during the spawning season (Period; pre-spawning = 16Oct14 and 18-20Oct14; spawning 28Oct14-01Nov14), between night and day (Time), and from spawning and non-spawning reefs. Within each time period, only 18 min per hour were sampled because of limitations of data storage. For example, during the 1200 hour, sounds were recorded from 1200 to 1203, not recorded from 1203 to 1210, recorded again from 1210 to 1213, and so on and so forth. The total hours sampled for each period are reported (Total Hours).

Data ID	Hydrophone	Dates	Location	Period	Time	Total Hours
1	1206	16, 18-20 Oct	Spawning	Pre-spawning	0000-0203, 0400-0503	3.6 h
2	1206	28Oct-01Nov	Spawning	Spawning	0000-0203, 0400-0503	3.6 h
3	1206	28Oct-01Nov	Spawning	Spawning	1200-1403, 1600-1703	3.6 h
4	1205	28Oct-01Nov	Non-spawning	Spawning	0000-0203	2.4 h
5	1203	28Oct-01Nov	Non-spawning	Spawning	0000-0203	2.4 h

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Table 2. Mean number of each type of sound detected per 3 minutes of observation at different locations (non-spawning sites, n=2; spawning site, n=1), spawning periods (pre-spawning versus spawning), and times of day (day versus night) at in Lake Huron near Drummond Island during 2014. Standard deviation of the mean is presented in parentheses. Down the column for each sound type, periods and times with different letters were significantly different as determined by general linear models.

Site	Period	Time	Snap	Growl	Gulp
Non-spawning	Spawning	Night	0	0	0
Spawning	Spawning	Night	0.78 (0.98) b	1.67 (2.27) b	0.11 (0.55) a
Spawning	Spawning	Day	0.21 (0.46) a	0.25 (0.48) a	0.06 (0.25) a
Spawning	Pre-spawning	Night	1.22 (1.67) c	0.22 (0.47) a	0.09 (0.28) a
		F-statistic	18.2	36.9	0.1
		df	2/272	2/272	2/272
		P-value	<0.001	<0.001	0.889

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Table 3. Candidate models explaining variability in the number of snaps and growls (response variable) that were heard in Lake Champlain at the Gordon Landing breakwall during 2015. Possible explanatory variables included visual observations of the number of lake trout observed and their spawning behaviors (Following, Parallel swimming, and Jockeying). Ranks were determined by weighted AIC (Wi) which were calculated from differences (Deltai) in Akaike's Information Criterion (AIC) values.

Response Variable	Explanatory Variable	F-statistic	p-value	R^2	AIC	Delta i	Wi	Rank
Snap	Trout	29.92	<0.001	0.34	357	0	0.83	1
Snap	Following	22.16	<0.001	0.25	363	5	0.08	3
Snap	Parallel swimming	22.68	<0.001	0.28	362	5	0.09	2
Snap	Jockeying	5.12	0.027	0.07	377	20	0.00	4
Growl	Trout	39.00	<0.001	0.41	394	0	0.83	1
Growl	Following	12.69	<0.001	0.18	413	19	0.00	4
Growl	Parallel swimming	22.64	<0.001	0.28	405	11	0.01	3
Growl	Jockeying	31.70	<0.001	0.36	399	5	0.11	2

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Table 4. The number of snaps, growls and thumps heard per hour at night in a laboratory flume stocked with 3 sexually mature males and 1 sexually mature female lake trout. Also reported is the % of times that lake trout were observed moving in the flume when the sound was detected. If lake trout were moving during the sound, the number of times only males were moving is reported. Numbers in parentheses are the standard deviation.

Sound	Number per hour	% of times fish moving when sound occurred	% of times only males were moving
Snap	6.4 (2.9)	67% (9%)	55% (16%)
Growl	9.5 (5.4)	77% (18%)	78% (20%)
Thump	12.0 (4.1)	80% (8%)	73% (20%)

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Figure Captions

Fig. 1. (a) Locations where digital spectrogram long-term acoustic recorders (DSG) were deployed at Drummond Island Lake Trout Refuge. Bathymetry is illustrated by color coding. The Lake Huron inset is not to scale. (b) The number of positions obtained from lake trout with acoustic telemetry transmitters during the pre-spawning (open bars) and spawning period (shaded bars) within 100 m of each DSG. (c) The number of positions obtained from lake trout with acoustic telemetry transmitters during the spawning period during the day (open bars) and night (shaded bars) within 100 m of each DSG. The numbers on top of the bars in (b) and (c) are the number of individual males and females detected within 100 m of each DSG during the specified period. The line within some bars in (b) and (c) illustrate the number of telemetry positions obtained from males and females; below the line are detections from females. Acoustic telemetry data are described in Binder et al. 2016.

Fig. 2. Waveforms (a & c) and frequency analysis (b & d) for representative growl (a & b) and snap (c & d) sounds recorded from lake trout spawning reefs. Inset diagrams in b and d represent the frequency distribution of each call from 0-500 Hz, the frequencies representing the main call energy for both calls. Power spectra were created with a Fast Fourier transform (FFT) filter size of 16384 with a Hanning window.

Fig. 3. Mean number of snaps, growls, and fish recorded during three days at a spawning site associated with the Gordon Landing breakwall, Lake Champlain during November 2015. Number of lake trout is presented as 0.1X the actual observations. Snaps and growls are presented as the number recorded during 3-minute sampling intervals. Error bars represent the standard deviation.

Fig. 4. Occurrence of snaps (top) and growls (bottom) as explained by the observed number of lake trout follows, parallel swims, and jockeys at a spawning site associated with the Gordon Landing breakwall, Lake Champlain during November 2015. Number of lake trout is presented as 0.1X the actual observations. Snaps and growls are presented as the number recorded during 3-minute sampling intervals.

Fig. 5. Percent of snaps, growls, and thumps that occurred with specific lake trout spawning behaviors (see methods) in an laboratory flume during December 2016. Jaw movement combines both nips and snaps as defined in the methods. 'No behavior' means that lake trout were moving in the flume, but not displaying any of the specific spawning behaviors defined in the methods. Error bars represent the standard deviation.

Fig 6. Waveforms (a) and frequency analysis (b) for representative thump sounds recorded from concrete raceways containing 3 male and 1 female lake trout. Inset diagram in b represents the frequency distribution of the call from 0-500 Hz, with the frequencies representing the main call energy. Power spectra were created with a Fast Fourier transform (FFT) filter size of 16384 with a Hanning window.

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Supplementary Material for Johnson et al., *Can. J. Fish. Aquat. Sci.*

Sound file S1: Representative example of a snap as recorded at the Gordon Landing breakwall spawning site in Lake Chaplain and illustrated in Figure 2a of the primary manuscript.

Sound file S2: Representative example of a growl as recorded at the Gordon Landing breakwall spawning site in Lake Chaplain and illustrated in Figure 2b of the primary manuscript.

Sound file S3: Representative example of a thump as recorded in concrete raceways at Hammond Bay Biological Station and illustrated in Figure 6 of the primary manuscript.

Supplementary video 1: Representative example of image and sound data captured from Lake Champlain during 2015. Need sound amplification

Supplementary video 2: Representative examples of snaps and associated lake trout spawning behaviors as observed in a laboratory flume.

Supplementary video 3: Representative examples of growls and associated lake trout spawning behaviors as observed in a laboratory flume.

Supplementary video 4: Representative examples of thumps and associated lake trout spawning behaviors as observed in a laboratory flume.

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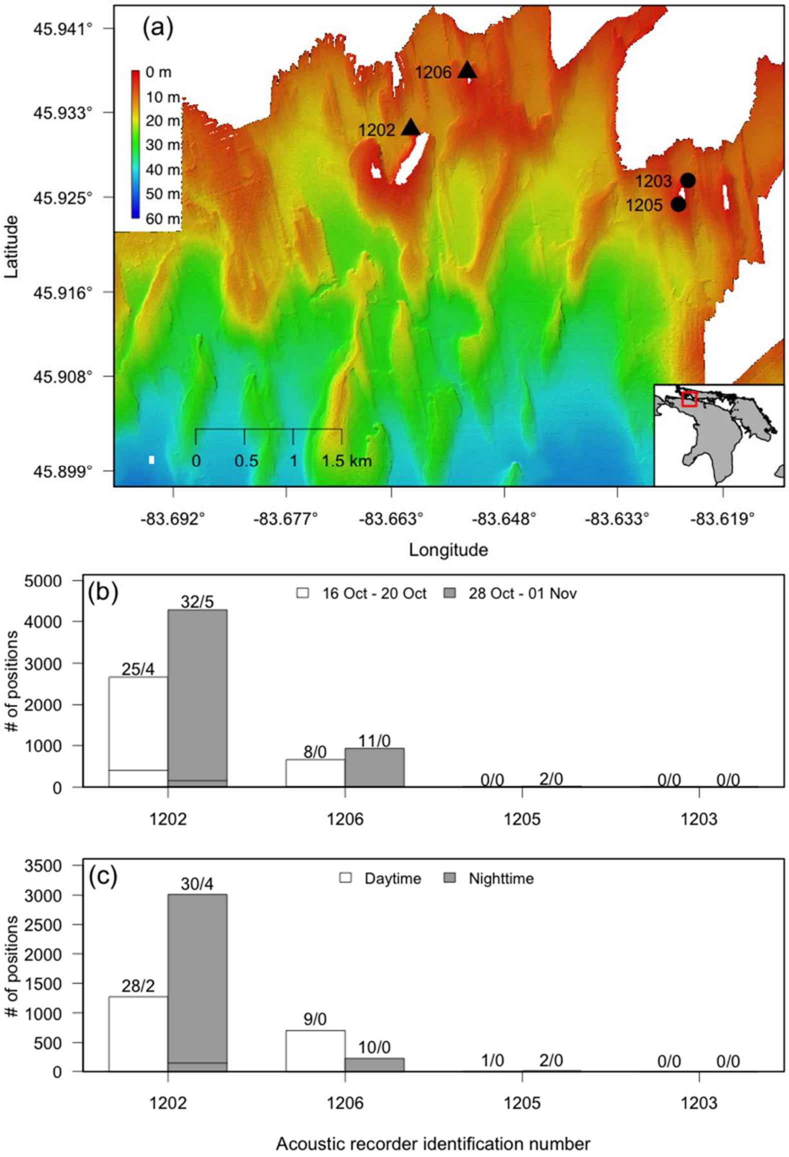

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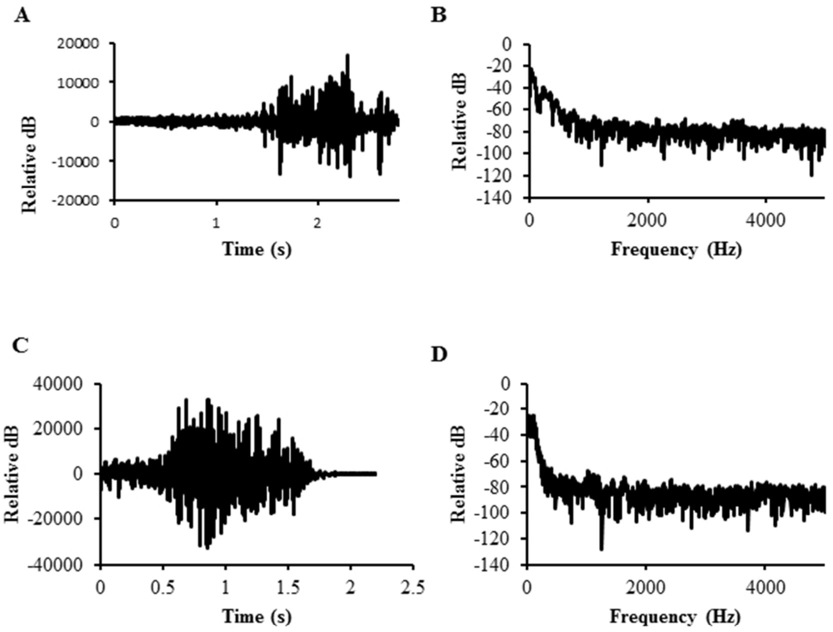

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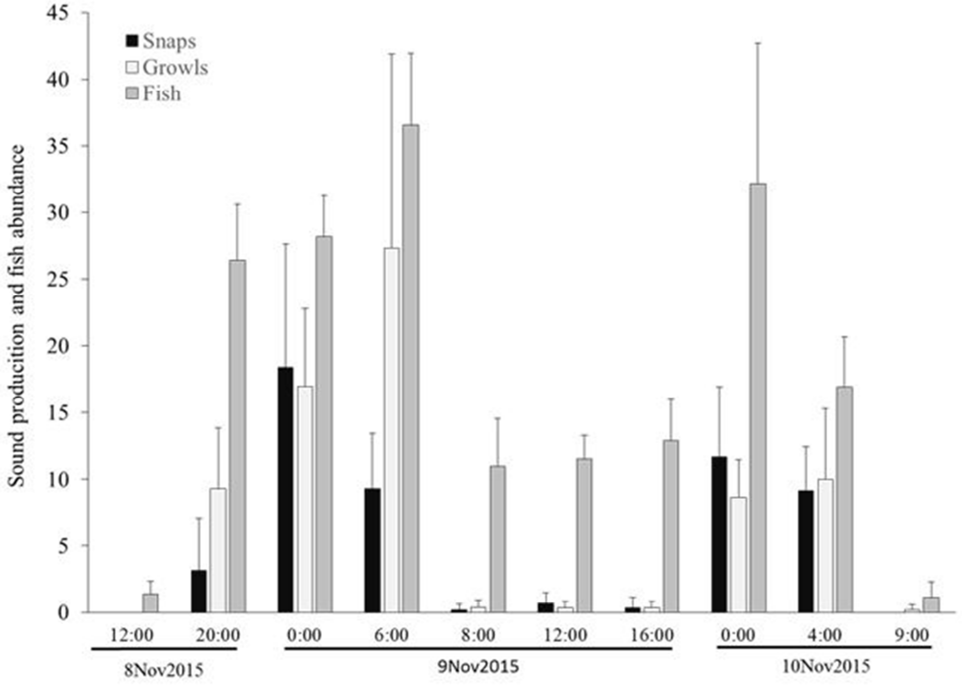

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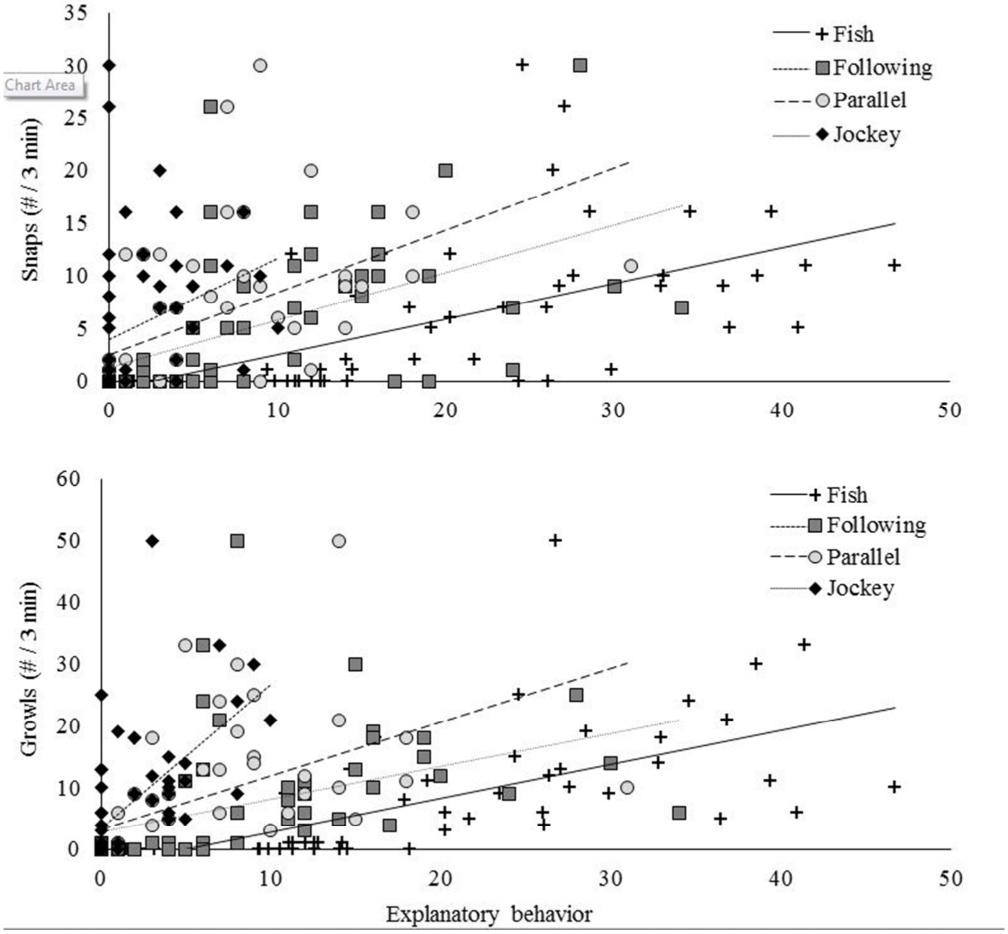

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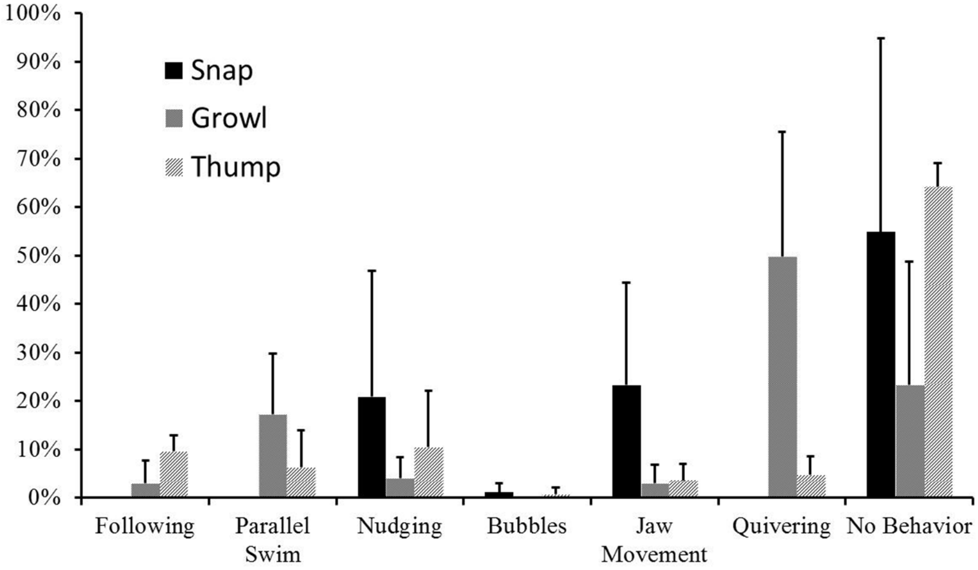

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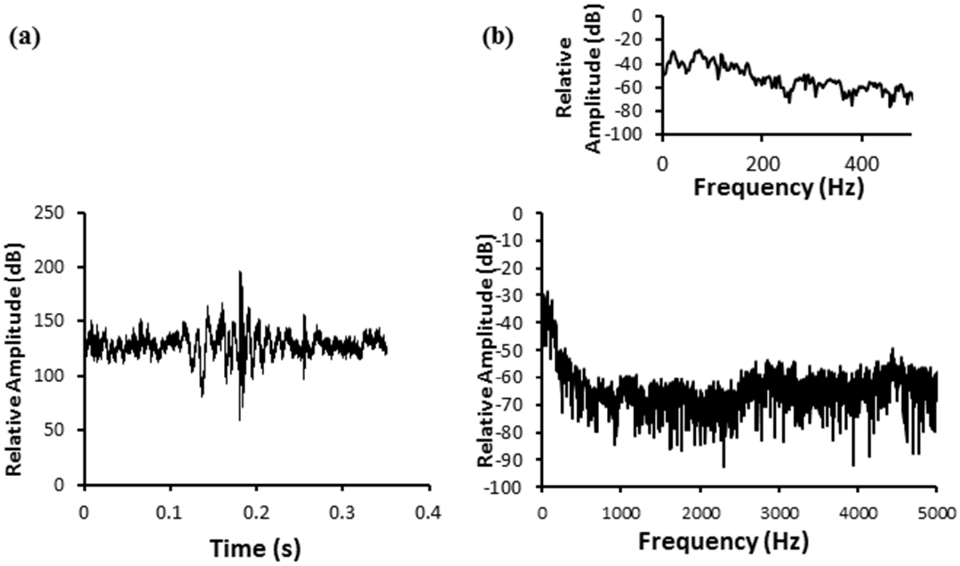

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181x105mm (96 x 96 DPI)