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Hearing capabilities and behavioural response of sea lamprey (*Petromyzon marinus*) to low frequency sounds

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Abstract:

Hearing ability is well studied across teleost fishes in general, and vertebrates more broadly, but little is known about sound detection abilities of lampreys (Petromyzontiformes), a basal extant vertebrate group. The sea lamprey (*Petromyzon marinus*) is a destructive invader of the Laurentian Great Lakes, while numerous lamprey species (including the sea lamprey) are imperiled in their native ranges. In both management scenarios, behavioral manipulation tactics to control movement and distribution are desired. Therefore, we describe the hearing ability and behavioral responses of adult and juvenile sea lamprey to sound to reveal how hearing may have evolved in vertebrates and determine possible management applications. Based on auditory evoked potentials, sea lamprey detected tones from 50-300 Hz with equal sensitivity, but did not detect sounds above 300 Hz. In a laboratory bioassay, sea lamprey behaviorally responded to sound from 50-200 Hz, with a general increase in swimming and a decrease in resting behaviours at both juvenile and adult stages relative to no-sound controls. To our knowledge, this is the first test of lamprey hearing and the results support that sound may be a means to modify lamprey behaviour for management purposes.

48 **Introduction:**

49 Sound is an important sensory modality for fish and is commonly used for predator/prey
50 detection, courtship/mating, and alarm cues (Fay & Popper 2000; van der Sluijs et al. 2011).
51 Hearing abilities vary widely between species, as some species exhibit general hearing
52 capabilities whereas others have specialized structures allowing them to hear a wider range of
53 sounds (Popper et al. 2003), but all species tested to date have some ability to detect and respond
54 to sound and it is likely a basal trait across vertebrates (Fay & Popper 2000).

55 Hearing ability can be measured either physiologically or behaviourally and while neither
56 technique is perfect, together they provide a more comprehensive measure of hearing. One
57 commonly used physiological technique for baseline hearing ability is the “Auditory Evoked
58 Potential” (AEP) technique. This technique measures electrical activity in the auditory brainstem
59 as a differential response between two electrodes in intact fish, (Kenyon et al. 1998; Ladich &
60 Fay 2013) and has a long history in hearing studies across a wide range of vertebrates (*e.g.* Jock
61 et al. 1996; Nachtigall et al. 2007). While not appropriate for true hearing thresholds, AEP can be
62 useful for a quick assessment of what frequencies can be detected by a given species. Based on
63 the presumed hearing range of a species using the AEP technique, behavioural studies can then
64 be performed to determine responses to detectable sounds.

65 Surprisingly, a systematic physiological evaluation of sound detection has not been conducted to
66 date for any agnathan, despite their importance for evolutionary studies. The ear of the sea
67 lamprey (*Petromyzon marinus*) possesses auditory hair cells and a large statolith in a common
68 sensory chamber called a *macula communis* (Maklad et al. 2014). The *macula communis* is likely
69 an evolutionary precursor to the three sensory maculae in teleosts, although the true homology of

these structures remains unsettled (Ladich & Popper 2004). Some research has been performed regarding the vestibular response of the lamprey ear (Lowenstein et al. 1968; Lowenstein 1970); however, there is currently no research concerning the response of the lamprey ear to sound or whether they show a behavioural response to acoustic stimuli (Popper 2005), leaving a large gap in how this sensory modality evolved in vertebrates.

Herein, we describe the hearing ability of both adult and juvenile sea lamprey and how they behaviorally respond to sound. We hypothesized that sea lamprey would hear low-frequency sounds and exhibit a change in normal behaviour when exposed to low frequency tones. To test our hypothesis, the AEP technique was used to discover sound frequencies sea lamprey can detect and a laboratory bioassay was used to assess the behavioral response (activity levels, duration of attachment, surface breaching) to detectable frequencies. In the current study, both juvenile and adult sea lamprey heard low frequency sounds and exhibited a change in behaviour when exposed to low-frequency tones.

Methods:

Animal Supply and Housing:

Work was conducted following Canadian Council for Animal Care (CCAC) protocols (University of Windsor AUPP 17-11). Adult sea lamprey were collected via U.S. Fish and Wildlife Service sea lamprey control program trapping operations conducted in the Ocqueoc, Cheboygan and Carp Lake rivers, Michigan during May – June 2017. Adults were held at Hammond Bay Biological Station (HBBS) in 2000 L flow-through tanks supplied with ambient Lake Huron water (~ 4 – 7° C) from June 1st-16th. Adults were transported to the University of Windsor Central Animal Care Facility in mid-June and were kept in a 560 L tank maintained at

4-6°C in a chilled room. Juvenile sea lamprey were collected via electrofishing as part of the USFWS sea lamprey control program assessment operations conducted in tributaries throughout the Great Lakes basin from October – November 2017. Juveniles were held at HBBS in 200 L flow-through tanks supplied with ambient Lake Huron water (~2 – 4° C) and then transported to the University of Windsor and held in a 560 L tank maintained at 4 - 6°C. Juvenile and adult sea lamprey were experimented on to determine if there was an ontogenetic difference in hearing abilities at different life stages.

Auditory Evoked Potentials:

Auditory evoked potential (AEP) technique was used to measure sea lamprey hearing ability (Belanger et al. 2010; Higgs & Radford 2013). A positive response to a sound stimulus was defined as a significant change in the brain waveform coincident with the offset of the sound stimulus (Garabon & Higgs 2017), with auditory threshold for a given sound stimulus recorded as the lowest sound intensity at which a change was seen (Fig. 1). Because no previous data on AEP waveforms in this species were available, a series of control trials with dead fish were also conducted. At no point did the control trials with dead fish show any “response” to the tones presented thus verifying that positive responses were detected in the live lamprey. Stimulus presentation and level were also verified with a hydrophone (Reson TC4013) placed at the position of the fish holder before trials were begun. To measure AEPs, sea lamprey (n=7 juveniles and n=9 adults) were held underwater in a purpose-built testing tank (2.6 cm diameter polyvinyl chloride pipe 1.17 m L; Belanger et al. 2010; Higgs & Radford 2013) under light anesthesia (2-phenoxyethanol 0.004 mol L⁻¹). Stainless steel 27 gauge electrodes (Rochester Electromedical) were placed under the skin of the sea lamprey; with one as a reference electrode placed in the front of the head, one as the recording electrode placed over the auditory brainstem

and a ground electrode placed under the body. Preliminary dissections were performed to identify external landmarks to the site of auditory nerve innervation to the brainstem to ensure proper location in anesthetized fish.

An underwater speaker (UW-30 Lubell Labs) was submerged at the end of the tank opposite the sea lamprey for delivery of sound stimuli. Sound stimuli consisted of tone bursts from 50-800 Hz and increased in 5 dB increments at each frequency until a characteristic response was detected. Each sound presentation was 34 ms with total recording window of 100 ms and each tone was presented at alternating phases and 200 responses at each phase averaged (400 total responses at each sound level and frequency) to reduce stimulus artifacts. Auditory threshold and bandwidth was then plotted as an audiogram to ascertain the hearing capabilities of juvenile and adult sea lamprey and to identify frequencies of greatest sensitivity. Sound level was measured both in terms of pressure units (dB re 1 μ Pa) using a hydrophone (Inter Ocean system inc. – Acoustic Calibration and System Model 902), as well as acceleration units (dB re 1 m s^{-2}) using a waterproofed accelerometer (model 4524 cubic triaxial deltatron, Brüel & Kjær). Sea lamprey were only expected to respond to the particle motion aspect of a propagating sound due to its basal auditory structures, thus, making the acceleration units the most appropriate. We also quantified the pressure response values as these are most likely to be used in any instream applications.

Behavioural Trials:

Behavioural trials were conducted in a 1020 L fiberglass tank (243 x 91 x 91 cm) with a water depth of 35 cm at a temperature of 6°C. Experiments were conducted under red light conditions as studies have shown that lamprey do not respond to red light (Govardovskii & Lychakov 1984; Binder & McDonald 2007). Approximately one third of the tank was sectioned off using an

138 acrylic plexiglas barrier (equipped with 1 cm holes in a 5 cm grid to allow for water flow) to
139 ensure lamprey stayed in the portion of the tank visible to overhead cameras. Sounds were
140 played from an underwater speaker (Clark Synthesis Diluvio AQ339; Lubell Labs) suspended at
141 the end of the tank with the lamprey, so as not to touch the sidewalls. The experimental setup
142 included the underwater speaker, connected to an amplifier (Scosche SA300), a 12 Volt PBS car
143 battery for power and an mp3 player to play the noise (Sony Walkman NWZ-E464). Background
144 noise levels were quantified in the experimental tank at different times of day and were
145 consistently measured between 114-121 dB re 1 μ Pa (particle motion ranged from 34-52 dB re 1
146 nm^2).

147 Sea lamprey were tested individually to avoid any follower bias and 17 individuals of each life
148 stage were tested for behavioural responses to sound. Trials generally commenced starting 2-4
149 hours after sunrise and sea lamprey were allowed one hour to explore and acclimate to the novel
150 environment before testing began (Li et al. 2002). Although sea lamprey are nocturnal,
151 performing experiments in dark conditions during the day can be a meaningful way to assess
152 avoidance responses (Barnett et al. 2016). Testing consisted of a one hour acclimation period
153 followed by presentation of sounds in a stepwise pattern (30-100 Hz 10 Hz steps) and 200 Hz
154 with a 1 min playing period followed by 5 min of silence until all detectable sounds were
155 presented (Rollo & Higgs 2008; Isabella-Valenzi & Higgs 2013). Each tone was played at 160
156 dB re 1 μ Pa, (particle motion, RMS, ranged from 34-52 dB re 1 nm^2 , dependent on frequency
157 played) as this is an ecologically relevant noise level present within lakes as small vessels
158 generally produce noise ranging from 140-167 dB re 1 μ Pa up to an approximate distance of 2 m
159 away (Arveson & Vendittis 2000). A comparison of sound levels in twelve freshwater lakes and
160 rivers, determined that ambient noise is significantly louder in rivers (Wysocki et al. 2007), and

as lamprey spawn in a river setting, we hypothesized that using 160 dB re 1 μ Pa would be comparable to noise present in their natural environments.

Sea lamprey behavior was filmed using a GoPro Hero3+ (Go Pro) for the duration of each experiment. Time spent actively swimming, time spent resting (attached to the tank), and number of surface breaches (a measure of disturbance behaviour) were determined for each sea lamprey during quiet and sound periods.

Statistical analysis:

AEP thresholds data were not normally distributed and could not be adequately transformed to meet normality assumptions of parametric analyses. Not all lamprey were exposed to every frequency due to the inherent difficulties in recording from the lamprey brain. Thresholds were therefore analysed with the Kruskal-Wallis H test (Field 2013) separately for juveniles and adults with frequency as the main effect. When a significant frequency effect was found, post hoc analysis was conducted on the mean rank frequency score of the most disparate ranked frequencies (Field 2013). Differences between mean activity levels in the behavioural trials for control and treatment groups were evaluated using repeated measures ANOVA for each metric; total time spent swimming, total time spent attached, and number of surface breaches. Behaviours were analysed as a difference metric between the 1 min sound presentation and the 1 min control period directly preceding sound presentation to account for possible behavioural differences due to time spent in tank or previous exposures. Statistical comparisons on the differences from control activity were evaluated with simple contrasts relative to 0 in the repeated measures design, with individual Bonferroni post hoc comparisons made when overall

significances were found. Behaviour data was tested for normality using descriptive statistics in SPSS.

Results:

Auditory evoked potentials

Juvenile or adult sea lamprey did not respond to tones above 300 Hz, so this was considered the limit of their physiological hearing range. Two juveniles and five adults responded to 300 Hz tones up to 160 dB re 1 μ Pa (-49.6 dB re 1m·s⁻²). In adult sea lamprey, there was no effect of frequency on particle motion thresholds (Fig. 2A; $H_4 = 4.79$, $p = 0.309$), so the ability to hear was independent of frequency. Mean thresholds ranged from -54 dB re 1m·s⁻² (144 dB re 1 μ Pa) to -50 dB re 1m·s⁻² (150 dB re 1 μ Pa). In juvenile sea lamprey, there was a significant effect of frequency on particle motion thresholds (Fig. 2B; $H_4 = 19.8$, $p = 0.001$) with mean rank frequency scores of 5.17 for 50 Hz, 12.5 for 90 Hz, 12.0 for 100 Hz, 23.17 for 200 Hz, and 24.5 for 300 Hz. Despite this overall omnibus significant frequency effect, there was not a statistical difference between individual frequencies ($|R_{50}-R_{300}| = 19.3$; $Z_{0.05, 20} = 22.2$; Field 2013). Juvenile hearing thresholds ranged from -55 dB re 1m·s⁻² (140 dB re 1 μ Pa) to -54 dB re 1m·s⁻² (155 dB re 1 μ Pa).

Behavioural trials

Both juvenile and adult sea lamprey displayed changes in behaviour when exposed to low frequency tones (Figs. 3, 4). There was a significant effect of sound on adult sea lamprey movement in the tank ($F_{1,14} = 16.566$, $p < 0.001$; $F_{9, 126} = 53.83$, $p < 0.001$; Fig. 3a). Post-hoc analyses showed significant changes in time spent moving of adult sea lamprey relative to the quiet period one minute before sound trial (control) with 30, 60, 70, 80, 90, and 200 Hz causing

reduced movement and 50 and 70 Hz increased movement relative to control trials. There was not a significant effect of sound on the time spent attached to the tank wall ($F_{9,126} = 1.07$, $p = 0.39$) but the duration of tank attachment seemed to decrease at 50, 90, 100 and 200 Hz relative to control periods (Fig. 3b). The number of surface breach events was affected by sound ($F_{9,126} = 2.12$, $p = 0.03$) with 60, 70, 100 and 200 Hz all showing a significant increase in breaching events compared to controls (Fig. 3c).

Juvenile sea lamprey had significantly ($F_{1,144} = 2.3$, $p = 0.02$, Fig. 4a) increased activity levels when exposed to low frequency tones, with 30-100 Hz all causing significantly more activity than control periods. For time spent attached to the tank (indicative of resting behaviour), juveniles were significantly affected by frequency ($F_{9,144} = 2.30$, $p = 0.02$, Fig. 4b) with a reduction in attachment at 30-100 Hz relative to controls. Surface breaches were also elevated with sound for juveniles ($F_{9,144} = 2.85$, $p = 0.004$, Fig. 4c), although for this behaviour only 40, 70, 80 and 100 Hz were different from controls. Behaviour data were normally distributed.

Discussion:

The goals of the present study were to assess the basic hearing capabilities of sea lamprey and the potential of sound to affect sea lamprey behaviour. As hypothesized, sea lamprey can detect low frequency sounds but their auditory bandwidth is limited just to those frequencies with a large particle motion component of the sound wave. Behaviourally we did see effects of a variety of these sounds on lamprey behaviour, largely showing a presumed disruptive effect, demonstrating the potential of sound as a disruptor that may help guide lamprey to traps or push them away from fishways, although extensive field trials are needed to show the utility of this approach.

226 *Auditory evoked potentials:*

227 The lamprey ear is morphologically less complex than that of other fishes (Lowenstein et al.
228 1968; Maklad et al. 2014), but does respond to angular accelerations perhaps important in
229 detecting swimming orientations (Lowenstein 1970). The portion of the ear containing the otolith
230 is a *macula communis* (Lowenstein et al. 1968; Maklad et al. 2014), unlike the three separate
231 auditory endorgans of other fishes, and it is here where the presumed auditory responses were
232 likely generated in the present study. To our knowledge, the present study is the first
233 demonstration of hearing abilities in any Agnathan and the low frequency bandwidth detection
234 does fit with expectations from the morphological descriptions. While it is not advisable to rely
235 on threshold estimates from AEP as an absolute measure (Higgs 2002), it is a useful technique to
236 estimate the frequencies of possible detection — as a lack of response at the level of AEP would
237 suggest that the fish cannot detect the frequency of interest. We are aware of the limitations due
238 to tank effects especially of low frequency tones in laboratory experiments (Parvulescu 1967),
239 but the current results do show the ability of the sea lamprey ear to respond to frequencies from
240 50-200 Hz. As a basal vertebrate, sea lamprey provide us with a window to estimate how hearing
241 evolved in lineages that led to teleosts, even though lamprey are a separate evolutionary offshoot.
242 Other basal vertebrates that have been tested, such as elasmobranchs (e.g. Casper et al. 2003;
243 Casper & Mann 2009) and Holosteans (Lovell et al. 2005), can hear a broader frequency range
244 with more evidence of a finer tuned audiogram. The flat audiogram of lamprey with a limited
245 threshold range suggests that hearing initially evolved for low frequency sound detection,
246 possibly for acoustic orientation or to locate spawning areas (Johnson et al. 2015), but expansion
247 and specialization was quickly selected for. While there is clearly a need for a more rigorous
248 comparative analysis of hearing across “fish” (e.g. Fay & Popper 2000; Fay & Popper 2012), the

results presented here give us a baseline at which to ground this comprehensive phylogenetic approach.

Behavioural response:

Both adult and juvenile sea lamprey exhibited an increase in activity levels when exposed to certain low frequency tones. Sea lamprey often attach to flat surfaces using their oral sucker as a means of holding stationary in a current (Reinhardt et al. 2009) and sea lamprey held in captivity rarely detach from the wall of holding tanks (Chung-Davidson et al. 2004), therefore we have quantified attachment to tank walls as a measure of resting behaviour. When exposed to low frequency tones, juvenile and adult sea lamprey increased time spent swimming and decreased time spent attached to tank walls, which allowed us to conclude that noise elicited a change in normal lamprey behaviour. A change in normal behaviour is often the first sign of stress an animal exhibits and therefore a measure of activity levels can be a useful indicator of stress (Mickle & Higgs 2017). Characterization of anti-predator behaviours in sea lamprey include increased swimming and area avoidance (Pfeiffer 1977; Imre et al. 2010). When exposed to electrical fields sea lamprey swam consistently and did not stop moving until the stimulation was turned off (Chung-Davidson et al. 2004). The present results demonstrate that not only can sea lamprey hear low frequency sounds but, at least at high intensity levels, these sounds disrupt lamprey behaviour, which may be useful for directing their movements in a management context.

When exposed to some frequencies, adult and juvenile lamprey exhibited an increase in surface breach behaviour. There is little scientific evidence available to explain surface breach behaviour in sea lamprey, however other species have been shown to jump or escape the water as a means

of avoiding poor conditions or to evade predators (Baylis 1982; Gibb et al. 2011). Therefore, we hypothesize that juvenile sea lamprey exhibit surface breach behaviour as a likely response to avoiding an unfavourable condition. While we were not able to measure physiological stress in the current study, the breach behaviour does suggest that the juvenile lamprey experienced the sound as an aversive and perhaps stressful stimulus. It is unclear why there was a slight differential response in breaching between adults and juveniles. There may be stage-specific differences in auditory abilities in sea lamprey (adult behaviour changes at 200 Hz for all responses measured, however this is not observed in juvenile behaviour), as in some teleosts (Popper 1971; Higgs et al. 2002; Vasconcelos et al. 2015), but there is little known about behavioural differences with development in this species. The differences seen may also be just artifacts of sample size, so more research is needed on how auditory abilities may, or may not, change with development in this species.

As noise has been shown to cause changes in behavioural patterns of animals, researchers can use noise as a control method for species entering an undesirable area or to lure/scare animals into a trap. European eels (*Anguilla anguilla*) have been guided into traps after exhibiting an avoidance response to an 11 Hz sound source (Sand et al. 2000). Low frequency tones of 16 Hz have also proven effective in reducing impingement of cyprinid fishes (Sonny et al. 2006) and a broadband sound with frequencies spanning 1 Hz-10 kHz has proven effective at directing movements of the aggressive invader, silver carp (*Hypophthalmicus molitrix*), to alternate habitats (Vetter et al. 2015). Low frequency (10 Hz) sound initiated an avoidance response in Atlantic salmon smolt (*Salmo salar*), ultimately discouraging migrating salmon from swimming downstream (Knudsen et al. 1994) and high frequency noise has been shown to be effective at deterring alewives (*Alosa pseudoharengus*) from a power plant intake (Ross et al. 1993). Further,

noise may prove more effective paired with additional sensory cues such as olfactory alarm cues as observed in juvenile convict cichlids (Ferrari et al. 2008). Therefore, based on the results obtained from the current study more research should be attributed to using sound as a management tool for sea lamprey in both control and conservation applications.

Future considerations and conclusions:

In the Laurentian Great Lakes sea lamprey are invasive and destructive, however in the North Atlantic, they are native and endangered and a focus of conservation efforts, especially in Europe (Beamish 1980). Here, we determine that noise can be used to disrupt normal sea lamprey behaviour. Understanding sea lamprey hearing ability may reveal behavioural control tactics as has been done for other fishes (e.g. Ross et al. 1993; Knudsen et al. 1994; Sand et al. 2000; Vetter et al. 2015; Murchy et al. 2017; Zielinski & Sorensen 2017). Sea lamprey populations have been suppressed in the Great Lakes using selective pesticides that kill larval sea lamprey that reside in natal streams (Applegate et al. 1961). However, management agencies have called to diversify control techniques by improving trapping technologies for downstream migrating juvenile sea lamprey and upstream migrating adult sea lamprey (McLaughlin et al. 2007; Great Lakes Fishery Commission, 2011). In concept, sound could be useful to modify an effective and non-invasive technology to direct migratory sea lamprey into traps (Knudsen et al. 1994; Maes et al. 2004) or redistributing them back into their native range (Li et al. 2007) and would complement currently developing technologies such as attractive pheromones (Li et al. 2002; Johnson et al. 2013; Li et al. 2018) and repellent alarm cues (Wagner et al. 2011; Imre et al. 2014; Hume et al. 2015) and electrical fields (Johnson et al. 2016). In contrast, lamprey populations are declining through most of their native ranges (Renaud 1977; Close et al. 2002), where managers seek to guide migratory adults, not to traps but to fish passage devices at

migratory barriers (Pacific lamprey: Keefer et al. 2013; European river lamprey: Foulds & Lucas 2013) and juveniles away from sources of mortality such as hydropower intakes or irrigation offtakes (Bracken & Lucas 2013).

Hearing abilities of freshwater fish depends on the presence of specialized structures such as Weberian ossicles or auditory bullae, which allow for a broader hearing range (50 to 5000 Hz) compared to fish lacking specialized structures (50 to 1000Hz) (Popper & Fay 1999). Therefore, before implementing sound as a control technique for sea lamprey behaviour, it is important to determine the type of fish present in the area and the potential effects of low-frequency sound on behaviour and physiology, as this is a relatively unexplored area (Mickle & Higgs 2017). Some of the limitations of this study include the distortion of sound due to experiments being performed in a laboratory tank setting, and low frequency sound waves causing distortion at relatively short distances. The next steps of this project should include similar experiments in a field setting to determine relevance in a natural setting, to determine the effect of these low frequency sounds on native fish species, and if sea lamprey habituate to these tones (Imre et al. 2010).

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Figure Legend

Figure 1: Representative auditory evoked potentials (AEP) traces recorded from an anesthetized adult sea lamprey presented with a 90 Hz tone stimulus. The AEP response begins at the offset of the 34 ms stimulus presentation (black bar at the bottom of the figure) and is first evident at 145 dB re 1 μ Pa (-54.4 dB re 1 m s^{-2}). Arrows represent the beginning of the observed response.

Figure 2: Threshold audiogram of adult (A) and juvenile (B) sea lamprey hearing displayed as pressure units (closed circles; dB re 1 μ Pa) and particle motion (open circles; dB re 1 m s^{-2}) units.

Figure 3: Adult sea lamprey behaviour when exposed to noise.

- a) Mean activity levels of adult sea lamprey exposed to noise, relative to controls (silent period between noise). Error bars are representative of mean ($\pm$ S.E). Significant differences relative to control are indicated by an * while differences compared to other frequencies are indicated by different letters and lack of letters indicates no significant differences among treatments.
- b) Mean duration of tank attachment of adult sea lamprey exposed to noise, relative to controls. Error bars are representative of mean ($\pm$ S.E). Significant differences relative to control are indicated by an * while differences compared to other frequencies are indicated by different letters and lack of letters indicates no significant differences among treatments.
- c) Mean surface breach events of adult sea lamprey exposed to noise, relative to controls. Error bars are representative of mean ($\pm$ S.E). Significant differences relative to control

are indicated by an * while differences compared to other frequencies are indicated by different letters and lack of letters indicates no significant differences among treatments.

Figure 4: Juvenile sea lamprey behaviour when exposed to noise

a) Mean activity levels of juvenile sea lamprey exposed to noise, relative to controls (silent period between noise). Error bars are representative of mean ($\pm$ S.E). Significant differences relative to control are indicated by an * while differences compared to other frequencies are indicated by different letters and lack of letters indicates no significant differences among treatments.

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Figure 3: Adult sea lamprey

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Figure 4: Juvenile Sea Lamprey

- Mean activity levels of juvenile sea lamprey exposed to noise, relative to controls (silent period between noise). Error bars are representative of mean (+/- S.E). Significant differences relative to control are indicated by an * while differences compared to other frequencies are indicated by different letters and lack of letters indicates no significant differences among treatments.
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