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MANAGEMENT BRIEF

Do Native Pacific Lamprey and Invasive Sea Lamprey Share an Alarm Cue? Implications for Use of a Natural Repellent to Guide Imperiled Pacific Lamprey into Fishways

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Abstract
Instream barriers affect anadromous lampreys worldwide by preventing access to spawning habitat, resulting in the decline of several species. Because lampreys rely heavily on olfactory cues to choose movement paths during upstream migration in rivers, the manipulation of these cues may be used to guide individuals into the vicinity of fish passage devices and thereby mitigate the impacts of barriers during migration. However, because experimentation with imperiled species presents significant legal and ethical challenges, use of a surrogate species that exhibits similar responses may prove very useful. Our laboratory study established that (1) the odor derived from dead Pacific Lamprey *Entosphenus tridentatus* elicits an avoidance response from invasive Sea Lamprey *Petromyzon marinus* from the Laurentian Great Lakes, and (2) the magnitude of this response does not differ from the conspecific alarm cue present in Sea Lamprey. By presenting the odor on the side of a river channel opposite a lamprey fish passage device, migrating lampreys of conservation concern may be guided to fishways, if the behavioral response to the cue has evolved in these taxa. Due to their availability and well-studied chemical communication system, Sea Lamprey may prove to be a useful surrogate for identifying and producing chemosensory cues for use in guiding Pacific Lampreys towards fish passage devices and away from intakes and screens.

The use of an abundant species as a surrogate to develop the means to effectively manage a closely related imperiled species has considerable appeal (Caro et al. 2005; Wenger 2008). Rare and threatened species may be difficult to observe or collect and are subject to considerable legal protections that restrict experimentation. Researchers and managers have attempted to use surrogate species as response indicators to predict population changes after large-scale ecological or anthropogenic perturbation. The utility of surrogates at this scale has proven inconsistent due largely to a failure to verify that surrogate and target species exhibit similar population responses to complex ecological drivers (Lindenmayer et al. 2002; Mortelliti et al. 2009; Murphy et al. 2011). Alternatively, surrogate species may prove effective in addressing small-scale mechanistic questions where the responses of the individual animal are key to the creation of successful management practices. Here, the surrogate is more akin to a medical model species, and the underlying assumption of conserved biology (e.g., physiology, sensory capacity, behavior) may be more easily established.

Surrogate species may be particularly useful in the discovery of new means to guide imperiled migratory fishes into fishways at dams, where success or failure at the population scale is determined by numerous individual acts of passage through a manmade device. Barriers to upstream migration are a threat to anadromous lampreys worldwide because they prevent migrants from accessing spawning habitat (reviewed in Maitland et al. 2015; Figure 1). Of particular note, the Pacific Lamprey *Entosphenus tridentatus*, a species of significant cultural and ecological importance, has experienced a drastic population decline over the past 50 years (Close et al. 2002). The species is now considered at-risk (ODFW 2006;

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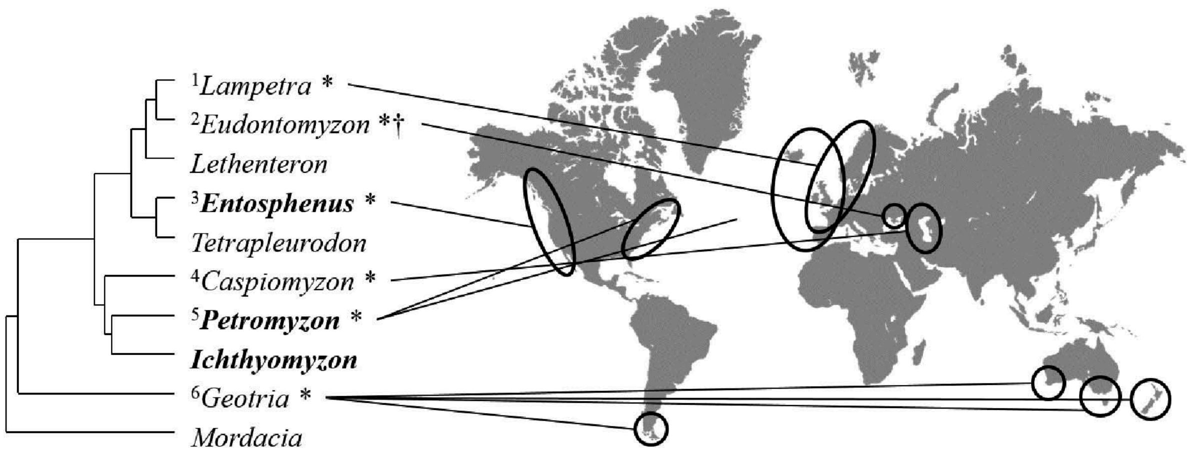

FIGURE 1. Cladogram based on Cyt*b* molecular data (derived from Potter et al. 2015), representing all extant lamprey genera. Black ellipses indicate geographical areas where a single anadromous species (indicated by an asterisk) belonging to that genus is currently threatened by instream barriers, resulting in the adoption of conservation legislation. Abbreviations: (†) indicates an anadromous species (*Eudontomyzon* sp. nov. migratory) now extinct, partially as a result of instream barriers (Kottelat et al. 2005). Additional explanations for preceding uppercase numbers: (1) *Lampetra fluviatilis* (IUCN 2013; JNCC 2010), (2) *Eudontomyzon* sp. nov. migratory (Kottelat et al. 2005), (3) *Entosphenus tridentatus* (ODFW 2006), (4) *Caspiomyzon wagneri* (IUCN 2008), (5) *Petromyzon marinus* (JNCC 2010; OSPAR 2009), (6) *Geotria australis* (IUCN 2014). Genus names in bolded font are known to possess a putative alarm substance.

WDFW 2015), and large-scale restoration projects are underway across the Pacific Northwest (Keefer et al. 2009; Maitland et al. 2015). In the Columbia River basin, 12 lamprey passage systems (LPS; a purpose-built ramp fishway designed to exploit the Pacific Lamprey's ability to climb wetted surfaces) have been installed at barriers to facilitate upstream passage. An LPS device is installed as a separate system at traditional fishways and is often integrated into some element of the existing fishway (e.g., is placed into auxiliary water supply channels or adjacent to existing fishway entrances). Once entered, the passage efficiency of an LPS can be greater than 90% (Moser et al. 2011). However, too few migrating lampreys locate the relatively small LPS entrance to achieve population management goals, particularly in large river systems where encounter rates may be less than 40% (Moser et al. 2002a, 2002b; Keefer 2013). There is a pressing need to increase encounter rates with LPS fishways to protect the Pacific Lamprey.

Guidance towards an LPS entrance may be achievable by manipulating the information the animal uses to select movement pathways in rivers. Migratory movements of lampreys are thought to respond to plumes of semiochemicals, conspecific odors that lead migrants towards high quality habitat and away from areas of risk (Buchinger et al. 2015). For example, the closely related and heavily studied Sea Lamprey *Petromyzon marinus* relies extensively on two odors to guide movements during their nocturnal upstream migration in rivers. The odor emitted by conspecific larvae guides migrants into streams with suitable spawning and rearing habitat (Sorensen et al. 2005), and the application of this odor can be used to lead migrants into tributaries or near one bank of a river channel (Wagner et al. 2006, 2009). However, movement along river banks also brings the animal into potential contact with nocturnal shoreline predators (e.g., raccoon), increasing the risk of predation. A second odor, a natural repellent contained in the tissue of live lamprey that is released when the skin is ruptured (putatively an alarm cue), causes migrants to move to the opposite side of the channel while continuing to move upstream (Bals and Wagner 2012; C. M. Wagner, unpublished data). By applying this natural repellent to one side of the channel to evoke migrants to the opposite bank during migration, Sea Lampreys quickly encountered a trap entrance placed opposite the odor plume (Hume et al. 2015). The movement process associated with encountering and entering traps is similar to finding and entering a fishway (Bravener and McLaughlin 2013).

Overlap has been demonstrated among lampreys in their behavioral responses to attractive semiochemicals (Fine et al. 2004), including Sea and Pacific lampreys (Robinson et al. 2009; Yun et al. 2011, 2014), suggesting that Sea Lamprey may be a suitable candidate for surrogacy for the Pacific Lamprey. At least one other lamprey species (Silver Lamprey *Ichthyomyzon unicuspis*) produces the compound (s) that elicit the alarm response in Sea Lampreys. Whether any other lamprey has evolved the alarm response has not been investigated. However, alarm signaling is more likely to be conserved across related taxa (versus reproductive pheromones) because the risk of predation is often shared, whereas the benefit of reproductive opportunities is not (Mirza and Chivers 2001). If conserved, the alarm response could prove to be a very useful tool in guiding imperiled lampreys into the vicinity of fish passage devices by inducing them towards the river bank associated with the LPS entrance. Because experimentation with Pacific Lampreys is strictly controlled, we report an initial test of the hypothesis that the odor produced by dead Pacific Lamprey contains one or more natural repulsive compounds that elicits the known alarm response in migratory Sea Lamprey. We tested our hypothesis using a standard laboratory space-use assay to ascertain whether Sea Lamprey were repelled by either the death odors of Pacific Lamprey and/or Sea Lamprey (versus a control). Odors were applied to one side of a laboratory raceway and the resulting lamprey distribution was analyzed for evidence of repulsion or attraction. We predicted (1) that Sea Lampreys would respond by avoiding extract derived from Pacific Lamprey, and (2) that the avoidance response would be similar in magnitude to the response from a conspecific extract.

METHODS

Odor collection.—We individually extracted the odors of one fresh-killed adult male Pacific Lamprey (304 g, obtained from the lower Columbia River, Washington) and one fresh-killed adult male Sea Lamprey (238 g, obtained from the Ocqueoc River, Michigan), following the Soxhlet extraction procedures of Bals and Wagner (2012). Briefly, we used separate 1-L 71/60 Soxhlet apparatuses (Ace Glass Inc., Vineland, New Jersey) with a water-cooled Allihn condenser and a 1-L solvent reservoir heated by a hemispherical mantle to 75–80°C. One liter of solvent (50:50 weight/weight of 200-proof ethyl alcohol and deionized water) was added into the solvent reservoir. A single carcass was then placed within the body of the extractor. Each extraction cycled three times. The resulting extracts were filtered and stored at –20°C until use.

Apparatus.—Because lampreys are nocturnal during their spawning migration, all trials were conducted at night (2200–0300 hours) between May 31 and June 26, 2015. Trials took place at the Hammond Bay Biological Station (HBBS, Millersburg, Michigan) in two concrete raceways (20 × 1.84 m) separated into an upstream holding area (7.5m long), an experimental arena (5.0 m), and a tailrace (7.5 m) with net barriers (Figure 2). Collimators were placed upstream of each experimental arena to promote smooth flow and distinct odor plumes. Each raceway received a continuous flow of water from Lake Huron through an offshore intake pump (temperature 7.4–11.9°C). Discharge was maintained between 6.7 and 12 L/s. Each experimental arena was equipped with one infrared-sensitive video camera (Axis Communications; Q1604 Network Camera) placed directly overhead, as well as two infrared lights (Wildlife Engineering; Model IRLamp6). A live feed from the cameras was observed on video monitors in a separate room, and trials were recorded onto digital media for analysis.

Stimulus odors were introduced into one side of the raceway via peristaltic pumps (MasterFlex model 7533-20) at a rate of at 20 mL/min at the upstream end of the experimental arena 15.2 cm from the left or right side. Prior to experimentation we mixed 8 mL of stimulus extract into 420 mL of lake water collected from the raceway in a 500 mL Erlenmeyer flask that was continuously stirred with a 2-cm magnetic stir bar. The final dilution of raceway water to extracted odor was 1 μL/L, a dilution that achieved full repellence in conspecific trials (Bals and Wagner 2012). To ensure no cross-contamination of odors, we used separate pump tubing, flasks, and stir bars for each stimulus odor.

Experimental subjects.—Wild male Sea Lampreys (365–578 mm, mean = 482 mm, SE = 2.62) were obtained by the U.S. Fish and Wildlife Service as part of an annual Sea Lamprey monitoring program during May and June 2015. The lampreys collected were actively migrating into two tributaries of Lake Huron (Cheboygan and Ocqueoc rivers, Michigan) and one of Lake Michigan (Manistique River, Michigan). During migration, male and female Sea Lampreys exhibit equal responses to the death odor containing a putative alarm cue (Bals and Wagner 2012).

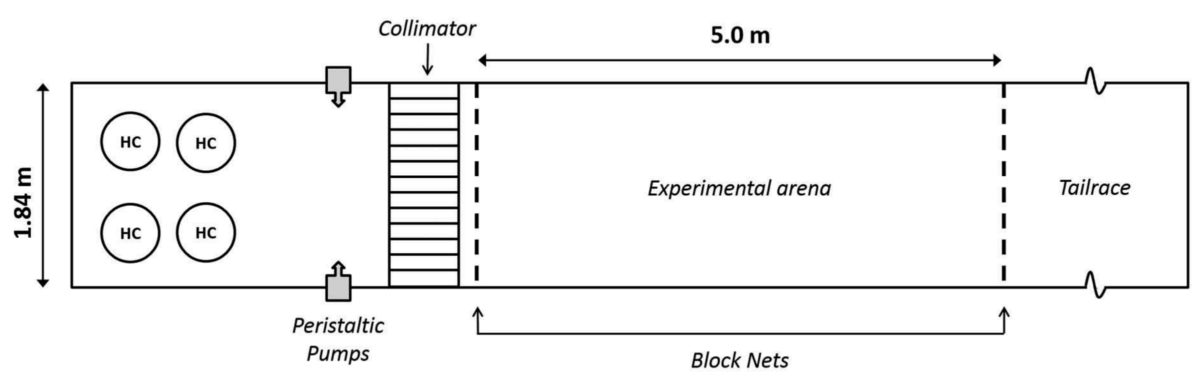

FIGURE 2. Overhead view of the raceway setup for behavioral space-use testing. Each raceway was separated into three zones: upstream holding area (7.5 m long), experimental arena (5 m long), and downstream tailrace (7.5 m long). Water flowed from left to right in the figure. Prior to introduction into the experimental arena, groups of lampreys were placed in holding cages (HC) in the upstream area. The odors were introduced via peristaltic pumps on the left or right side of each raceway. The bottom of each raceway was lined with white plastic and marked into four equal-sized rectangles to assign the position of each animal to a side of the raceway from the recorded video.

Following capture, the lampreys were transported to the station, separated by sex via external characteristics per Siefkes et al. (2003), and placed into 1,000-L holding tanks receiving a continuous fresh flow of water from Lake Huron (100% exchange every 2 h). All experimental subjects were held at HBBS for a minimum of 48 h prior to use and observed to ensure normal activity. Only specimens lacking external injury were used, and each lamprey was used in a single trial. All procedures for subject handling and experimentation were approved by the Michigan State University Institutional Animal Care and Use Committee (permit AUF 01/14-007-00).

Experimental procedure.—Prior to the beginning of a trial at approximately 1500 hours, four groups of immature male Sea Lamprey (10 individuals per group) were placed into separate holding cages in upstream section of each raceway. At 2200 hours, a trial began when a single cage was moved into the middle of the experimental arena of a raceway and the subjects were released. Trial duration was 30 min, comprising a 10-min preexposure period and a 20-min exposure period. The preexposure period began when a majority (≥6) of Sea Lamprey were actively moving. During the exposure period, one of three stimulus odors—extracted Pacific Lamprey death odor, extracted Sea Lamprey death odor, or a solvent control —was introduced into one side of each raceway. We completed eight replicates for each stimulus odor. To eliminate possible effect of raceway identity (channel one or two) or odor application side (left or right), each odor was tested with an equal number of replicates in either raceway (four in channel one, four in channel two), and the application side was alternated across replicates within each raceway; i.e., for a single treatment four replicates were performed in each raceway, with the odor pumped twice on the left side and twice on the right side within a raceway. At the end of each trial, we recorded the total length (mm) and wet weight (g) of each individual.

Data analysis.—From the video recordings we determined the position of each individual's head every 30 s after the start of the trial. Positions were assigned to either the stimulus (control or death odor application side) or nonstimulus side of the raceway. Only the final 10 min of the stimulus period were used for analysis to provide time for the distribution of lamprey to stabilize after introduction of the stimulus. To confirm no effect of raceway or side of the raceway receiving the stimulus odors, we first ran a one-way ANOVA with odor identity (factor), raceway, and treated side as random effects, testing the transformed proportion of animals on the stimulus side as the response. The results confirmed an effect of odor identity ($F_{2,\ 19} = 10.24$, $P < 0.001$) and no effect of raceway ($F_{1,\ 19} = 0.18$, $P = 0.67$) or side ($F_{1,\ 19} = 3.03$, $P = 0.09$). Raceway and treated side were omitted from subsequent analysis. To determine whether space use differed in response to stimulus odors (versus control), data were analyzed with a second one-way ANOVA. The transformed proportion of lampreys on the stimulus side was the response variable and odor identity (Sea Lamprey extract, Pacific Lamprey extract, or solvent control) was a fixed factor, with water temperature and discharge as random covariates. Post-hoc pairwise Tukey's honestly significant difference (HSD) tests were performed to test for significant differences in the proportion of lampreys on the stimulus side in all stimulus odor pairs. Prior to analysis, all proportions were arcsine-transformed and tested for normality via Shapiro–Wilk's test. The transformed data were normally distributed ($W > 0.95$, all $P > 0.38$). All statistical analyses were performed in SPSS at $\alpha = 0.05$.

RESULTS

The overall statistical model was significant (ANOVA: $F_{4,\ 19} = 4.59$, $P = 0.009$), with a significant effect of odor identity on the distribution of animals within the raceway ($F_{2,\ 19} = 6.08$, $P = 0.009$) but no effect of water temperature ($F_{1,\ 19} = 0.23$, $P = 0.635$) or discharge ($F_{1,\ 19} = 0.34$, $P = 0.567$; Figure 3). Post-hoc pairwise comparisons of odors confirmed the predicted patterns in that (1) the extracted odors of dead Pacific Lamprey (Tukey's HSD, $P = 0.004$) and dead Sea Lamprey (Tukey's HSD: $P = 0.002$) significantly repelled Sea Lampreys versus the solvent control, and (2) the magnitude of the repulsion elicited by Pacific Lamprey death odor and Sea Lamprey

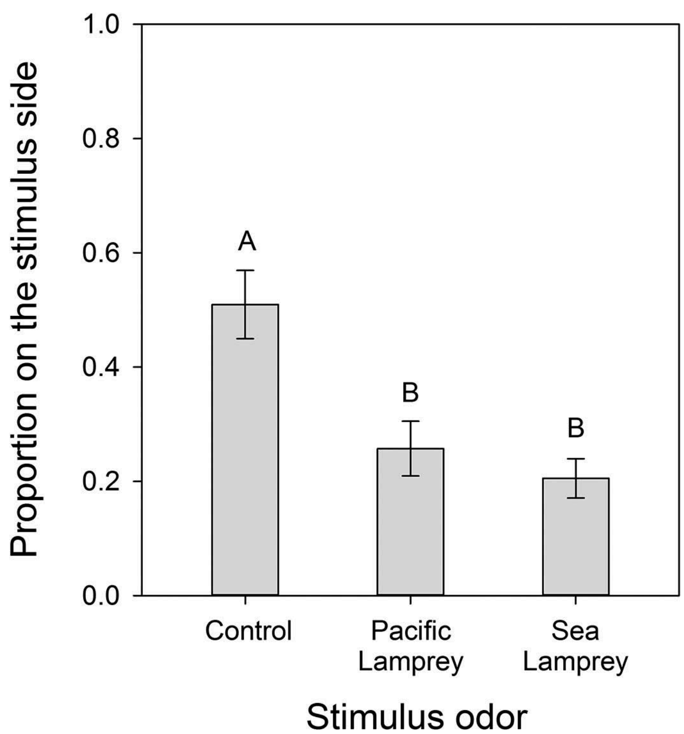

FIGURE 3. Mean (±1 SE) proportion of migratory male Sea Lampreys on the stimulus side of the raceway after exposure to death odors collected from fresh-killed whole carcasses of a male Sea Lamprey and a male Pacific Lamprey. Treatments with differing letters were significantly different per Tukey's honestly significant difference test after one-way ANOVA ($N = 8$ for each bar). The analysis was performed on data that were arcsine-transformed but are displayed as the observed proportions.

death odor did not differ (Tukey's HSD: $P = 0.93$). Generally, during the prestimulus period of trials, Sea Lampreys actively swam around the edges of the experimental arena in either a clockwise or counter-clockwise fashion, spending less time swimming in the middle of the arena. When exposed to the solvent control, the same patterns of movement occurred. However, when either of the death odors (Pacific or Sea Lamprey) was introduced, individuals who encountered the plume altered their trajectories by turning away from the activated side and either moving towards the nonstimulus side or downstream to the block net in an apparent attempt to escape. The magnitude of responses varied from simple turning and avoidance to a striking flight response where the animal burst-swam downstream.

DISCUSSION

Migratory Sea Lampreys strongly and consistently avoided the odor extracted from fresh-killed Pacific Lamprey, indicating that a repulsive compound or compounds, putatively an alarm cue (Imre et al. 2010; Bals and Wagner 2012), may be present in both taxa. Regardless of the chemical nature of the material (an alarm cue or other natural repellent), the observed response establishes the potential viability of using invasive Sea Lamprey from the Great Lakes as a source of material for testing guidance of live Pacific Lampreys towards fishway entrances. Utilizing Sea Lampreys as a behavioral surrogate species for Pacific Lamprey responses to semiochemicals and other odors requires further evaluation and rigorous hypothesis testing because differences in their biology are known (Clemens et al. 2010). However, olfactory receptor morphotypes appear conserved from lampreys to teleost fishes, and it is likely that their behavioral affiliations in reproduction, food acquisition, and risk perception are similarly conserved (Hansen and Zielinski 2005; Hamdani and Døving 2007; Laframboise et al. 2007; Døving and Lastein 2009). Sea Lamprey also avoid the odor extracted from dead Silver Lamprey (Bals and Wagner 2012), suggesting that the cue is present in the two major clades of Petromyzontiformes (Figure 1). Because both Sea and Silver lampreys are basal to Pacific Lamprey (Potter et al. 2015), the cue inducing this alarm response may have been present in a common ancestor.

Importantly, whether Pacific Lampreys have evolved a similar alarm response is yet to be determined. The evolution of an alarm response to chemical cues released upon injury in teleost fishes is hypothesized as a secondary function of the compounds involved. Specifically, the substances contained in ostariophysan club cells (located in the skin) function as antimicrobial agents in response to epidermal infections and protective agents against ultraviolet light exposure. Olfactory perception of the compounds as injury-related odors evolved later (Chivers et al. 2007; Ferrari et al. 2010). Thus, evolution of the alarm response may be derived from ecological circumstances that dictate selective pressures. Those circumstances may include the nonhoming migration, which requires movement into and through unfamiliar areas with new predators where alarm cues may be important signals of predation risk. Lampreys rely extensively on olfactory cues to locate habitat and mates while avoiding predation during their terminal migration (reviewed in Johnson et al. 2015). If the alarm response that is clearly demonstrated by Sea Lampreys is conserved across lamprey taxa, it could be applied in situations where behavioral manipulation, such as guiding migrants to fish passage devices, is used to protect species of conservation concern. Clearly, the next step is to evaluate whether alarm responses have similarly arisen in other anadromous lamprey species, particularly the Pacific Lamprey.

In addition to successful upstream passage, lampreys newly transformed into the parasitic life phase must survive a downstream migration through a gauntlet of threats caused by instream barriers. During downstream migration, juvenile Pacific Lamprey can become impinged on intake screens or entrained in irrigation canals; they may experience other physical injury resulting in direct mortality (Moser et al. 2015). Prior research has considered aversive stimuli to direct juvenile lampreys, including electrical guidance (Applegate et al. 1952; Johnson and Miehls 2014) and other nonphysical stimuli such as carbon dioxide barriers (Dennis et al. 2016). These technologies often require costly infrastructure, making whole-channel implementation difficult and expensive. Further, they tend not to be species-specific in action and, thus, may have negative effects on nontarget fishes. If the chemical alarm signaling system of lampreys is present across multiple life stages, application of the natural repellent upstream of entrainment and impingement areas may guide downstream migrants away from the dangerous areas. Evidence for the conservation of the alarm signaling system and behavioral response exists within Sea Lamprey larvae (Perrault et al. 2014), and newly transformed emigrants have been observed to respond to the cue (Wagner, unpublished data). Thus, if conserved among petromyzontid lampreys and their life stages, the lamprey repellent may be used to direct adult migrants toward an LPS for fish passage and direct emigrating juveniles away from danger.

The Sea Lamprey is currently a model organism in the fields of genomics, (McCauley et al. 2015), medicine (Cai et al. 2013), and biomimetics (Ijspeert et al. 2013). Our results add to a body of work, suggesting that the invasive population in the Great Lakes may prove useful as a model of behavioral, physiological, and ecological responses to olfactory cues during odor-mediated migration. In particular, the availability of invasive Sea Lampreys as experimental subjects and a source of experimental olfactory cues, along with the substantial research infrastructure supported primarily by the Great Lakes Fishery Commission, creates a circumstance whereby this invasive pest may become a valuable surrogate for lampreys of conservation concern. Confirming a behavioral alarm response within Pacific Lamprey and other lampreys of conservation concern and identifying the chemical structure of the repulsive compounds will be important next steps.

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