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Articles

Behavioral Responses of Pacific Lamprey to Alarm Cues

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Abstract

Pacific lamprey (*Entosphenus tridentatus*), an anadromous ectoparasite, faces several challenges during adult migration to spawning grounds. Developing methods to address these challenges is critical to the success of ongoing conservation efforts. The challenges are diverse, and include anthropogenic alterations to the ecosystem resulting in loss of habitat, impassable barriers such as dams, climate change impacts, and altered predator fields. We conducted a behavioral study to understand how adult migrating Pacific lamprey respond to potential alarm cues: White Sturgeon (*Acipenser transmontanus*), human saliva, decayed Pacific lamprey, and river otter (*Lontra canadensis*). Research has shown that some species of lamprey can be guided to a location using odors and similar cues may be useful as a management tool for Pacific lamprey. Experiments were conducted over 2 nights and measured the number of entries (count) and duration of time spent (occupancy) by adult lamprey in each arm of a two-choice maze. During the first night, no odor was added to test for selection bias between arms. During the second night odor was added to one arm of the maze. Contrary to expectations, lamprey were significantly attracted to the river otter odor in both count and occupancy. No significant differences were found in the response of lamprey to the other three odors. Results from this study indicate that Pacific lamprey do respond to some odors; however, additional tests are necessary to better identify the types of odors and concentrations that elicit a repeatable response.

Keywords: Pacific lamprey; predator avoidance; lamprey; anadromous; Columbia River; olfaction; two-choice maze

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Introduction

During the past 50 y, Pacific lamprey (*Entosphenus tridentatus*) have experienced unprecedented population declines and have been extirpated from the upper reaches of many rivers and tributaries in Washington, Oregon, California, and Idaho, including the Umatilla River in Oregon (Close et al. 1995). Counts of returning adults at Columbia River dams and tributaries have dropped from historical highs of over a million individuals to lows in the thousands (CRITFC 2011). In recent years only a few hundred fish have been recorded at Lower Granite Dam on the Snake River (Ward et al. 2012), with 106 fish counted in 2016.

Multiple factors have contributed to the decline of lamprey, including navigational hazards, dewatering, water pollution, intentional poisonings, culverts, stream channelization, and predators (Beamish and Northcote 1989; Close et al. 1995; Clemens et al. 2012). Historical tribal accounts describe that during lamprey migrations in the Columbia River, Celilo Falls was “black with eels” (CRITFC 2011). Despite their decline in abundance, lamprey continue to hold a place of cultural and natural significance among many Pacific Northwest tribes and are used for ceremonial, medicinal, spiritual, and subsistence purposes (Close et al. 1995, 2002, 2004; Larson and Belchick 1998); A limited harvest of a few thousand adult lamprey still occurs in some locations during the upriver migration (CRITFC 2011; Baker et al. 2014).

Pacific lamprey are anadromous and undergo extensive migrations during juvenile and adult phases (Beamish 1980; Robinson and Bayer 2005). Adults spend approximately 1 to 3 y in the ocean environment as ectoparasites, where continued growth occurs. Upon returning to freshwater, adults are known to migrate hundreds of kilometers inland to suitable spawning habitat when unimpeded (Torgersen and Close 2004; McIlraith et al. 2015). Upon onset of the freshwater migration, they cease feeding and begin upstream migrations in the late spring. During this time, body length decreases by approximately 20% (Beamish 1980). Changes in water temperature and flow events partially influence the initiation of upstream movement (Hardisty and Potter 1971; Keefer et al. 2009; Binder et al. 2010; Lampman 2011) and warm water induced maturation in lamprey in laboratory experiments (Clemens et al. 2009). Adult Pacific lamprey reside in freshwater for approximately 1 y, then migrate farther upstream to spawning habitat during the following spring after first entry into freshwater (Beamish 1980; Clemens et al. 2013). There is evidence that some lamprey may over winter more than 1 y prior to spawning, while others may mature in the ocean and spawn shortly after entry into freshwater (Baker et al. 2014; Clemens et al. 2013).

Most lamprey do not appear to home to their natal streams (Hatch and Whiteaker 2009) and the factors that guide their migration are complex. Recent genetic studies of Pacific lamprey support the conclusions that lamprey lack philopatry (Spice et al. 2012). Instead, olfactory cues (including bile acids, amino acids, and sex

pheromones) apparently guide adult anadromous lamprey movements during both migratory and spawning phases (Li et al. 1995; Johnson et al. 2009; Clemens et al. 2012; Moser et al. 2015). For example, sea lamprey (*Petromyzon marinus*) initially locate freshwater spawning habitats using chemical cues consisting of bile acids released by larval conspecifics and are further guided by sex pheromones released by spermiating males (Li et al. 2002; Johnson et al. 2005). It is likely that the same holds true for Pacific lamprey (Yun et al. 2011).

Several species of fish, marine mammals, piscivorous birds, and humans prey upon Pacific lamprey in their freshwater and saltwater life stages (Close et al. 1995; Orlov et al. 2009; Riemer et al. 2011). Olfactory cues function in predator recognition in lamprey and other fishes (Wagner et al. 2011; Buchinger et al. 2015) and may be especially important during migrations, which expose lamprey to increased risk of predation when passage is delayed at dams (Kirk et al. 2015). Although many studies have investigated fish passage problems and anthropogenic structural barriers and solutions, less is known about natural impediments to passage such as the presence of predators (Jackson and Moser 2012; Keefer et al. 2014).

Injured prey can produce chemical “alarm cues” when the skin is damaged and “kairomones” can be released by predators during a predation event. The chemical cues may be beneficial to the signaler or to the recipient and the strength of the signal can depend on the amount of damage to prey, number of predators and number of prey present, and diet of predators (Wisenden and Chivers 2006; Schoeppner and Relyea 2005). Response to chemical cues from predator diets are a way that a naïve prey may avoid novel predators (Roberts and Leaniz 2011). Adaptive traits such as the ability to respond to alarm cues (“Schreckstoff” response; Mathuru et al. 2012) from predator-injured conspecifics or the ability to learn to recognize predators in the aquatic environment is critical to fitness (Korpi and Wisenden 2001).

Fish use a wide variety of sensory adaptations to monitor their environment and to improve their survival (Munoz and Blumstein 2012; Smith 2012). Several studies indicate that sea lamprey show a strong behavioral response to odors and some predator odors appear to repel lamprey (Wagner et al. 2011; Imre et al. 2014). Imre et al. (2014) tested a variety of predator odors in a seminatural stream channel and observed that sea lamprey had a strong avoidance response to predator odors and responded to alarm cues from conspecifics and sympatric heterospecifics. Strong responses to repellent odors could be used to influence the behavior of migrating fish. For example, manipulation of invasive sea lamprey in the Laurentian Great Lakes using odors has met with some success (Wagner et al. 2011; Di Rocco et al. 2014; Imre et al. 2014; Hume et al. 2015) and similar strong responses by Pacific lamprey could be an important management tool. Using odors to repel Pacific lamprey from locations at dams that hinder successful passage while guiding them with attractants toward installed lamprey passage structures is one example of



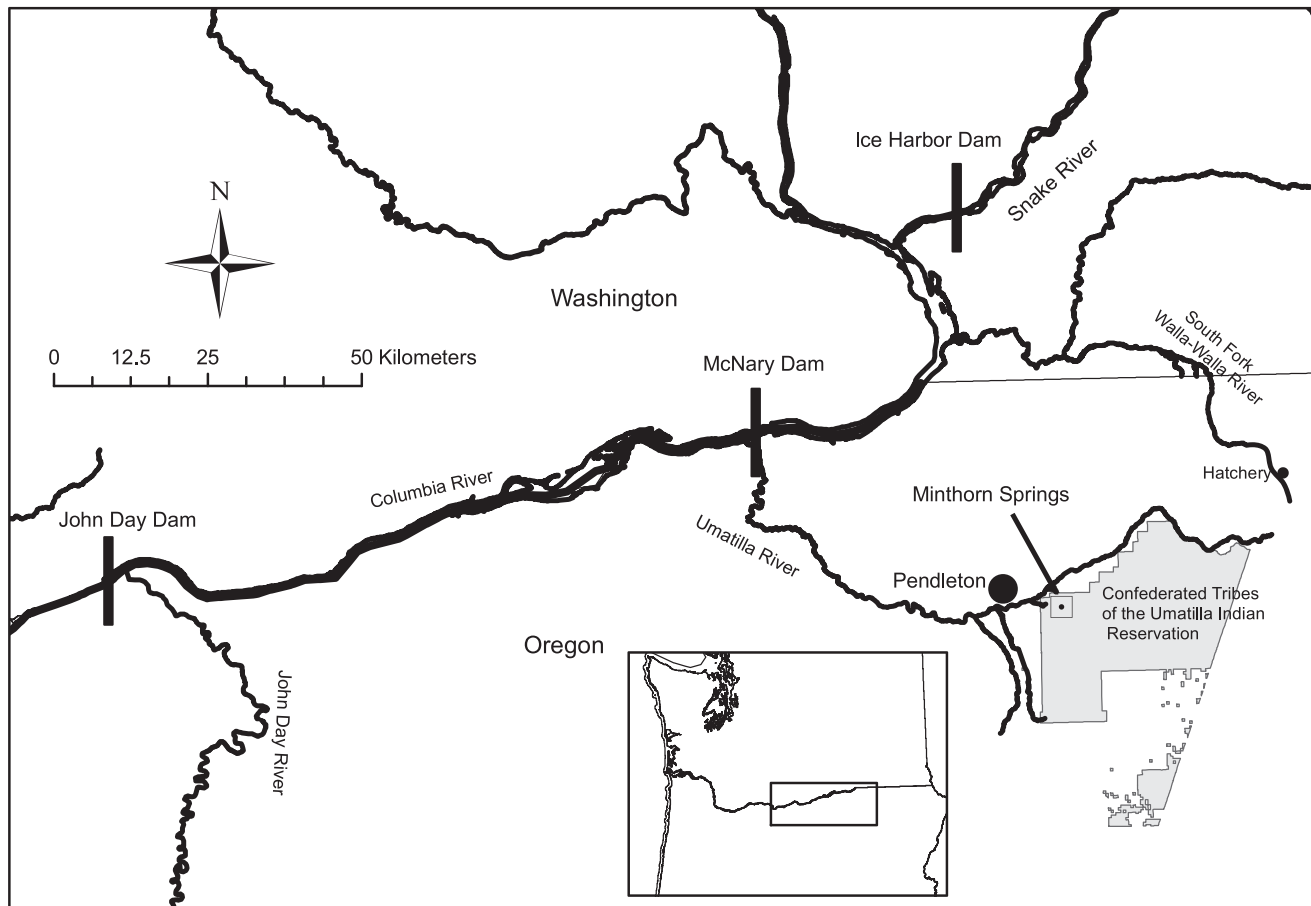


Figure 1. Map showing location where two-choice maze experiments were conducted to test the behavioral responses of Pacific lamprey (*Entosphenus tridentatus*) to four alarm odors during July–October 2014. Indicated sites include the experimental site (Minthorn Springs), locations where lamprey were collected at Columbia River mainstem dams, and an additional holding facility on the South Fork of the Walla Walla River.

their use as a management tool. Additionally, repelling adult migrants from unsuitable reaches or tributaries that have low water quantity or quality and guiding them to better-quality habitat is another way to improve chances for success in ongoing conservation and translocation efforts. However, to our knowledge no studies have been conducted on the response of Pacific lamprey to repellent odors.

In this study, we examined the response of adult, migrating Pacific lamprey to a suite of possible repellent odors: White Sturgeon (*Acipenser transmontanus*), river otter (*Lontra canadensis*), human saliva, and decayed adult Pacific lamprey. We selected these odors on the basis of previous research or local information that suggested that each odor would likely influence the behavior of lamprey. We tested lamprey behavior using a two-choice maze to compare the occupancy time and the total number of entrances fish made when they were exposed to an alarm cue compared with a control (background) odor. In addition, we provide information on lamprey activity patterns during the nighttime hours. The results of this study could have direct implications for use of repellent odors as management tools to effect

positive behaviors and increase lamprey abundance and access to historical spawning areas.

Methods

Experimental animals

We conducted behavioral tests on adult, migratory-phase lamprey at the Minthorn Springs Juvenile Acclimation and Adult Holding Facility, near Pendleton, Oregon (Figure 1). Biologists of the Confederated Tribes of the Umatilla Indian Reservation collected the lamprey at the John Day Dam on the Columbia River (rkm 347) during lamprey migration to spawning grounds (Figure 1). The sex of the fish was unknown because these fish overwinter in Columbia River tributaries before sexual maturation and do not spawn until the following spring. Biologists collected the fish in July 2014 from funnel traps installed at the north and south fishways of the dam. They placed the fish into 300-gallon oxygenated tanks and transported them directly to holding tanks at Minthorn Springs. After acclimating for several days we anesthetized the fish with a buffered solution of 50 mg/L tricaine methane sulfonate (MS 222) and the fish were

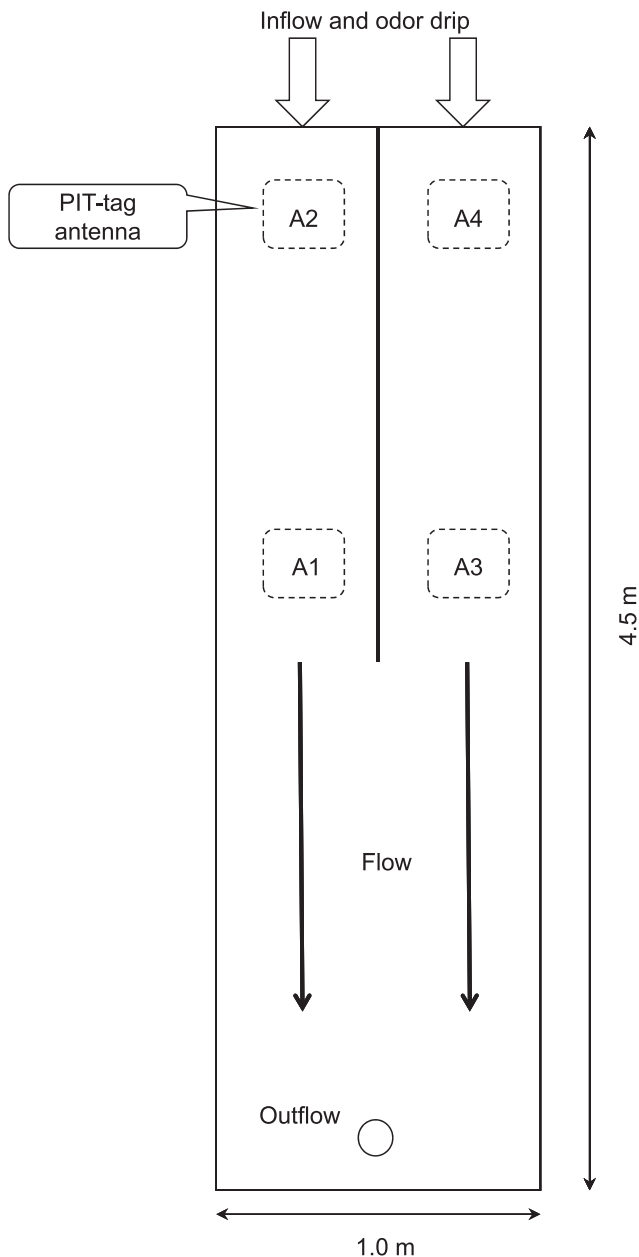


Figure 2. Diagram of the two-choice maze used to test the behavioral responses of Pacific lamprey (*Entosphenus tridentatus*) to four alarm odors during July–October 2014. The diagram shows direction of flow and the location of passive integrated transponder-tag antennas, A1, A2, A3, A4, that were positioned underneath the maze to detect fish movement.

fitted with 23-mm half-duplex passive integrated transponder (PIT) tags using methods from Keefer et al. (2009). We inserted the tags into the body cavity just off the ventral midline and in line with the anterior insertion of the first dorsal fin (Keefer et al. 2009). We measured and weighed the fish and allowed them to recover before then returning the fish to the holding tanks. Because of mortalities, we obtained four additional individuals in September and October from the South

Fork Walla Walla Hatchery (Figure 1). The additional fish were from a mixed group of fish obtained earlier at Bonneville, The Dalles, or John Day dams (Figure 1) during their upstream migration in June through August of 2014. Individuals used for the experiments ranged in length from 610 to 722 mm, mean of 662 mm (SD = 32), and weighed 340 to 570 g, mean of 439 g (SD = 60).

We conducted experiments from July through October 2014. We did not feed the fish throughout the holding period because during the migratory phase of their life cycle adult lamprey do not eat (Beamish 1980). We used each fish only once for each odor experiment, except for one fish that we used twice during the river otter experiment. Overall, we used 13 individuals for the experiments (9 to 10 fish per experiment), but only five fish completed all four odor experiments. The 13 fish ranged in length from 610 to 722 mm, mean of 662 mm (SD = 32), and weighed 340 to 570 g, mean of 439 g (SD = 60).

Experimental conditions

We conducted the experiments in two 4.5 (length) × 1 (width) × 0.6 (height) m fiberglass tanks covered with black plastic to maintain a dark environment. Each tank (hereafter, maze) was divided in half lengthwise over part of its length to make two arms and a reservoir section (Figure 2). We pumped water from Minthorn Springs continuously into the upstream end of each arm at a rate of 6 L/min and water depth in the maze was 20 cm. Water velocity was 0.01 m/s. We measured and recorded water temperatures at the inflow and outflow of each maze daily (Table 1).

Antennas

To detect fish movement we used antennas designed to read PIT tags. We positioned the antennas underneath each arm to detect the fish as they entered and exited the arms: one at the entrance of each arm (A1 and A3) and one at the upper end of each arm (A2 and A4) where the odor was introduced (Figure 2). We did not place antennas under the reservoir portion of the maze; therefore, we detected a fish only as it entered or exited one of the arms. A half-duplex PIT detector for each maze recorded the antenna number and time of each PIT detection. We downloaded the resulting file of all PIT-tag detections at the completion of each experiment. We conducted quality control for PIT antenna performance by using a wand with a PIT tag to assess antenna range and test the accuracy of detection data.

Experimental design

We conducted experiments using four potentially repellent odors: White Sturgeon, human saliva (0.006% solution), decayed Pacific lamprey, and river otter. We selected White Sturgeon for testing because they are known predators of lamprey (Close et al. 1995; Orlov et al. 2009), and it is possible that sturgeon delay the travel

Table 1. Date ranges when experiments were conducted and mean and range of water temperature (°C) from the inflow and outflow of two two-choice mazes used to test the behavioral responses of Pacific lamprey (*Entosphenus tridentatus*) to four alarm odors during July–October 2014.

Odorant	Dates	Mean (range) of inflow	Mean (range) of outflow
White Sturgeon	July 8–25, 2014	13.6 (11.5–17.5)	14.8 (12.0–18.0)
Human saliva	July 28–August 22, 2014	14.1 (13.0–17.0)	15.2 (14.0–18.5)
Decayed lamprey	September 10–29, 2014	12.8 (11.5–15.0)	13.5 (12.0–15.0)
River otter	September 29–October 9, 2014	13.3 (11.5–15.0)	14.0 (12.0–16.0)

times of lamprey during their freshwater migration because sturgeon aggregate at the base of dams (Schultz et al. 2014; Kirk et al. 2015). We obtained water containing sturgeon at the Pacific Northwest National Laboratory from a 1.9-m³ tank holding 84 juvenile sturgeon with an average weight of 1 kg/fish (i.e., 44.2 kg/m³). Water flow at the entrances to Bonneville Dam averages 0.662 m³/min, so we approximated conditions where there would be 0.003 kg of Sturgeon per cubic meter, or approximately one adult White Sturgeon in a 5 × 10 × 200 m fishway entrance area. We expected that the concentration of the sturgeon odor was well above the level that lamprey are exposed to in the natural environment in the Columbia River, and should have been detectable in the mazes. We obtained the control water from the same source (Columbia River) used to rear sturgeon. We froze all odor samples until needed and used the samples undiluted.

We chose human saliva odor on the basis of results from similar studies with sea lamprey (Bals and Wagner 2012; Imre et al. 2014) and on tribal knowledge and personal experience by one of the authors (A.D.J.) that suggests that human saliva can have a repellent effect on Pacific lamprey. It has been reported that saliva is used to assist in harvesting lamprey, as fish will leave resting spots when saliva enters the water. We used a saliva concentration of 0.006% (6 mL of saliva to 6 L of water) on the basis of previous studies of concentrations that elicited a response (Imre et al. 2014). We collected the saliva no more than 24 h before testing from one of the authors (L.L.P.) who did not eat or drink at least 1 h before collection. We obtained the control water from Minthorn Springs. We held all saliva odor samples in the refrigerator until use.

Use of decayed Pacific lamprey as a repellent odor was based on previous studies (Wagner et al. 2011; Bals and Wagner 2012; Imre et al. 2014). To create the decayed Pacific lamprey odor, we placed a partially decomposed, frozen lamprey into a 5-gallon bucket with 1 L of Minthorn Springs water, and allowed it to thaw at ambient air temperature. After an additional 24 h, we divided the water and poured it into 10 glass jars filled to 100 mL and frozen. We removed samples from the freezer 24 h before each experiment to thaw. Once thawed, we mixed a 100-mL odor sample with 4.9 L of Minthorn Springs water, resulting in a 2.0% solution for testing. Previous studies suggest that one fish is sufficient to elicit a response. Although our collection

methods differed slightly from previous studies (Wagner et al. 2011; Bals and Wagner 2012; Imre et al. 2014), lamprey are sensitive to the scent of decayed conspecifics in the natural environment and we anticipated a response in the small experimental mazes.

We selected North American river otter as a test odor on the basis of research that suggests that otters regularly feed on fish (Penland and Black 2009; Toweill 1974) and on personal observations by the authors that otters are frequently observed in the Umatilla River where lamprey aggregate (A.D.J., M.L.M.). Additional information indicates that some aquatic mammals commonly consume Pacific lamprey (Roffe and Mate 1984); therefore, we thought it likely that a mammal-based odor would stimulate a response from our experimental animals. We obtained odor for the otter experiment from an outdoor tank that provided habitat for two North American river otters at the Woodland Park Zoo (Seattle, WA). On the basis of the tank volume and exchange rate (maximum volume 1,568 L, water exchange five times/h) the odor concentration was likely much greater than would occur in a natural stream. We filled 12 buckets each with 12 L of Seattle City water, the source water for the otter tanks, to use for the controls. We immediately transported all otter odor samples to a freezer, stored until used in experiments, and used undiluted.

Odor experiments

We tested 10 Pacific lamprey in each experiment except for the White Sturgeon experiment when we used only 9 fish. We randomly chose each fish from a holding tank that contained only fish not previously used in that experiment. We captured a single fish using a dip net, scanned for a PIT-tag code, and then transferred the fish to one of two randomly assigned mazes and tested over two consecutive nights. We placed each fish into its maze during the daytime, typically from 1000 hours to 1400 hours, and the antennas were turned on at this time; however, we did not expect searching activity to occur until sunset, as lamprey are not active during daytime hours (Robinson and Bayer 2005; Di Rocco et al. 2014). Before the beginning of each experiment, we randomly determined which arm of the maze would receive the odor treatment (hereafter, treatment arm). Subsequently, we alternated the odor treatment between arms. During the first night, we did not add odor to either arm of the maze to evaluate behavior to

measure arm bias by individual fish. During the second day between the hours of 1500 to 1800, we started dripping water containing a repellent odor or water used as a control to the two different arms of each maze. An exception was for two fish during the saliva experiment on one date when we started the odor treatment at 2039 hours. We added the repellent odor and control water via plastic tubing using a peristaltic pump set to drip at a rate of 5 mL/min. We monitored the pumps for at least 10 min to ensure they were working properly and they ran for at least 12 h, subjecting the fish to a minimum of 12 h of odor.

At the completion of each test, we placed each lamprey in the “tested” tank. In addition, we measured any remaining odor solution to ensure that we exposed each fish to the odor treatment at the desired rate for the full 12 h. We filled and rinsed each maze three times to ensure that no residual odor remained before starting a new test. We measured the water inflow temperature and outflow temperature of the mazes and monitored the condition of all fish daily as required by U.S. Geological Survey Animal Care and Use Permit #2008-33.

Statistical analysis

We collected data for the entire time the fish was in the two-choice maze. However, lamprey are active at night and tend to rest during daylight hours; therefore, we chose to analyze fish behavior only for the data collected during the 12-h nighttime period of 1800 to 0600 hours. Using a custom script written in the R language (R Core Team 2013), we processed the raw data (Table S1, *Supplemental Material*) to recognize and remove any erroneous detections. These errors included records that did not follow a logical detection series such as fish being detected in the upstream arm without a detection at the entrance to the upstream arm, and detections of fish in the adjacent maze due to bleed-over of the signal. We analyzed the clean data set for the number of entries (counts) and duration of time spent in each arm. We then compared the counts and duration between the treatment arm and the control arm. We used a conservative approach to counting entries and duration by using only the data from the A2 and A4 antennas (those closest to the drip end of the arms rather than at the entrance to the arm). We found no significant arm bias during any of the experiments ($P > 0.05$; Wilcoxon signed-rank test) and to determine odor effects on fish behavior, we analyzed the data from the second night using a two-tailed Wilcoxon signed-rank test of correlated samples (Whitlock and Schluter 2015) with a significance of $P < 0.05$.

We summarized the start and end times for fish activity by recording the first time the fish began movement in the evening hours after 1800 hours and the last movement detected in the morning before 0600 hours, our designated end time. A few fish continued to move outside of the hours that we set for data analysis,

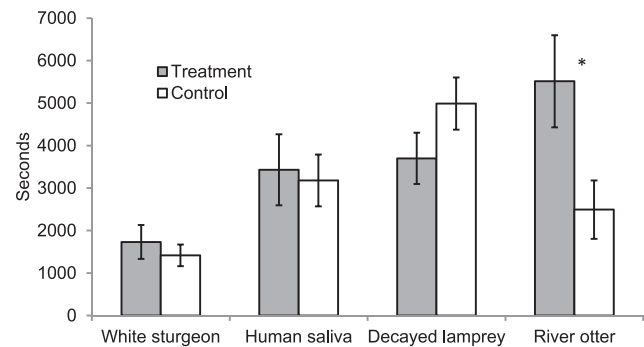


Figure 3. Mean (SE) duration of time spent in the treatment (odor added) or control arms of a two-choice maze used to test the behavioral responses of Pacific lamprey (*Entosphenus tridentatus*) to four alarm odors during July–October 2014. Asterisk indicates a significant difference between bar pairs (control night and treatment night, Wilcoxon test, $P < 0.05$).

but most fish movement occurred during this time range. We also computed the start time relative to sunset (time = 0) on each night of each test (<https://www.weather.gov/climate/astronomical.php?wfo=pdf>). That is, we subtracted the time of sunset from the start time of fish activity to produce a value for time from sunset. We used analysis of variance to assess the effects of fish (five fish were used in all four experiments), night (control vs. treatment), and experiment (four odor experiments) on time from sunset. The model also included all interaction terms and we used the Tukey multiple comparison test to identify differences among means for significant effects.

Results

Duration of time

During the experiment using the river otter odor there was evidence for a significant attractant effect on the duration of time that adult lamprey spent in each arm of the maze (Wilcoxon signed-rank test, $P < 0.05$; Figure 3). The mean duration of time in the control arm was 2,493 s ($n = 10$, SE = 687) compared with 5,514 s in the treatment arm ($n = 10$, SE = 1,084). Experiments for White Sturgeon ($n = 9$), human saliva ($n = 10$), and decayed lamprey ($n = 10$) resulted in no significant differences in time spent in each arm when the odor treatment was added.

Number of entries

Results for the number of entries into each arm (control arm vs. treatment arm) (Figure 4) were similar to the results for duration with a significant attractant effect of river otter odor. There was no evidence for significant differences in entries for White Sturgeon, human saliva, and decayed lamprey ($P > 0.05$). However, there was a significant difference in the number of entries for the river otter odor ($P = 0.005$), with an average of 69 counts (8 SE) for the control arm compared with 110 counts (12 SE) for the treatment arm (Figure 4).

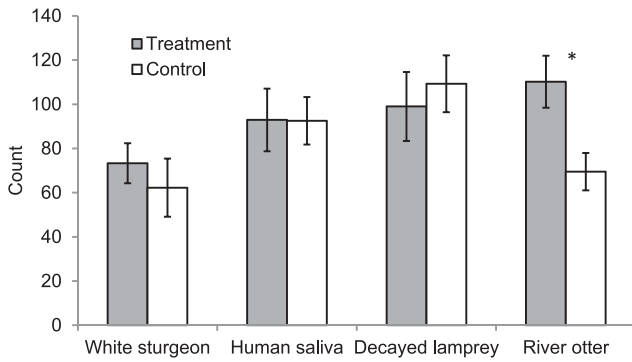


Figure 4. Mean (SE) number of counts for fish entering the treatment or control arms of a two-choice maze used to test the behavioral responses of Pacific lamprey (*Entosphenus tridentatus*) to four alarm odors during July–October 2014. Asterisk indicates a significant difference between bar pairs (control night and treatment night, Wilcoxon test, $P < 0.05$).

Fish activity

The lamprey tested in our experiments were consistently active at night. There was a significant difference in the number of entries between tests conducted on the first night when no odor was added and the second

Table 2. Mean number of entries made by adult Pacific lamprey (*Entosphenus tridentatus*) into the arms of a two-choice maze during the 12-h control night (night 1) and the 12-h treatment night (night 2) during experiments to test the behavioral responses to four alarm odors (n = number of fish tested) during July–October 2014.

Night	Odor			
	White Sturgeon ($n = 9$)	Human saliva ($n = 10$)	Decayed lamprey ($n = 10$)	River otter ($n = 10$)
Control	205	228	262	264
Treatment	112	185	208	180
Difference	93	43	54	84

night when odor was added ($\chi^2 = 8.42$; $df = 3$; $P < 0.03$; Table 2). The majority of fish appeared to move little during daylight hours and typically started activity in the early evening (Figure 5). On the basis of the five fish used in all four experiments, the mean time that movement started in the sturgeon odor experiments was significantly later ($F = 14.21$, $df = 3$, $P < 0.01$; 162 min after 1800 hours) than in the saliva experiment (91 min) or the decayed lamprey and river otter experiments (both 54

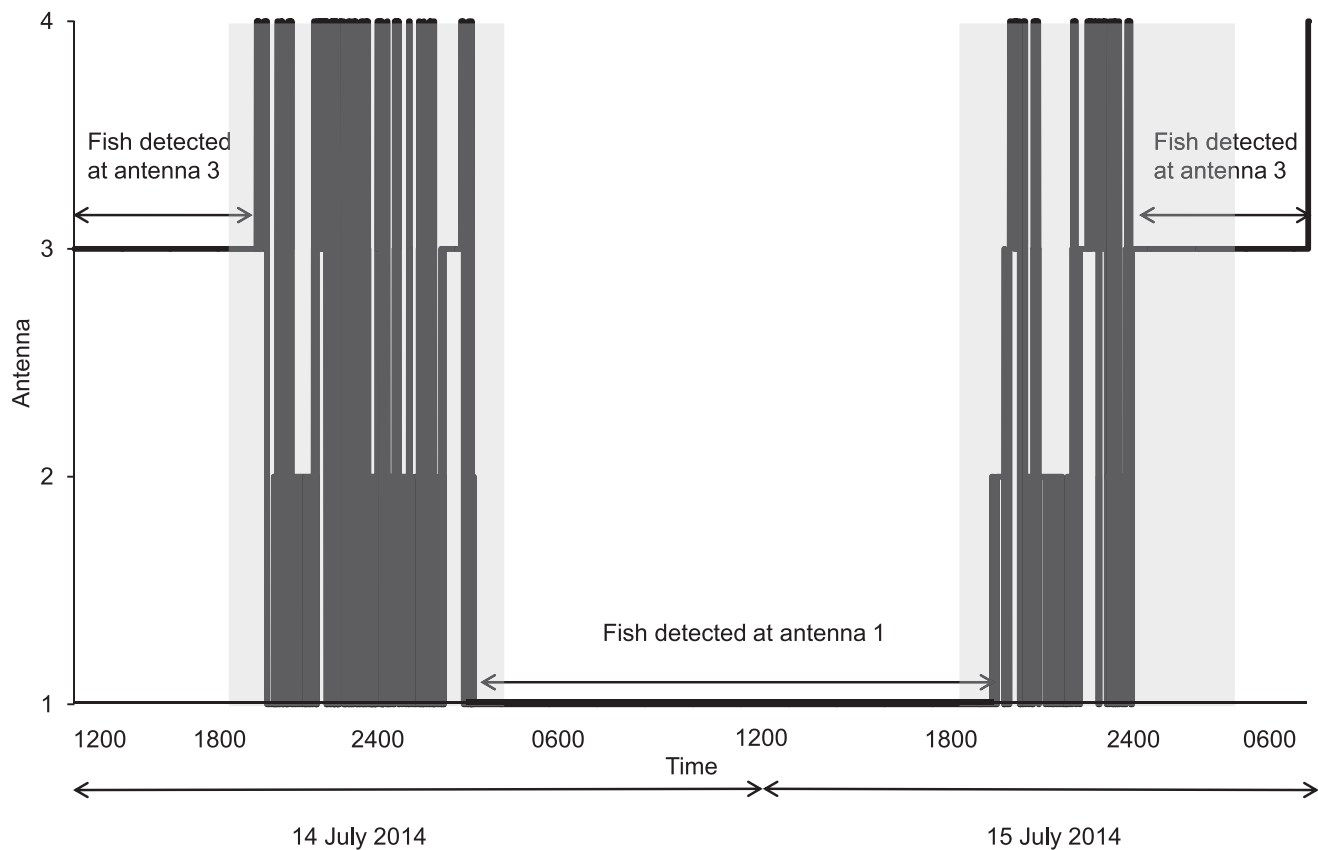


Figure 5. Bar graph showing an example of typical activity over 12 h based on passive integrated transponder -tag detections for one fish detected at each of four antennas in a two-choice maze used to test the behavioral responses of Pacific lamprey (*Entosphenus tridentatus*) to four alarm odors during July–October 2014. Bars at each height represent a detection at the associated antenna. Antenna numbers 1 and 3 represent the entrances to each arm of the two-choice maze, whereas antenna numbers 2 and 4 were nearest the inflow and odor drip in each arm of the maze. The shaded areas represent nighttime periods (sunset to sunrise).

min). This effect was likely related to when sunset occurred: mean sunset time for each experiment was: White Sturgeon 2041 hours; saliva 2002 hours; decayed lamprey 1926 hours; river otter 1833 hours. The analysis of the start of activity relative to sunset (time from sunset) revealed a significant difference among experiments ($F = 6.37$, $df = 3$, $P < 0.01$). On average, fish in the saliva experiment started moving approximately 43 min before sunset, whereas fish in other experiments started activity near sunset (range -8 to 14 min). A small but significant effect between nights (i.e., treatment vs. control; $F = 5.44$, $df = 1$, $P = 0.03$) was also found. On average, during the first night of testing (no odor added) fish started moving 21 min before sunset, whereas movement on the second night (odor added) was 2 min after sunset. Mean start times among individual fish were not significantly different ($F = 2.55$, $df = 1$, $P = 0.06$) and no interactions were significant ($P > 0.12$).

Discussion

We tested four potential repellent odors for effects on the behavior of Pacific lamprey. Of the odors tested, only river otter (aquatic mammalian predator) odor resulted in a significant difference in the duration of time and in the number of entries between the treatment and the control arms of the maze. However, it appeared to attract, not repel, lamprey. Some fish respond to predator cues by decreasing swimming activity or seeking cover if available (Lehtiniemi 2005). Fish response may also be dependent on water temperature or fish activity when exposed to the odor. For example, Di Rocco et al. (2014) tested the daytime response of sea lamprey to predator cues (2-phenylethylamine and human saliva) at varying water temperatures and found that when the water temperature reached a mean of 13.7°C lamprey that were already moving responded to the predator cue with increased movement; however, lamprey that were resting or hiding remained in place. Thus, it was possible that for our study, a fish that remained in an arm after we released odor may have been resting or exhibiting antipredator behavior by decreasing movement or changing location vertically and moving to the bottom or sides of the tank within the odor arm. Similarly, studies on juvenile Chinook salmon (*Oncorhynchus tshawytscha*) showed that fish responded to predator cues of native northern pikeminnow (*Ptychocheilus oregonensis*) by staying motionless for 70% of the time during the lab experiment, whereas in the field experiment they spent time near the substratum, fleeing, or reducing movement (Kuehne and Olden 2012). In a predator-avoidance experiment with shark (*Chiloscyllium punctatum*) embryos, the embryos ceased gill movement to avoid detection when presented with an electrical impulse that mimicked a predator cue (Kempster et al. 2013).

The response of adult lamprey to the odor from human saliva (mammalian predator) did not show any significant effects. On the basis of traditional tribal

knowledge, it should have repelled the lamprey (A.D.J., personal communication), and Imre et al. (2014) noted that sea lamprey likely recognize a component in human saliva that is present in other mammalian prey species, thus recognizing humans as predators. However, we derived the odor sample for this experiment from only one person and this may have been insufficient to cause an effect. Further testing to determine whether Pacific lamprey respond consistently to human odors is particularly important for assessment of lamprey passage at dams where Pacific lamprey adults may be regularly exposed to human odors (from people conducting dam maintenance). In addition, the presence of human odors on structures used to aid lamprey passage could limit their efficacy. In fact, Pacific lamprey exhibit reduced use of newly installed structures (Moser et al. 2011). A better understanding of lamprey sensitivity to human odors and the effects of human odor on migratory behavior is clearly important.

We also expected a response to White Sturgeon (aquatic predator). Sturgeon are known to prey on lamprey and lamprey are often used as sturgeon bait by anglers. Diet cues from predators are known to produce a behavioral response in prey (Mirza and Chivers 2001; Roberts and Leaniz 2011) and a fish encountering a novel predator may be alerted when the chemical odor from a consumed conspecific passes through the digestive tract of the predator and is released to the aquatic environment. In our study, neither the river otter nor the White Sturgeon was fed a diet that included Pacific lamprey and thus the response may have differed from what would be expected in the natural environment. However, because Pacific lamprey are a conservation concern, using them as fish food in our study was not an option. Understanding the effects of predator odors on lamprey behavior has practical applications at dams where predators congregate. Kirk et al. (2014) noted that the vertical position of lamprey in the water column was affected by presence of White Sturgeon. Hence, the presence of sturgeon could potentially prevent lamprey from finding or using fishway entrances. It is possible that the hatchery-reared juvenile sturgeon that produced the odor used in our experiments were not producing compounds that lamprey respond to. It is also possible that lamprey behavior in the presence of sturgeon is mediated by a combination of sensory stimuli: olfactory, electrical, and visual cues.

A repellent effect from decayed lamprey odor (conspecific alarm cue) was anticipated. Similar studies have been conducted where sea lamprey responded to conspecific and heterospecific alarm cues by avoiding the laboratory stream channel where the odor was released (Wagner et al. 2011; Imre et al. 2014). Moreover, Byford et al. (2016) recently reported that odor extracted from a dead Pacific lamprey produced an avoidance response in sea lamprey. It is possible that the concentration of dead lamprey odor we used was lower than necessary or that a different preparation technique was required to alter the behavior of adult Pacific lamprey. For example, grinding the skin of sea lamprey

produced a stronger repellent effect than intact skin (Bals and Wagner 2012). Moreover, the chemical responsible for the alarm cue may have dissipated to an undetectable or barely detectable level by the time we collected the decayed lamprey for use in our experiment. Although our experiment did not show a significant effect of decayed lamprey odor on fish behavior, this odor did appear to reduce the time lamprey spent in the treatment arm in most tests (7 of 10). This was also the only experiment in which the duration of time spent in the treatment arm was lower than that spent in the control arm. For these reasons, further investigation with more experimental animals is recommended.

The chemical cues that result in a behavioral response in prey are complex and involve signals released from both the predator and prey; cues differ during different stages of predation, allowing prey to evaluate the severity of the risk they face (Wisenden and Chivers 2006). Lamprey may be responding to a combination of sensory inputs (not solely scent) when reacting to predators or alarm cues. A study of teleost fish found that the sight and scent of an injured conspecific combined with the scent of a novel predator produced a greater repellent response than scent of the novel predator alone (Ward and Figiel 2013). We conclude that the response of adult Pacific lamprey to both White Sturgeon and human saliva was neutral; however, it was possible that the concentrations of our extracts were not sufficient to elicit a response or that we may have seen a stronger response if we had combined the conspecific alarm cue with the saliva and sturgeon odors, similar to results of Lautala and Hirvonen (2008).

Pacific lamprey were consistently active during the nighttime. In the future, tests may need to be conducted for a shorter period of time. Analysis of a subset of data from 1800 to 2400 hours produced similar results to those presented here. The cause for the reduction in the number of entries from the first night (no odor drip) to the second night (odor drip) for all experiments is unknown but may have been a result of lamprey acclimation to the experimental mazes. Differences in activity could also have accounted for the reduction in entries; however, differences in means for first lamprey movement from sunset between the first and second nights of experimentation were small (21 min). Although the data did not show significant differences in the initiation of movement among individual fish, mean start times were variable (range 35 min before sunset to 10 min after sunset) and other observations of lamprey behavior have provided evidence for significant effects of individual lamprey temperament (Moser et al. 2013; R. L. McLaughlin, University of Guelph, personal communication). The ability to track activity of a larger number of lamprey over more sequential nights would help to tease out this component.

Conclusion

As an anadromous fish, it is imperative that lamprey are able to migrate successfully to suitable spawning habitat if restoration efforts are to be effective. During

their freshwater migration, lamprey navigate through a series of dams on the Columbia River and its tributaries and these structures can be barriers to migration (Jackson and Moser 2012; Keefer et al. 2014). Using fishes' natural response to odors to guide them away from hazards and toward preferred routes could be a useful management tool, as it often requires small amounts of a chemical cue for detection over long distances (Hume et al. 2015; Sorensen and Stacey 2015). Perceived barriers that slow lamprey at the dams are complex and may consist of a combination of predators, flow, and structural challenges (Kirk et al. 2014; Keefer et al. 2015). Although the current study showed only limited effects from the repellent odors tested, future research into Pacific lamprey responses to chemical signaling is needed. For sea lamprey, extensive efforts to isolate and synthesize specific chemicals that stimulate lamprey behavior have increased options available for management of this species in the Great Lakes (Hume et al. 2015). A similar program to identify repellent odors or alarm cues in Pacific lamprey may provide new techniques to manage and recover this imperiled species (Moser et al. 2015; Byford et al. 2016).

Supplemental Material

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Data S1. Raw data from two-choice maze experiments in a text file from passive integrated transponder tag readers for each individual fish in White Sturgeon trials. Each row of data represents a fish detection at a specific antenna at a specific time. The data may include anomalous records that require data processing before analysis. Columns one through eight represent 1) date, 2) time stamp, 3) total duration, 4) tag type, 5) tag number, 6) antenna number, 7) number of tag detections, 8) number of empty scans before the tag was detected.

Found at <http://dx.doi.org/10.3996/042016-JFWM-033.S1> (836 KB zip).

Data S2. Raw data from two-choice maze experiments in a text file from passive integrated transponder tag readers for each individual fish in the human saliva trials. Each row of data represents a fish detection at a specific antenna at a specific time. The data may include anomalous records that require data processing before analysis. Columns one through eight represent 1) date, 2) time stamp, 3) total duration, 4) tag type, 5) tag number, 6) antenna number, 7) number of tag detections, 8) number of empty scans before the tag was detected.

Found at <http://dx.doi.org/10.3996/042016-JFWM-033.S2> (970 KB zip).

Data S3 Raw data from two-choice maze experiments in a text file from passive integrated transponder tag readers for each individual fish in the decayed Pacific

lamprey trials. Each row of data represents a fish detection at a specific antenna at a specific time. The data may include anomalous records that require data processing before analysis. Columns one through eight represent 1) date, 2) time stamp, 3) total duration, 4) tag type, 5) tag number, 6) antenna number, 7) number of tag detections, 8) number of empty scans before the tag was detected.

Found at <http://dx.doi.org/10.3996/042016-JFWM-033.S3> (1396 KB zip).

Data S1. Raw data from two-choice maze experiments in a text file from passive integrated transponder tag readers for each individual fish in the river otter trials. Each row of data represents a fish detection at a specific antenna at a specific time. The data may include anomalous records that require data processing before analysis. Columns one through eight represent 1) date, 2) time stamp, 3) total duration, 4) tag type, 5) tag number, 6) antenna number, 7) number of tag detections, 8) number of empty scans before the tag was detected.

Found at <http://dx.doi.org/10.3996/042016-JFWM-033.S4> (1460 KB zip).

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