Push and pull of downstream moving juvenile sea lamprey (*Petromyzon marinus*) exposed to chemosensory and light cues

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Visual and olfactory stimuli induce behavioural responses in fishes when applied independently, but little is known about how simultaneous exposure influences behaviour, especially in downstream migrating fishes. Here, downstream moving juvenile sea lamprey (*Petromyzon marinus*) were exposed to light and a conspecific chemosensory alarm cue in a flume and movement were monitored with overhead cameras and nets. When exposed to light, sea lamprey were more likely to be captured in a net closest to the light array. When exposed to the alarm cue, sea lamprey transit rate through the flume increased, but sea lamprey did not avoid the alarm cue plume by moving perpendicular to flow. When the alarm cue and light were applied simultaneously in a push and pull configuration, the alarm cue still triggered enhanced downstream movement (push downstream) and more sea lamprey was still captured in the net nearest the light (pull to the side), resulting in twice as many sea lamprey being captured in the lighted net relative to controls. To our knowledge, this is the first study using multiple sensory cues in a push-pull configuration to modulate fish outmigration. Push and pull of juvenile sea lamprey with sensory cues could be useful to reduce turbine entrainment where native and enhance trap catch where invasive.

**Key words:** Alarm cue, lamprey, light, migration, push-pull

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**Introduction**

Fish behaviour is modulated by sensory information about the aqueous environment (Atema *et al.*, 2012). For example, many migrating fishes use olfactory and gustatory cues to locate natal streams (Hara, 1994; Dittman and Quinn, 1996) and avoid predators (Wisenden, 2015), photoreceptors to image their environment and influence movement timing and location (Guthrie, 1986) and superficial neuromasts to detect flow fields and adjust swimming speed and trajectory (Montgomery *et al.*, 1997). As such, artificially modifying the sensory information landscape to manipulate fish movement may be a useful means to achieve restoration and invasive species control objectives (Noatch and Suski, 2012). However, constructing an effective intervention requires an understanding of how multimodal sensory information modulates...
physiology and behaviour in both laboratory and natural environments (Douglas and Hawryshyn, 1990; Johnson and Li, 2010) and how the roles of internal and external context regulate movement decisions (Nathan et al., 2008).

Two classes of sensory information hold particular promise for manipulating fish behaviour. Artificial light has been investigated as a cue to modify fish behaviour for nearly 60 years. Most fishes have photoreceptors that discern wavelength, intensity and direction (polarity) of light. Exposure to artificial light, both continuous and pulsed, can induce negative (Noatch and Suski, 2012) or positive phototaxis (Rich and Longcore, 2005; Ford et al., 2018). Salmonids detect wavelengths ranging from ultra violet through the visible spectrum (Bowmaker and Kunz, 1987) and strobed arrays of white light have frequently been tested to induce avoidance responses in outmigrating salmon smolts to reduce entrainment at hydropower dams (Brown, 2000; Hamel et al., 2008). The application of odours that convey information between and within species to modify fish behaviour (semiochemicals) also has received considerable interest. Most fishes have acutely sensitive olfactory systems (Hara, 1994) and can be attracted or repulsed by a wide array of odours (Sorensen and Johnson, 2016). For example, odours produced when fishes are injured (damage-released alarm cues) often repel conspecifics and are closely related heterospecifics (Dalesman et al., 2007; Hume and Wagner, 2018). Hume et al. (2015) recently demonstrated that this odour may be used to guide migrating adult sea lampreys towards traps in Great Lakes tributaries. Research into the use of semiochemicals in management to modify fish behaviour, whilst holding promise (Sorensen and Johnson, 2016) is poorly understood (Johnson et al., 2013) and is especially understudied in downstream migrating fishes (Schmucker et al., 2017).

Behavioural modification tactics integrating two or more sensory stimuli can induce more consistent behavioural responses in fishes than individual stimuli. Information from multiple sensory modalities can act synergistically, complementarily, be redundant, or conflict (Moller, 2002; Montgomery et al., 2002). Sounds, light and bubbles are often tested together (Sager et al., 1987) with some success. The integration of acoustic stimuli within visual stimuli (bubble curtains) deterred a high proportion (~95%) of bighead carp (Hypophthalmichthys nobilis) in a lab-based experiment (Taylor et al., 2005). Some sensory stimuli can complement each other in push-pull configurations, where one stimulus induces an avoidance response and the other induces attraction (Miller and Cowles, 1990; Cook et al., 2007; Hume et al., 2015). However, to our knowledge, the combination of attractant light and repellent odour has not been tested in fishes, but should operate complementarily in push-pull configurations.

Sea lamprey (Petromyzon marinus) is targeted for restoration in its native range (North Atlantic) and control where invasive (Laurentian Great Lakes; Hansen et al., 2016). Hydropower dams interrupt sea lamprey life history by blocking some adults from reaching spawning grounds and by entraining outmigrating juveniles (Mailtland et al., 2015; Moser et al., 2015). Artificial light pollution from urban areas could influence sea lamprey outmigration behaviour and impact conservation, especially since many sea lamprey producing streams flow through large cities near their confluence with the ocean (Marchesan et al., 2005; Gaston et al., 2013). Depending on the goal, manipulating juvenile sea lamprey migration behaviour with sensory cues could be useful to reduce harmful effects where native and enhance trap entrainment where invasive (Guo et al., 2017).

Here, we hypothesized that emigrating juvenile sea lamprey detects and behaviourally responds to light and olfactory stimuli to reduce risk of predation. Juvenile sea lamprey emigrates from natal streams at night during high discharge events (Sotola et al., 2018), presumably to minimize risk of predation (Potter, 1980). Therefore, sea lamprey may use light and odour cues to guide or modulate the trajectory and speed of outmigration. Physiologically, juvenile sea lamprey are sensitive to individual photons of light (Morshedian and Fain, 2015) and low-intensity white light (10 lux; Binder et al., 2013). Behaviourally, juvenile sea lamprey moved towards and were more likely captured in nets closest to the wall of a large flume when white light were activated along the wall at low intensity (10 lux) relative to high intensity (100 lux) or off (darkness; Haro et al., submitted). Juveniles of the closely related European river lamprey (Lampetra fluviatilis) show an increase in migratory activity in the field when light levels decrease below 0.1 lux and locomotor activity increases at night in laboratory experiments when light level is below 0.9 lux (Zvezdin et al., 2018). Sea lamprey also have well-developed olfactory organs and exceptionally large olfactory bulbs relative to the brain (Kleerekoper, 1972). This anatomically dominant system is highly sensitive to compounds that regulate prey-searching (Kleerekoper and Mogensen, 1959, 1963) and upstream migration of adults (Teeter, 1980; Buchinger et al., 2015). An alarm cue contained in the skin and tissue of conspecifics induces antipredator behaviour in upstream migrating adult sea lamprey including spatial avoidance (Bals and Wagner, 2012; Imre et al., 2014) or altered movement speed and timing if the alarm cue cannot be avoided (Lühring et al., 2016). Larvae burrowed in river sediments exhibit less downstream drift when exposed to the alarm cue (Wagner et al., 2016). The response to alarm cue has not been tested on downstream migrating juveniles following metamorphosis into the parasitic feeding phase. Therefore, an outstanding knowledge gap is: if and how downstream migrating sea lamprey behaviourally responds to chemosensory alarm cues and how the response to the alarm cue changes when exposed to artificial light?

Our objective was to determine how speed and direction of juvenile sea lamprey downstream movement were influenced by exposure to chemosensory alarm cues and light. We predicted that (i) exposure to light would slow
downstream movement and induce movement towards the lighted structure as previously described (Haro et al., submitted), (ii) exposure to the alarm cue would increase the probability of downstream movement and swimming speed as a means to increase distance from a predator and (iii) exposure to light and alarm cue simultaneously in a push-pull configuration would cause more sea lamprey to move downstream away from the source of alarm cue (push downstream) and towards the lighted structure (pull to the side). The objective was accomplished by exposing juvenile sea lamprey moving downstream in a large hydraulic flume to light, alarm cue, light and alarm cue combined and no artificial sensory cues. Variables monitored included: (i) spatial distribution of sea lamprey at the end of the trial with nets, (ii) time sea lamprey arrived at downstream end of the flume with video and (iii) swimming speed and orientation of sea lamprey in a video observation area within the flume.

Material and methods

Experimental animals

Recently, metamorphosed juvenile sea lamprey were hand collected on 18 September 2017 following a reservoir drawdown at a hydropower intake canal on the Connecticut River near Turners Falls, MA, USA. Sea lamprey were held at the adjacent US Geological Survey, S.O. Conte Anadromous Fish Research Laboratory (Conte Lab) in 2 m diameter tanks with ambient water from the Connecticut River and mesh nylon netting (1.3 x 1.3 cm) for shelter. Recently metamorphosed juvenile sea lamprey generally do not feed in streams, so no food were provided (Davis, 1967). Sea lamprey were used first in the experiment testing light cues described in Haro et al., (submitted). Sea lamprey were reused for two reasons. First, the number of sea lamprey were limited. Second, the goal was to understand how sea lamprey respond to the alarm cue alone and alarm and light cues. Therefore, trials testing only light and control trials with sea lamprey already tested by Haro et al., (submitted) were used to confirm consistency in the behavioural response to light and the utility of the bioassay for testing responses to the alarm cue. Experimental protocols involving sea lamprey were in accord with United States federal guidelines for care and use of animals as approved by the American Fisheries Society through the ‘Use of Fishes in Research Committee’, 2014.

Experimental arena

A hydraulic open-channel flume at the Conte Lab was used for behavioural trials (Fig. 1). The total length of the test arena was 22.8 m and consisted of a 2 m wide and 7 m long channel in the middle of the flume from which sea lamprey were released (release channel). Upon exiting the release channel, sea lamprey entered a 6 m wide section of the flume that was 15.8 m long (observation channel). Sea lamprey were introduced into the upstream end of the release channel after acclimating in a bottomless floor-mounted release cage that was lifted out of the water at the start of a trial. The cage was 0.6 m high and 0.5 m wide and constructed of perforated sheet aluminium (Miehls et al., 2017a). Five sea lamprey collection nets were arrayed across the width of the channel to catch sea lamprey exiting the downstream end of the flume (Miehls et al., 2017a). Nets were constructed of 9.5 mm delta mesh nylon netting with mouth openings 2.0 m tall and 1.2 m wide and were 7.9 m long from mouth to end of codend. Net codends were constructed of buckets (18.9 l) fitted with a conical funnel made from the same 9.5 mm delta mesh netting.

The flume was supplied with water directly from the Connecticut River to produce a depth of 0.5 m and a target water velocity of 0.25 m sec⁻¹. Supply water was passed through flow straighteners at the upstream end of the flume to produce linear flow throughout the test arena. Water velocity was measured 0.25 m from the substrate on a 1.6 m grid throughout the test arena using a Marsh-McBirney model 201D flowmeter with a 1D electromagnetic probe (Fig. 2a).

Sensory cues

The light stimulus were introduced using a linear light array consisting of four light emitting diode (LED) linear tape lights (SuperBrightLEDs; model SE-WFLS-CW300X3; 6500 K, 1027 lumens/m) attached to the inside of a 9.7 m long and 7.5 cm wide aluminium C-channel (herein, termed ‘light array’). Light output was controlled with a dimming circuit (SuperBrightLEDs; model LDK-8A; pulse width modulating dimmer) connected to each tape light. This light array was mounted to the east wall (herein, referred to as ‘left wall’ as referenced looking downstream) 0.5 m above the water to project light vertically down at the substrate (Fig. 1). The light array and intensity were the same as in Haro et al., (submitted; 10% above water setting) and induced the strongest positive phototaxis in the Haro et al., study. Light intensity was measured 0.25 m from the substrate on a 1.6 m grid throughout the test arena using a LI-COR LI-1000 light meter with SPQA-1186 spherical quantum sensor (nearest 1 lux; minimum light sensitivity 0.27 lux). Non-linear extrapolation between sample points was used to estimate light intensities throughout the flume (Fig. 2b).

Sea lamprey alarm cue was extracted from larvae sea lamprey. The cue is contained in larval tissue and both larvae and migrating sub-adults respond to the larval cue, suggesting no life-stage specific variation in its chemical composition (Bals and Wagner, 2012; Wagner et al., 2016). Sea lamprey larvae ranging from 60 to 110 mm were collected from the Platte River, MI, during May 2017 by staff of the US Fish and Wildlife Service. Larvae were transported to US Geological Survey, Great Lakes Science Center, Hammond Bay Biological Station and held in 1000 l tanks supplied with ambient water from Lake Huron and containing 10 cm of sand for larval burrowing. Larvae were fed brewer’s yeast once weekly (Hanson et al., 1974). During September 2017,
Figure 1: Plan view of laboratory flume facility approximately to scale, showing layout of release, observation and recovery areas, where responses of recently metamorphosed sea lamprey to light and chemosensory alarm cues were evaluated. Water flow is from left to right. White zones of observation areas indicate areas covered by retroreflective sheeting. Orange shading in release channel is where the chemosensory alarm cue were applied.

Table 1: List of treatments, associated number of trials, the total number of sea lamprey released over all the trials per treatment and the final disposition of each sea lamprey at the end of the trial according to the locations illustrated in Fig. 1.

| Treatment         | Trials | Number released | Release channel | Observation channel | Net 1 (east-light) | Net 2 | Net 3 | Net 4 | Net 5 (west) |
|-------------------|--------|-----------------|-----------------|---------------------|-------------------|-------|-------|-------|--------------|
| Control           | 5      | 145             | 36              | 14                  | 32                | 15    | 16    | 11    | 21           |
| Odour only        | 5      | 145             | 18              | 16                  | 37                | 9     | 15    | 21    | 29           |
| Light only        | 4      | 119             | 33              | 20                  | 38                | 5     | 10    | 6     | 7            |
| Odour and light   | 5      | 154             | 21              | 8                   | 65                | 17    | 9     | 15    | 19           |

10.0 kg of larvae (~10 000 larvae total, 1 g each) were dug out of the holding tanks, euthanized and frozen in plastic bags at −80°C. Larvae carcasses were extracted on 31 October 2017 at Michigan State University using a pair of 2.1 m Soxhlet extractors each equipped with water-cooled Allihn condensers and 12 l solvent reservoirs heated with hemispherical mantles to 75–80°C. Larvae were divided equally between the two extractors and extracted with a 50:50 solution of 200 proof ethyl alcohol and deionized water for three cycles. Extract was then rotoevaporated at 35°C under a vacuum to remove most of the ethanol, producing 8.3 l of the alarm cue that was aliquoted into 1 l bottles and stored at −20°C. Given this extraction protocol, 1 ml of extract consists of the odour of roughly 0.588 g of larvae carcass.

Sea lamprey alarm cue was introduced into the test arena using a diffuser hose (Bubble Tubing®, Canadian.pond.ca). The hose were positioned perpendicular to streamflow 1 m upstream of where the release channel exited into the observation area (Fig. 2c). The diffuser hose were doubled back over the release channel (2 m wide) and placed 0.25 m above the substrate to increase chances that sea lamprey exiting the release channel would immediately be exposed to the alarm cue. Prior to experimentation, 225 ml of the alarm cue (equivalent to ~150 g of extracted sea lamprey) was added to 30 l of water and the solution were pumped (Little Giant Pump; Model 2E-38N) into the arena for 12 min at 2.5 l per min (0.201 g of extracted larvae per second) through the 4 m diffuser. Given the discharge of the flume (250 l sec⁻¹) and application rate of the alarm cue (0.201 g of extracted larvae per sec), each litre of water in the flume were activated with 0.80 mg of extracted larvae if fully mixed at the downstream section of the flume, which is similar to the rate reported by Bals and Wagner (2012; 1.1 mg of extracted larvae per l of water in the experimental arena). The distribution of the alarm cue in the arena was mapped using rhodamine dye (Turner Designs, Rhodamine WT, Sunnyvale, CA, USA) using the method described in Johnson et al. (2009) by sampling the same locations as water velocity and light intensity (Fig. 2c).
**Experimental procedure**

Experiments were conducted from 28 November 2017 to 02 December 2017 between 20:00 and 00:00. Four treatments were tested each night: (i) control—no light or alarm cue, (ii) light only, (iii) alarm cue only and (iv) a combination of light and alarm cue. Treatment order was shifted each night to avoid potential confounding effects with time of night. To conduct a trial, between 25 and 31 juvenile sea lamprey were placed in the release cage to acclimate for 10 min. The number of sea lamprey used per trial varied because of changes in the availability of sea lamprey and human error. After 10 min of acclimation, sensory stimuli were activated (light and/or alarm cue depending on treatment) and after 2 additional minutes of acclimation when sensory stimuli were applied, sea lamprey were released. Sea lamprey were allowed 10 min to explore the flume observation area. After 10 min, the entrance to the collection nets at the downstream end of the flume were blocked and the nets were emptied. Sea lamprey remaining in the release channel and observation channel were recovered with dip nets. The number of sea lamprey captured in each collection net, the release channel and observation area were tallied. After a 10 min
flume flushing period, another batch of sea lamprey were placed in the release cage to acclimate for the next trial.

**Observation of sea lamprey behaviour in the flume**

Sea lamprey behaviour and distribution were monitored at three transects in the flume using cameras: (i) one camera monitored where the release channel exited into the observation area (herein termed ‘release observation’; Fig. 1), (ii) two cameras monitored a transect 4.9 m downstream of the release channel (herein termed ‘flume observation’; Fig. 1) and (iii) three cameras monitored the downstream end of test arena, which were 15.8 m downstream of the release channel (herein termed ‘net observation’; Fig. 1).

Low-light sensitive video cameras (AXIS models Q1604, Q1635 and P1365 MkII) were mounted overhead and camera fields of view were illuminated by infrared LED illuminators (Larson Electronics model LEDEU14; 12 W, 850 nm) positioned next to the video camera lens. Retroreflective (3M Diamond Grade, series 3990) background panels 1.2 m in width, spanning the entire width of the test arena, were attached to the bottom of the flume channel beneath each camera to reflect light from the illuminators back up through the water column to the camera, enhancing image contrast. Marks on the retroreflective panel at the net observation area were used to visually divide the panel into five sections, each 1.2 m wide that corresponded to the lateral panel zone in front of each collection net. Video imagery (black and white, 1280 × 720 pixel resolution per camera; frame rate of 30 fps) were recorded from all six cameras simultaneously using a computer workstation running AXIS Camera Station video recording software. Video recordings were reviewed and the time of net entry of each sea lamprey were recorded to the nearest sec. Any sea lamprey exiting back upstream out of a net were subtracted from the counts dataset for that net. The release observation camera were reviewed to determine if any of the sea lamprey that swim into the observation area swam back upstream into the release channel during the trial.

**General behavioural metrics evaluated**

To determine if the direction and speed of juvenile sea lamprey movement were influenced by exposure to alarm and light cues, three general behavioural metrics were evaluated: (i) spatial distribution of sea lamprey at the end of the trial as determined by net catches (broad-scale directional behavioural outcome), (ii) the time it took to transit the flume from release cage to nets (Fig. 1; broad-scale temporal behavioural outcome) and (iii) swimming speed and orientation as determined by overhead cameras at the flume observation area (Fig. 1; fine-scale directional and temporal behavioural outcomes).

**Spatial distribution of sea lamprey at the end of the trial**

First, the influence of the alarm cue and light on the likelihood of sea lamprey being found in the nets (all nets combined), flume observation area, or release channel at the end of each trial were modelled by comparing counts in each location (nets, observation area, or released channel) amongst treatments using general linear models. The proportion of sea lamprey present at all locations within the flume were calculated relative to all sea lamprey that were found at the end of each trial. Screening at the upstream end of the flume provided shelter and not every individual released were accounted for at the end of the trial; hence, sample size were not always 30 individuals. To determine the influence of the alarm cue and light on the general distribution within the flume, we modelled proportion within each flume section (release channel, observation area or nets) as a function of treatment (distribution model 1). Then, the proportion of the sea lamprey that moved into each net (net 1, 2, 3, 4 or 5) relative to only those sea lamprey that moved downstream (distribution model 2) and relative to all sea lamprey released for testing (distribution model 3) were modelled as functions of treatment. Models were developed using general linear models and all *post hoc* pairwise contrasts were made using Tukey’s multiple comparison of means with trial as the replicates (Hothorn et al., 2008).

**Transit rate to nets**

Video data at the net observation area were used to determine the time sea lamprey arrived in nets relative to when the release cage was opened and if transit rate was influenced by light or alarm cue application. Time when release cage were lifted was subtracted from time when sea lamprey entered a given net for each sea lamprey observed, and that difference in time was used to determine cumulative catch relative to transit time for each trial. Transit rates through the flume (event = capture in net) were then modelled as functions of treatment using Cox proportional hazards analysis (Therneau, 2015) for all captures combined.

**Swimming behaviour in flume: location, orientation and speed**

Behavioural metrics were extracted from video collected at the flume observation area including (i) location of arrival, (ii) orientation when arriving, (iii) lateral displacement whilst transiting the observation area and (iv) movement speed through the observation area as calculated by dividing total distance (x, y) moved whilst transiting the observation area. The flume observation area was positioned at a location where sea lamprey had been exposed to the alarm cue for 4 m and where light intensity were increasing (Fig. 2b) and was our best *a priori* guess as to where changes in sea lamprey behaviour would most likely occur. Data were only collected on sea lamprey that entered the panel from upstream and
exited downstream so that the behaviour of the same sea lamprey was not measured twice. Transects for sea lamprey that crossed multiple camera views were stitched together during post-processing and considered a single transect.

To extract behavioural metrics from video, a lens corrected grid overlay with 2.5 cm resolution was created for the flume video observation area using python programming language with reference point (0,0) located in the upstream, left corner (looking upstream; Supplementary Fig. 1). The grid overlay was matched to the flume video using ImageJ (Schneider et al., 2012). As sea lamprey entered the flume, video observation area (entire body over the observation area), an x, y coordinate was recorded for the head and a line drawn from head to tail bisecting the centreline of the body. The line was then used to determine orientation angle relative to the lighted wall of the flume (left wall = 0°; left was determined from the perspective of the fish as migrating downstream). These measurements were repeated as soon as any part of the body contacted the downstream edge of the observation area. Coordinates were used to calculate lateral distance from lighted wall (x; left wall) as sea lamprey entered and exited the observation area, change in lateral distance from left wall whilst transiting the observation area (x enter—x exit) and actual distance travelled when transiting the observation area (x, y enter—x, y exit). Actual distance travelled was divided by transit time to determine movement speed within the observation area.

Lateral distance from the left wall upon entering the observation was modelled as a function of treatment using linear regression. Lateral displacement whilst transiting the observation panel and overall movement speed were modelled as functions of treatment and distance from left wall (x coordinate upon entrance into observation area), Orientation data were provided for descriptive purposes only and were not statistically evaluated (Agostinelli and Lund, 2017; supplementary material). Data analysis were conducted using R environment for statistical computing 3.5.1 (R Development Core Team, 2018).

Results

Water velocity, light intensity and alarm cue distribution in flume

Water temperature was ambient and ranged from 3.2 to 3.7°C during experimentation. Turbidity was low (<10 NTU) and did not change over the duration of the study. Water velocity averaged 0.25 m sec⁻¹ and did not vary substantially across the flume immediately upstream of drift nets (Fig. 2a), but where the release channel emptied into the flume, water velocity was 0.15 m sec⁻¹ along the left wall, 0.30 m sec⁻¹ in the middle and 0.20 m sec⁻¹ along the right wall. Light intensity was as high as 140 lux near the light array on the left wall, but quickly dissipated such that light intensity in most locations more than a meter from the east wall was less than 10 lux and most locations more than 2 m from the left wall was less than 0.27 lux (the limit of detection of the meter; Fig. 2b). Therefore, sea lamprey could avoid light exposure by swimming away from the light array. Dye concentration (surrogate for alarm cue distribution) varied laterally across the flume and concentration were highest in the middle of the flume both at upstream and downstream cross sections of the flume. A metre from the left and right walls dye concentration were near zero (Fig. 2c), meaning that exposure to the alarm cue dropped if sea lamprey moved towards either wall.

General observations

Five trials each were completed for control, light and light plus alarm cue treatments; four alarm cue only trials were completed. Of the sea lamprey released during all trials, 91.2% were observed on video exiting the release channel (Fig. 1, release observation area); 59.8% were oriented downstream, 13.7% were oriented upstream, 13.0% were oriented to the right and 13.5% to left. Most sea lamprey moved downstream soon after release with a median transit time to reach the in-flume observation area of 50 s as determined by video examination at the release observation area (Fig. 1).

Spatial distribution of sea lamprey at the end of the trial

Distribution amongst nets, flume and release channel—all sea lamprey released

Generally, more sea lamprey were observed in the nets when the alarm cue were applied and more sea lamprey were found in the flume or release channel when light were applied (Fig. 3) relative to control. Specifically, a greater proportion of sea lamprey were in nets following treatments with the alarm cue relative to treatments with light only (light only—alarm cue only: z = 2.880, P = 0.021; light only—light + alarm cue: z = 3.632, P = 0.002). The proportion of sea lamprey remaining in the flume did not differ significantly amongst treatments (α < 0.05), but the proportion remaining in the flume after light only trials trended higher than control, alarm cue and alarm cue + light. The proportion of sea lamprey found in the release channel at the end of the trial were higher during light only trials relative to trials with the alarm cue only (light only—odor only: z = 2.714, P = 0.034). The difference between proportions in the release channel following light only versus light + alarm cue (z = 2.477, P = 0.064) and following control versus alarm cue only (z = 2.411, P = 0.075) treatments were marginally different (α = 0.10). Further review of video observation counts at the release channel (release observation area 1 in Fig. 1) revealed that less sea lamprey were observed in the release channel after trials with the alarm cue because they were less likely to move back upstream into the release channel during trials
Figure 3: Proportion of juvenile sea lamprey present in the release channel (release), observation flume (flume) and downstream capture nets (nets) following 10 min trials testing the influence of light, chemosensory alarm cue and both light + alarm cue treatments on downstream movement. Treatments with different letters differed significantly (α = 0.05).

when the alarm cue were applied compared to trials with no alarm cue ($\chi^2$ test: $z = -2.392, P = 0.017$).

**Probability of capture in specific nets—only fish captured in nets**

More sea lamprey were captured in the left wall net during trials with light treatment relative to control ($z = 2.952, P = 0.017$) and relative to alarm cue only trials ($z = 2.628, P = 0.043$; Fig. 4). The proportion captured in any other nets amongst the treatments of control, light, alarm cue and light + alarm cue did not differ significantly.

**Probability of capture in specific nets—all sea lamprey released**

The overall proportion of all sea lamprey released that were captured in the left wall net (lighted side; net 1) were greater during light + alarm cue trials compared to control ($z = 2.94, P = 0.018$) and alarm cue only ($z = 2.36, P = 0.085$) trials (Fig. 5). The contrast between light + alarm cue and alarm cue only trials were not significantly different ($z = 1.45, P = 0.466$).

**Transit rate through flume**

Not only did more sea lamprey move downstream when the alarm cue were applied, they also exhibited a greater transit rate (Fig. 6). Specifically, the catch rate during the alarm cue only and light + alarm cue trials was significantly greater than control trials ($z = 2.68, P = 0.007; z = 2.35, P = 0.019$) and light only trials ($z = 2.70, P = 0.007; z = 2.44, P = 0.015$). Catch rate did not differ between control and light trials ($z = 0.49, P = 0.627$) or between the alarm cue only and light + alarm cue trials ($z = 0.35, P = 0.727$). Overall, treatment had a significant effect on rate of cumulative catch ($\chi^2 = 13.07, df = 3, P = 0.004$).

**Swimming behaviour in flume: location, movement, swim speed and orientation**

Fine scale analysis of sea lamprey behaviour in the flume (flume observation area in Fig. 1) showed that upon entry into
Figure 4: Proportion of juvenile sea lamprey that moved downstream and were captured in each of five nets positioned from left to right across the downstream end of a 6 m wide flume. Trial duration were 10 min testing influence of light, alarm cue and both light + alarm cue treatments on the downstream movement of juvenile sea lamprey relative control conditions with no light or alarm cue active. Net 1 were on the left wall nearest the light array. Proportion of lamprey in net 1 following light treatment trials were significantly greater than control and alarm cue only trials. No other catch proportions differed significantly in other nets.

the observation area sea lamprey distributions were shifted slightly left of centre during the alarm cue trials and slightly right of centre during all other treatments (Supplementary Fig. 2). We observed a significant interaction where lateral position within the flume influenced the effect of treatment on lateral displacement of sea lamprey (side-to-side movement) whilst transiting the video observation area. During control trials, lateral displacement was not significantly different from zero ($t_{1,47} = 0.50, P = 0.617$). However, the distance from the left wall when entering the observation area did influence the effect of treatment for light only ($t_{1,40} = 2.79, P = 0.007$), alarm cue only ($t_{1,69} = 3.01, P = 0.004$) and light + alarm ($t_{1,69} = 3.01, P = 0.004$) trials. When light and alarm cue treatments were applied, sea lamprey tended to move towards the nearest wall (Supplementary Fig. 3). Movement speed through the observation area showed no significant difference amongst treatments (Kruskal-Wallis $\chi^2 = 4.2838, df = 3$, $P$-value = 0.23; Supplementary Fig. 4). In general, sea lamprey were predominately oriented downstream when entering the video observation panel with slight bias towards the walls on either side of the flume (Supplementary Fig. 5).

**Discussion**

**Responses of juvenile sea lamprey to light**

When exposed to light, more juvenile sea lamprey moved back upstream and fewer sea lamprey move downstream to the nets compared to control trials with no light. Sea lamprey that did move downstream during lighted trials were more likely to be captured in the net closest to the light array compared to control trials. These results are consistent with observations of Haro et al., (submitted) using the same experimental system, animals and light setting.
confirming that previous work in the bioassay could be replicated.

Here, detailed analysis of sea lamprey swimming behaviour in the flume revealed that sea lamprey on the right side of the flume (non-lighted side) were more likely to swim away from the light during light treatments relative to control (Supplementary Fig. 3), a result that is not fully consistent with a hypothesis of positive phototaxis. Although light levels were less than 0.27 lux in the right side of the flume during lighted trials, juvenile sea lamprey can detect single photos of light (Morshedian and Fain, 2015) and in theory may have still been able to detect and swim towards the light source. Therefore, given these results, future research could investigate if sea lamprey avoid light at relatively low lux values (1–10 lux) when contrasts in light intensity can be perceived by their sensory system (Jekely, 2009), but are unable to detect contrasts and navigate away from the light when exposed to light exceeding 100 lux Therefore, in circumstances where their sensory system is overwhelmed, like those experienced within 2 m of the light array in this study, maybe sea lamprey slow down and search for refuge from the light, rather than flee. In other words, when near the light source, sea lamprey may not have been attracted to the light, but rather attracted to the wall and structure illuminated by the light. In the same way, it is conceivable that during lighted trials that the right wall may have reflected light originating from the left wall and therefore, sea lamprey on the right side of the flume were also swimming towards an illuminated structure. Responses of fishes to light often vary with intensity. Juvenile walleye (Sander vitreus) aggregated near low intensity light even when higher intensity options were available (Bulkowski and Meade, 1983). Juvenile pikeperch (Sander lucioperca) also moved towards to the lowest intensity light available (Luchiari et al., 2006).

Therefore, although sea lamprey detect and behaviourally respond to light, more research is needed to understand
how context influences juvenile sea lamprey responses to light before testing in management scenarios. Behavioural responses of fishes to light can vary for many reasons (Brown, 2000) such as intensity, orientation, (Haro et al., submitted), wavelength (Ford et al., 2018), water depth (Hamel et al., 2008), water turbidity (McIninch and Hocutt, 1987) and time of day (Marchesan et al., 2005). Even behavioural studies on adult sea lamprey found inconsistent responses to light that were likely related to light intensity, distance sea lamprey were from the light source and spatial scale of the experiment (Purvis et al., 1985; Stamplecoskie et al., 2012).

In concept, light could be used in several ways to improve sea lamprey control in the Great Lakes region. One option may be to use light arrays to drive sea lamprey towards the bottom and banks where nets can efficiently fish through high discharge events. Another option may be to use high intensity light arrays as ecological traps; light attracts visual predators (Ślusarczyk et al., 2005; Nightingale et al., 2006) and sea lamprey become more vulnerable to predation if they slow down in response to light. Predation traps can be an unintended consequence of passing valued fishes around dams and through fishways (Blackwell and Juanes, 1998; McLaughlin et al., 2013), so conceptually the same could be true for sea lamprey.

**Responses of juvenile sea lamprey to alarm cue**

When exposed to the alarm cue whilst moving downstream, transit rates to downstream nets increased, were less likely to move upstream back into the release channel and did not move laterally away from the plume. To our knowledge, this is the first study documenting a behavioural response to a chemosensory alarm cue in downstream migrating fish. The only other previous attempt were in a raceway flume testing downstream migrating American silver eel (*Anguilla rostrata*) to odour from dead eel, but no changes in movement trajectory, activity level or proximity to the odour source.
were observed (Schmucker et al., 2017). The behavioural response expressed by juvenile sea lamprey is consistent with predator avoidance; swimming downstream at a faster rate will increase distance from the predator more consistently than freezing or turning perpendicular to flow to navigate out of the alarm cue plume. Interestingly, analysis of sea lamprey movement speed in the flume observation area did not reveal that sea lamprey were swimming faster at that location (Supplementary Fig. 4). One possible explanation is that our observation area was positioned in the wrong location in the flume to observe differences in movement speed. Another explanation is that sea lamprey may not swim faster downstream when the alarm cue is applied, rather, fewer sea lampreys pause downstream movement when the alarm cue is applied. A final explanation is that sea lamprey do not swim faster when exposed to the alarm cue, but instead swim at the same rate but take a more direct path downstream. The 1.2 m observation area observed was not sufficient for evaluating these options and therefore, could be the focus of future work. Future studies could determine if the alarm cue also triggers sea lamprey to change depth in the water column. If the primary threat of predation is from other fishes, sea lamprey may swim towards the water surface to further increase distance from the predatory fish or towards the substrate to seek physical cover. If the primary threat of predation is from shorelines mammals, birds or reptiles, sea lamprey may swim deeper towards the middle of the channel.

Similar to light cues, responses of fishes to alarm cues vary according to ecological context (Ferrari et al., 2010). Even with sea lamprey, responses to the alarm cue vary amongst and within life stages (Buchinger et al., 2015). When upstream migrating adult sea lamprey are exposed to the alarm cue activating half the stream channel, they move upstream slower and avoided water scented with the alarm cue (Di Rocco et al., 2016). When the alarm cue activated the entire river channel, adult sea lamprey released offshore the river mouth were more likely to enter the river and moved upstream at a faster rate, whereas those sea lamprey released in the river during the same alarm cue treatments continued to move upstream, but at a slower rate (Luhring et al., 2016). Laval sea lamprey, which are sedentary filter feeders burrowed in the sand (Applegate, 1950), are less likely to drift downstream when exposed to the alarm cue in a laboratory microcosm (Wagner et al., 2016), but in an experiment where larvae did not have access to burrowing substrate, larvae increased the rate of directional changes when exposed to the alarm cue compared to control solvent (Perrault et al., 2014).

Therefore, although juvenile sea lamprey detect and behaviourally respond to the alarm cue, more research is needed to understand how context influences responses prior to application in management. Like larval sea lamprey, recently, metamorphosed sea lamprey burrow in substrate during the day. If burrowed metamorphosed sea lamprey are exposed to the alarm cue during the day, it is not clear if they would be more or less likely to emigrate at nightfall. Furthermore, the likelihood of outmigration after exposure to the alarm cue may be contingent on stream flow and turbidity. Juvenile sea lamprey mostly emigrate during high flows in the fall, winter and spring (Applegate, 1950; Swink and Johnson, 2014; Baer et al., 2018), so sea lamprey may only be more likely to leave their burrows after exposure to the alarm cue if discharge and turbidity is also high. Context could also influence how downstream moving sea lamprey respond to the alarm cue. In low velocity stream environments, characteristic of pools and drowned river mouths, sea lamprey may flee in all directions and increase turning rates when exposed to the alarm cue. Similar speculation could be made for how sea lamprey would respond in shallow, deep, turbid, clear, wide and narrow rivers. Testing various circumstances will allow managers to better understand when application of the alarm cue may and may not be useful to achieve control and restoration objectives.

**Responses of juvenile sea lamprey exposed to light and alarm cue in a push-pull configuration**

When the alarm cue and light were applied simultaneously in a push-pull configuration, the cues were complementary because alarm cue still triggered greater downstream transit rates and more sea lamprey were still captured in the net near the light. To our knowledge, this is the first time that the combined effects of a light stimulus and an alarm cue were tested in tandem in any fish, whether migrating upstream or downstream. This is also a rare example of using two sensory cues in a push-pull configuration to modify fish behaviour (Hume et al., 2015).

Other sensory cues have been integrated to modify animal behaviour with mixed results; sometimes behavioural responses cancel out, add up or synergize. Combinations of light, sound and bubbles have been tested to modify migratory behaviour of salmonids (Perry et al., 2014) and Asian carps (Taylor et al., 2005) with some success, but minimal response to these stimuli were exhibited by adult sea lamprey in a y-maze (Miehls et al., 2017a). In some cases, responses of fish to combined stimuli can be unexpected. In laboratory experiments, brown trout (Salmo trutta) avoid accelerating velocities, but show positive phototaxis. When brown trout were exposed to accelerating velocity and light, the avoidance response to the velocity gradient were enhanced rather than suppressed (Vowles and Kemp, 2012). Therefore, predicting how sea lamprey will respond to combinations of light and alarm cues as stream flow, depth, turbidity change is tenuous and needs to be evaluated experimentally (Nestler et al., 2008). Future research could also conceivably try to integrate light, alarm cue and pulsed direct current to produce complementary or synergistic responses because downstream migrating sea lamprey avoid fields of pulsed direct current (Johnson and Miehls, 2014; Miehls et al., 2017a).
Conclusion

Downstream moving juvenile sea lamprey detect and behaviourally respond to light and alarm cues and these cues may be useful in management when integrated. The use of light and alarm cue nearly doubled the catch in the lighted net relative to the control. Statistical significance of results were lacking in some cases because the power of the experimental approach were limited by the four to five trials conducted per treatment. Further inquiry into light and alarm cues to modify juvenile sea lamprey behaviour could reveal ways to enhance the response. A light array deployed over a longer distance may result in a greater proportion of sea lamprey moving towards or away from the light. Responses of sea lamprey may be different when migrating downstream on their own volition in a natural stream with dynamic depth and flow characteristic. Furthermore, an interaction between water velocity, light and alarm cue seems probable and could be investigated further (Nestler et al., 2008; Vowles and Kemp, 2012). Taken together, these cues hold some promise to modify behaviour to improve control or restoration of sea lamprey, but additional systematic experiments will be needed to understand how responses are influenced by context and the presentation of the stimulus.

Supplementary material

Supplementary material is available at Conservation Physiology online.

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