Canadian Journal of Fisheries and Aquatic Sciences
Journal canadien des sciences halieutiques et aquatiques

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Journal:	<i>Canadian Journal of Fisheries and Aquatic Sciences</i>
Manuscript ID	cjfas-2016-0445.R1
Manuscript Type:	Article
Date Submitted by the Author:	20-Jan-2017
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Keyword:	INVASIVE SPECIES < Organisms, MANAGEMENT < General, BEHAVIOR < General, TELEMETRY < General, LAMPREYS < Organisms

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Spatial mismatch between sea lamprey behaviour and trap location explains low success at trapping for control

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January 2017

Abstract:

Understanding the space use and the environmental features affecting it can be crucial to the management of invasive species. Improved understanding of space use in invasive Sea Lamprey (*Petromyzon marinus*) could help discern why trap success in large rivers is lower than needed for effective control. We tested if manipulating discharge nightly could increase trap success at a hydro-generating station on the St. Marys River. We quantified numbers of acoustic tagged Sea Lampreys migrating up to, and their space use at, the hydro-generating station. In 2011 and 2012, 78% and 68% of tagged Sea Lampreys reached the generating station, respectively. Sea Lampreys were active along the face, but more likely to occur at the bottom, and away from the traps near the surface, especially when discharge was high. Our findings suggest that low probabilities of encountering traps was due to spatial (vertical) mismatch between the space use of Sea Lamprey and the trap locations and that increasing discharge did not alter space use in ways that increase trap encounter. Understanding the space use of invasive species can help managers assess the efficacy of trapping and ways of improving trapping success.

Introduction

The frequency of species invasions and their ecological and economic impacts are pressing scientists to develop ways of protecting and restoring natural ecosystems (Palmer et al. 2004; Pimentel et al. 2005). Trapping is a potentially valuable form of control, often used as part of an integrated control program, but could become more prevalent if managers could improve the success of individual traps and the overall proportion of the population trapped (trapping efficiency). For example, improvements in trap success have contributed to better control of insects in a variety of regions (El-Sayed et al. 2006) and invasive American mink (*Neovison vison*) in Scotland (Roy 2011). Understanding the behaviour of the target species can be crucial to trap success, because coming in proximity to, entering, and remaining in a trap (encounter, entrance, and retention, respectively) can depend strongly on a species' behaviour (Bravener and McLaughlin 2013).

We tested explanations for how space use of invasive Sea Lampreys (*Petromyzon marinus*) migrating in the St. Marys River, the connecting channel between Lake Superior and Lake Huron, could explain low encounter rates with traps used for control and whether experimental increases in discharge could improve encounter rates with traps and overall trap success. The Sea Lamprey is a parasitic fish that feeds on the blood of other large fishes (hosts). It entered the upper Laurentian Great Lakes between 1924 and 1938 (Christie and Goddard 2003; Smith and Tibbles 1980). Following this invasion, Sea Lamprey populations increased rapidly in Lakes Erie, Huron, Michigan, and Superior and contributed to the declines in Lake Trout (*Salvelinus namaycush*), Lake Whitefish (*Coregonus clupeaformis*), Burbot (*Lota lota*), Walleye (*Sander vitreus*), and several species of catostomids in the mid 1900's (Smith and Tibbles 1980). In response to these changes, the Great Lakes Fishery Commission (GLFC) was created under

the *Convention on Great Lakes Fisheries* (1954)—a treaty between Canada and the United States. The GLFC is responsible for Sea Lamprey control in the Great Lakes with field operations contracted to the Department of Fisheries and Oceans Canada (DFO) and the United States Fish and Wildlife Service. Sea Lamprey control currently relies on two methods: periodic lampricide treatment of tributaries where larval Sea Lampreys rear for the first three to five years of their life and barriers that deny migrating adult Sea Lampreys access to spawning habitat in tributaries. Trapping (removal) of migrating adult Sea Lampreys prior to reproduction would provide a third control option if trapping success could be improved. In its most recent strategic vision document, the GLFC pledged to increase the development and implementation of effective and efficient trapping methods (Pillar 2, Goals 1 and 2; Great Lakes Fishery Commission 2012).

Improvements in trapping success could be particularly valuable for Sea Lamprey control in large rivers, such as the St. Marys or Nipigon River. Treatment with lampricides is more challenging for large rivers, due to the size and complexity of large river systems and the increased cost and logistics of lampricide application. In the St. Marys River, trapping has been used historically for population assessment and to collect males for a sterile-male release program that was discontinued in 2012 (Adair and Sullivan 2015; Bravener and Twohey 2016). Annual trapping efficiency across the river, estimated from mark-recapture methods, is approximately 39%, on average over a ten year period from 2004-2014. Since 2007, two decision analyses comparing different management options for the St. Marys River have suggested that a trapping efficiency of greater than 70% is needed for trapping to be an effective additional control method (Haesaker et al. 2007; Jones et al. 2015). Over this time, two tracking studies of Sea Lampreys in the river have also suggested that trapping efficiency could be closer

to 10% (Bravener and McLaughlin 2013; Holbrook et al. 2016a), because the proportions of Sea Lampreys coming within approximately 1.0 m of a trap (encounter) over the period of trap operation (0.05-0.13), entering a trap upon encounter (0.08-0.31), and returning to traps upon leaving are all low (Bravener and McLaughlin 2013; Dawson et al. 2016). The proportion of Sea Lampreys retained in a trap upon entering is high (Bravener and McLaughlin 2013).

Understanding the space use of invasive animals can be crucial to increasing encounter rates with traps, and ultimately trapping success. For Sea Lampreys, the current trapping strategy involves positioning a relatively small number of traps in locations where migrating adult lamprey are expected to occur, usually near barriers that impede upstream migratory movements and create flows believed to attract lamprey. The success of this approach relies on a high proportion of Sea Lampreys passing near, and therefore encountering, traps. However, it may not fully account for potential changes in space use behaviour under variable environmental conditions. Actual measurement of space use in these conditions, at spatial scales relevant to trapping, has been limited. The nocturnal behaviour of Sea Lampreys, high water velocities, entrained air, and deep water at trap sites in large rivers have made it difficult to quantify Sea Lamprey behaviour.

Identifying environmental features that affect the space use of Sea Lampreys can create further opportunities to improve trapping success. Greater understanding could be valuable for trapping fishes because water flow can influence fish behaviour and be manipulated (Johnson et al. 2012; Olden et al. 2014). On the one hand, the idea that modestly fast and turbulent flows can attract migrating, fluvial fishes to traps and fishways appears widely in the literature (Coutant 2001; Dow 1962; Pratt et al. 2009; Weaver 1965). On the other hand, the emphasis on attraction can obscure the multiple and complex ways in which flow can influence fish behaviour (Lacey et

al. 2012; Liao 2007). For example, moving water could simply induce a rheotactic response in migrating fishes that results in aggregation at bottlenecks to movement, without any attraction per se, and irrespective of the magnitude or variability of water velocity beyond some minimal threshold. High water velocities can also stimulate the intensity of activity and space use of fishes, including lampreys (Almeida et al. 2002; Castro-Santos 2004; Keefer et al. 2011), without attraction, possibly because increased discharge coincides with elevated water levels, and the creation of potential passage routes along river margins (Matheney and Rabeni 1995) or the deepening of riffle areas that would be obstacles to movement under lower flows (Lonzarich et al. 2000; Schaefer 2001). Very high and unpredictable water velocities can even deter fishes, either because they exceed the swimming abilities of the fish or they unacceptably increase the energetic costs of swimming (Almeida et al. 2002; Lacey et al. 2012).

Our investigation of space use tested three potential explanations for why previous studies observed low proportions of Sea Lampreys encountering traps in the St. Marys River. First, we tested whether the proportion of Sea Lampreys encountering traps is low because the lampreys stop moving upstream before reaching trap locations on the downstream face of a hydro-generating station that serves as a barrier to upstream migration. This could happen in two ways. Sea Lampreys could stop short of the generating station because discharge from the station creates challenging swimming conditions (e.g. fast flows or turbulence; Quintella et al. 2004) or because there is suitable spawning habitat downstream of the generating station. Next, we tested whether the proportion of Sea Lampreys encountering traps is low because their behaviour at the downstream face of the generating station does not favour encounters with traps. This could happen in two ways. Sea Lampreys could aggregate at locations away from the trap sites, either because they are attracted to the discharge from the draft tubes of the generating station or

because the lamprey tend to be bottom oriented (Bravener 2011; Holbrook et al. 2015) while traps are located near the water surface. Alternatively, Sea Lampreys could be spread-out (dispersed) and immobile along the face of the generating station. In an earlier study, tagged Sea Lampreys approaching the generating station took widely different upstream routes (Bravener 2011). Near the generating station, the Sea Lampreys may also attach to surfaces with their oral disc because of the fast water velocities (Keefer et al. 2010; Kemp et al. 2011; Quintella et al. 2004). These explanations are not mutually exclusive. After considering these explanations, we tested whether increasing nightly discharge from the generating station altered the space use of Sea Lampreys in ways that would favour increased encounter with traps.

Materials and methods

Description of the Study Site

Field tracking of Sea Lampreys was conducted between 26 June to 25 July 2011 and 8 June to 7 July 2012 in the tailrace of the Francis H. Clergue Generating Station (hereafter the Clergue generating station) on the St. Marys River connecting Lakes Huron and Superior. The St. Marys River is 112 km long and drops approximately 6.8 m over its length. Mean annual discharge is 2100 m³/s (Duffy et al. 1987). A series of gates spanning the head of the St. Marys Rapids is used to control outflow from Lake Superior through the rapids while diverting water to four hydro-generating stations and three shipping canals. The Clergue generating station is a run-of-the-river hydroelectric dam. Its tailrace is approximately 70 m wide and 16 m deep at the downstream face of the station, with depth decreasing to 12 m approximately 20 m downstream. Water passing through three turbines is discharged from three 10 x 10 m draft tubes along the

downstream face of the station. Mean daily discharge is approximately $1000 \text{ m}^3\text{s}^{-1}$ (Duffy et al. 1987).

Sea Lamprey Trapping Operations

Five Sea Lamprey traps are operated along the downstream face of the generating station. The North (NAWT) and South Attractant Water Traps (SAWT) are permanent structures (Fig. 1, top panel). The NAWT has two entrances. The SAWT has four entrances. Both traps direct attraction flow out of the trap entrances. Three portable traps are also installed seasonally between the NAWT and SAWT. Portable traps are designed like a “minnow-trap”, with two funnel openings at opposite ends (See Fig. 1, Mclean et al. 2015). They are oriented perpendicular to the discharge from the generating station and placed in areas of high discharge exiting the draft tubes. All traps fish at depths of 1 - 3 m below the water surface and are checked and emptied daily. There are four additional trap locations on the St. Marys River: the St. Marys Rapids and three other hydroelectric generating stations. One to six traps are operated at each of these other locations.

Manipulation of nightly discharge

During the study period, discharge from 2300-0700h was manipulated from the normal low for this time of year on one night (2300h-0700h; mean = $475 \text{ m}^3\text{s}^{-1}$) to a discharge comparable to daytime discharge (0800h-2200h; mean = $910 \text{ m}^3\text{s}^{-1}$) the next night. Discharge was manipulated at night because that is when Sea Lampreys are most active (Binder and McDonald 2007). Under normal operations, discharge is reduced overnight when electricity demand is low. The hydro operator strived to alternate discharge nightly, but deviations were necessary due to demand for electricity.

Acquisition, tagging, and release of Sea Lampreys

Sea Lampreys used in our project were obtained from trapping locations on the US side of St. Marys River. These Sea Lampreys were assumed to be representative of Sea Lampreys unfamiliar with the Clergue generating station. Acquiring naïve Sea Lampreys from other rivers was not feasible; those Sea Lampreys had already spawned. Sea Lamprey migration occurs later for the St. Marys River than for other tributaries, due to the St. Marys River's much larger size and slower warming of water temperature. Based on catch records for traps at the Clergue generating station, the migration period covered 3 June to 25 July and 22 May to 16 July in 2011 and 2012, respectively. Collecting experimental Sea Lampreys from the St. Marys River via means other than trapping (e.g., divers) was impractical.

Upon removal from traps, experimental Sea Lampreys were transported to a holding facility adjacent to the Clergue generating station, placed in sex-specific holding tanks (6 m diameter, 1 m deep), provided with constant gravitational discharge from the St. Marys River (turnover rate <30 min), and held 1-3 days prior to tagging. Two types of tag were surgically implanted into 108 Sea Lampreys (1:1 sex ratio) in each study year. Acoustic tags (Hydroacoustic Technology, Inc. (HTI), Seattle, WA) were used to obtain 3-D positions of Sea Lampreys in the water column downstream of the generating station. Each acoustic tag transmitted a repetitive signal with a unique and precise period (2003 ms to 4571 ms depending on the tag in 2011 and 3003 ms to 5571 ms in 2012). PIT tags (3.4 mm x 23 mm, 0.6 g in air, Texas Instruments, Dallas, TX) were used for tracking the encounter, entrance into, and departure from traps (Rous 2014). The model of acoustic tag differed across years. In 2011, HTI model 795G (11 x 25 mm, 4.5 g in air) was used. In 2012, HTI model 795GP (11 x 36 mm, 4.6 g in air) was used. A new tag was deployed in 2012 because it allowed us to measure depth (Z)

positions based on both 3D acoustic positioning (similar to 2011), and 2D acoustic positioning plus depth estimated from water pressure. Depth positioning using acoustic signals becomes less accurate when the depth axis becomes smaller than the two horizontal (X,Y) axes.

For tag implantation, each Sea Lamprey was netted from a holding tank and held in an aerated bath of MS 222 (50 mg/L; Syndel Laboratories Ltd, Nanaimo, Canada) until it reached stage 3 of anaesthesia (partial loss of equilibrium). It was then measured for total length (± 1 mm) and transferred to a damp foam pad for surgery. The ventral area of the lamprey was rinsed with a Povidone-iodine solution (5 g/L; Sigma-Aldrich, St. Louis, USA) and then with sterile saline solution (9 g/L). A 5 mm incision was made near the ventral midline, and an acoustic and PIT tag were inserted into the peritoneal cavity using forceps. The incision was closed with three independent sutures (Ethicon Monocryl 3/0; Ethicon, Somerville, USA). During surgery, the lamprey was periodically irrigated with a maintenance dose of anaesthetic (30 mg/L) in oxygenated water. Scalpels, forceps, and tags were disinfected in a Virkon solution (1 g/L) and rinsed with sterile saline solution (9 g/L) prior to each surgery. Scalpel blades were changed after every fifth surgery to ensure the blades were sharp. Following surgery, the tagged lamprey was transferred to a recovery tank, monitored during recovery from the anaesthesia, and held for 1-4 days prior to release in the St. Marys River.

Tagged Sea Lampreys were released approximately 300 m downstream from the generating station. The release distance was selected to give tagged lampreys ample opportunity to select their upstream path, yet ensure they were likely to enter our study area rather than move elsewhere in the river. The tagged lampreys were released on six dates, separated by 48 hours. Release dates covered early, middle, and late points of the peak in migration. On each date, six lampreys (1:1 sex ratio) were released from each release site. Releases occurred at approximately

226 2000h to minimize predation of tagged animals immediately post-release and because Sea
227 Lampreys are most active at night.

228 **3D tracking of space use**

229 The tagged Sea Lampreys were tracked using an HTI acoustic telemetry receiver (ATR;
230 Model 290). Each year a 16 hydrophone (model 590, HTI) array was positioned in the tailrace of
231 the generating station extending 70 m across the face of the station and approximately 70 m
232 downstream (Fig. 1, bottom panel). Eight hydrophones were mounted on the face of the
233 generating station (Fig. 1, bottom panel) and fastened to 2.5 cm diameter stainless steel pipes
234 anchored into the downstream face of the generating station (#'s 1-8: Fig. 1, bottom panel). Four
235 of these hydrophones were mounted approximately 1 m below the water surface and four were
236 mounted approximately 2 m above the river bottom (16 m deep). Eight more hydrophones were
237 positioned downstream of the generating station. Four (#'s 9-12) were positioned approximately
238 20 m downstream of the generating station. Two (9 and 12) were mounted to 2.5 cm stainless
239 steel pipes extending from the shore into the water column and secured with piled rock and
240 braided steel cable. Two others (#'s 10 and 11) were attached to weighted, pyramid shaped metal
241 towers (1 m high with a 1 m x 1 m base) placed on the river bottom. The final four hydrophones
242 (#'s 13-16) were positioned approximately 70 m downstream. Two of these (#'s 13 and 16) were
243 also attached to pipe extending from shore. The remaining two hydrophones (14 and 15) were
244 mounted approximately 1 m above the river bottom on vertical pipes (diffusers) from an effluent
245 system extending across the river in a north-south direction. This array geometry was selected
246 based on tag range tests conducted in 2010, and consultation with personnel from HTI and with
247 professional divers familiar with conditions in the tailrace. Spacing of hydrophones was selected
248 to minimize the effects of sound attenuation from entrained air and maximize line of sight

between tags and the hydrophones. Air entrained in the water of the tailrace, due to turbulence, can alter the speed of sound in water and introduce error in 3D positioning. At the end of the field season, the horizontal position of each hydrophone was measured by a professional land surveyor. Vertical position of each hydrophone was determined by measuring the length of a line dropped perpendicular from the water surface to the hydrophone. Speed of sound in water was estimated each day using mean daily water temperatures from temperature loggers operated by DFO at the traps.

Data processing and positioning

Processing and positioning was done in consultation with HTI. The software MarkTags (HTI) was used to assign acoustic signals detected by the hydrophones to individual tagged lampreys. In 2011 and 2012, the software AcousticTag (HTI) was used to estimate 3D positions for individual lampreys from signals detected on four or more hydrophones. In 2012, an additional data set was created by using AcousticTag to estimate 2D (XY) positions from signals detected on three or more hydrophones and the Z position from the pressure sensor in the tag.

Position accuracy was estimated using telemetry records for a set of Sea Lampreys caught in traps (13 in 2011, 8 in 2012) and for test tags (1 near the surface at the NAWT in 2011, 1 near the surface and 1 near the bottom at the NAWT in 2012). Distances between the estimated tag position (via telemetry) and true position (via GPS and depth measurements) were used to estimate error, including mean Euclidean distances in the X, Y, and Z directions, and four measures of spherical error that quantify the radius of a sphere centred on the estimated position that is expected to contain the true position 50%, 61%, 95%, and 99% of the time (Connolly 2012) (Supplemental Material: Tables S1-S3).

271 Data analysis

272 The farthest upstream position reached by each tagged individual was used to test
273 whether the low proportion of Sea Lampreys encountering traps observed by Bravener and
274 McLaughlin (2013) could be a consequence of lampreys halting their upstream movement before
275 reaching the downstream face of the generating station. A Sea Lamprey was considered to have
276 reached the face of the generating station if it entered the vertical slice of water extending 3 m
277 downstream of the face of the generating station. The criterion of 3 m was selected based on the
278 accuracy of our position estimates and because we considered it reasonable that a Sea Lamprey
279 within 3 m of a trap could be trapped. Numbers of Sea Lampreys entering the 3 m slice were
280 quantified using the software QGIS (QGIS Development Team, 2012, QGIS Geographic
281 Information System. Open Source Geospatial Foundation Project). The effect of discharge on
282 probability of arriving in the 3 m slice was tested using a mixed effect logistic regression model
283 relating the number of tagged individuals arriving in the slice within a sample night, relative to
284 the number available, with sample night modeled as a random effect and discharge on a given
285 night modeled as a fixed effect. The effect of discharge condition was tested using a log-
286 likelihood ratio test. Separate analyses were conducted for 2011 and 2012.

287 Four additional steps were used to test if the proportion of Sea Lampreys encountering
288 traps was low either because Sea Lampreys aggregated away from trap locations or because Sea
289 Lampreys were widely distributed and relatively immobile across the face of the generating
290 station. These steps were completed separately for the 3D acoustic data from 2011, 3D acoustic
291 data from 2012, and the 2D plus depth (pressure) data set from 2012.

292 First, the 3 m vertical slice of water downstream of the face of the generating station was
293 divided in 118 grid cells using QGIS. Each cell in the grid was approximately 3 m x 3 m x 3 m

(27 m³). Cells along the top and edges were less than 9 m³ because of the irregular shape of the dam face. The Spatial Query tool in QGIS was then used to assign all tag positions within the vertical slice into the appropriate cells.

Second, mixed effect logistic regression (occupancy) models were used to estimate the probability of a lamprey occupying a cell during a specified hour of a given night. Occupancy modelling was used because earlier research demonstrated that the probability of a Sea Lamprey being trapped increases with the time it spends near a trap (Bravener and McLaughlin 2013; McLean et al. 2015). These analyses were conducted with night-time observations only because Sea Lampreys are most active at night and discharge was manipulated from night to night and not during the day. Each model related the proportion of tag detections for an individual tag within a given cell over a 1 h period of the night to covariates known to influence Sea Lamprey behaviour based on previous studies and to specific predictor variables relevant to this study. The covariates considered were cell volume, time of night, and water temperature. These were modeled as fixed effects. Cell volume was considered to statistically control for any effects cell volume might have on the time spent in that cell. Time of night was considered because Sea Lamprey activity can vary during the night (Bravener and McLaughlin 2013). Water temperature was considered because it can be a strong predictor of Sea Lamprey activity and arrival at barriers (Binder et al. 2010; McLean et al. 2015; Rous 2014). Time of season was not included because it was highly correlated with water temperature. The predictor variables considered were discharge, water depth, and the statistical interaction between discharge and depth. All models also included cell identification number (Cell ID) as a random intercept effect to accommodate potential differences in tag detections across cells. Tag period (Individual ID) and time of day were modelled as a random slope effect to accommodate individual differences in occupancy

across time periods within a night. All occupancy models were estimated using the detections available for each Sea Lamprey (tag) in a given data set. Missing detections occurred as revealed by analyses of sequences of tag detections for individual tags in fixed positions (Table S4). Accommodations for missing detections were not feasible (see Discussion). Prior to analysis, time of day was transformed by taking the sine of each hour and multiplying it by $2\pi/24$ because time of day is a circular variable. The presence of tagged Sea Lampreys in traps could bias occurrence estimated for cells containing traps, because traps are not emptied until the morning. To minimize this, we examined the spatial locations of trapped Sea Lampreys and deleted detections after the time when the Sea Lamprey was estimated to have been trapped.

Third, multi-model inference was used to identify the best approximating model from a set of approximating models (Burnham and Anderson 2002). Two rounds of model comparisons were completed. The first round compared models involving the covariates only. The best approximating model from that round was carried forward to the second round that tested the added effects of discharge, water depth, and the interaction of discharge and depth, after accounting for the effects of the covariates identified as important predictors from the first round. In both rounds, the models were compared using the Bayesian Information Criterion (BIC). BIC was used for model comparison because it has been shown to perform better than other model selection metrics when sample sizes are large (Raffalovich et al. 2008).

Fourth, the variation in space use, and differences between nights of high and low discharge, were depicted using heat maps to visually differentiate cells where the occurrence of Sea Lampreys was high from cells where it was low. Plots of 2D movements in the X,Y dimensions were also used to visually evaluate whether Sea Lampreys exhibited restricted

movement along the face of the generating station, as expected if encounter with traps was low because Sea Lampreys were overdispersed and immobile along the face of the generating station.

All statistical analyses were performed using R version 3.0.2 (R Development Core Team, 2011), including the lme4 (Bates et al. 2015) and ggplot2 (Wickham 2010) packages. All Sea Lampreys were handled in accordance with Animal Utilization Protocol #1502 issued by the University of Guelph.

Results

In each study year, nightly discharges were alternated consistently over most of the study period of Sea Lamprey migration and trapping (Fig. 2). In 2011, nightly discharge was kept high (mean = $899 \text{ m}^3 \text{ s}^{-1}$) on 14 study nights and low (mean = $370 \text{ m}^3 \text{ s}^{-1}$) on 16 study nights.

Differences in discharge between high and low nights were smaller during the period from days 179 to 183 than for the remainder of the tracking period. The dam operator was also unable to alternate discharge from night to night between days 195 to 198 and days 201 to 203. In 2012, nightly discharge was kept high (mean = $935 \text{ m}^3 \text{ s}^{-1}$) on 16 study nights and low ($599 \text{ m}^3 \text{ s}^{-1}$) on 14 study nights. There were 6 days near the end of the tracking period where discharge was low on consecutive nights (days 176 to 181), followed by 7 days where discharge was high on consecutive nights (days 182 to 188).

There was little evidence that lampreys halted their upstream movement before reaching the face of generating station. In 2011, 91 of 108 tagged individuals (84%) were detected entering the hydrophone array. Eighty-four of 108 individuals (78%) reached the 3 m vertical slice of water downstream of the face of the generating station. Of the 17 tagged lampreys that were not detected entering the hydrophone array, three were caught at other trapping locations in

the St. Marys River. The remaining 14 were never detected or trapped following release. In 2012, 81 of 108 tagged individuals (75%) entered the hydrophone array. Seventy-three of 108 individuals (68%) reached the face of the generating station. Of the 27 lampreys not detected entering the hydrophone array, four were caught at other trapping locations and 23 were never detected following release.

We also found no evidence that upstream movement was deterred by high discharge or spawning opportunities. In 2011, the probability of a tagged Sea Lamprey arriving at the downstream face of the generating station was slightly higher on nights of high discharge than on nights of low discharge ($G = 4.02$, $df = 1$, $p < 0.05$). In 2012, there was no difference in probability of arrival at the dam face between nights of high and low discharge ($G = 0.09$, $df = 1$, $p > 0.75$). In addition, 2D tracks for individual lampreys suggested that many lampreys were trying to enter the draft tubes exiting from the generating station (Fig. 3) where water velocities can exceed 1 ms^{-1} . We found no evidence that upstream migration was deterred by the availability of spawning habitat downstream of the dam. In 2011, contract divers verified that Sea Lampreys were spawning within the hydrophone array, but 92% (84/91) of the tagged lampreys entering the hydrophone array moved all the way to the face of the generating station in 2011 and 90% (73/81) did so in 2012.

Three lines of evidence supported the explanation that the proportion of Sea Lampreys encountering traps is low because the occurrence of Sea Lampreys along the face of the generating station was concentrated away from the trap locations. First, for all three data sets, the best approximating model predicting the spatial occurrence of Sea Lampreys along the face of the generating station included discharge, water depth, and the statistical interaction between discharge and depth as predictor variables. The inclusion of water depth, and the statistical

interaction between water depth and discharge, indicated that across all three datasets the probability of Sea Lamprey occurrence varied vertically and the vertical distributions of occurrence varied with discharge (Tables 1,2). Second, for each data set, heat maps summarizing the probability of occurrence for different cells along the face of the generating station revealed high variability across cells, suggesting that the probability of occurrence was clumped across cells rather than uniform (Fig. 4). The heat maps further indicated that the probability of occurrence was generally higher in cells at the bottom of the generating station in the deepest part of the tailrace and cells along and in front of the draft tubes exiting the generating station (dark red in Fig. 4). Sea Lampreys were much less likely to occur at the top corners of the face of the generating station near the shore where water velocities were slow (dark blue in Fig. 4). They were also less likely to occur near the water surface where the traps are located. Third, examination of 2D horizontal tracks demonstrated that most Sea Lampreys moved along much of the face of the hydro-generating station and were not over-dispersed and immobile along the face (Fig. 3).

The expectation that under high discharge Sea Lampreys would alter their space use in ways that would favour increased encounter with traps was not strongly supported. As noted above, Sea Lampreys were more likely to reach the face of the generating station on nights when discharge was high, than when discharge was low, in 2011, but not 2012. The probabilities of Sea Lampreys occurring in specific cells along the face of the generating station also varied with discharge (Tables 1, 2). For all three datasets, the model including a term for the depth by discharge interaction was the best approximating model in each of the model sets (Table 1). On nights of high discharge, the probabilities of Sea Lampreys occurring in cells including, and adjacent to, traps tended to be lower than the probabilities for nights of low discharge, while

probabilities of Sea Lamprey occurring in cells along the bottom of the river and near the draft tubes tended to be higher on nights of high discharge than on nights of low discharge (Fig. 4). However, when visually comparing the heat maps, the differences in occurrence for individual cells at low and high discharge were quite small (Fig. 4).

Discussion

Our findings support two main conclusions. First, the low proportions of Sea Lampreys encountering traps observed by Bravener and McLaughlin (2013) at this trap location were likely due to a vertical (spatial) mismatch between the space use of the Sea Lampreys and the locations of traps, although movement of released animals in directions away from the trapping location was probably also a contributor. Second, increasing discharge did not alter space use in ways that would appreciably increase rates of encounter and success for traps in their current location at the top of the water column.

Our conclusion that encounter with traps is low because of a vertical mismatch between Sea Lamprey space use and trap locations is supported by two lines of reasoning. First, the 2D telemetry tracks and our occupancy analyses suggested that Sea Lampreys actively moved along the face of the generating station, but were much more likely to occur near the bottom of the water column, and near the draft tubes, well away from the traps ~15 m above. Further, many of the telemetry tracks suggested that individual Sea Lamprey were entering the draft tubes exiting the generating station. While doing so, those lampreys would be unavailable to encounter traps at the surface. These findings were inconsistent with the explanation that encounters with traps are low because the lampreys were over-dispersed and attached (immobile) for extended periods of time. The affinity for the river bottom is consistent with observations of adult Sea Lampreys

migrating in river sections downstream of any migration barrier (Araújo et al. 2016; Bravener 2011; Holbrook et al. 2015). It provides a unique demonstration of how vertical space use can be important to trapping success (but see Engeman et al. 1999). Second, there was little support for the hypothesis that Sea Lampreys entering the hydrophone array were not reaching the downstream face of the generating station, either because of limitations on swimming capability, or because they stopped at spawning sites downstream of the face of the generating station. Over 90% of Sea Lampreys entering the array reached the face of the generating station in each year, even though contract divers video-recorded spawning activity downstream of the generating station. We also found no evidence that fast water velocities were impeding upstream progress, as observed for lampreys in other river and passage systems (Almeida et al. 2002; Johnson et al. 2012; Keefer et al. 2011).

Our findings suggest that both fallback from release points and reversals could also contribute to the low encounter probabilities with traps. We consider fallback to be the immediate reversal from a release point. However, we cannot be certain whether fallback is a response to handling or occurs naturally (Holbrook 2015). Alternatively, we consider the response a reversal if an individual moves upstream, approaches the barrier and then reverses their movement downstream. Depending on the year, 16- 25% of released Sea Lampreys never entered the hydrophone array downstream of the generating station. The magnitude of these percentages is consistent with Bravener's (2011) earlier observation that only 67% (22/33) of acoustic tagged Sea Lampreys entered a hydrophone array (~100m x 100m) positioned in the river section immediately downstream of our study site. In our study, 7 tagged Sea Lampreys were captured at trap locations kilometers away from our study traps. Furthermore, migrating adult Sea Lampreys are known to display reversals in movement (Almeida et al. 2002; Applegate

1950; Dawson et al. 2016; Dolinsek et al. 2008; Holbrook et al. 2016b; Kelso and Gardner 2000). Reversals occur in other fishes too (Frank et al. 2009; McLaughlin et al. 2013). Such reversals could add to the challenges of trapping in large rivers that offer a diversity of possible movement routes, especially if the animals do not return to previously visited trap locations (Bravener and McLaughlin 2011)

Our conclusion that increasing discharge from the generating station did not alter space use in ways that would increase encounter and success for traps in their currently operated positions is supported by analyses considering both the approach to the face of the generating station and space use along the face. The probability of Sea Lampreys reaching the face of the generating station was not appreciably higher on nights of high discharge than on nights of low discharge, providing little evidence that higher nightly discharges were more attractive to, or stimulated upstream movement of, migrating Sea Lampreys, in the way described for other systems and species of lamprey (Almeida et al. 2002; Castro-Santos 2004; Keefer et al. 2011). Further, on nights of high discharge, probabilities of Sea Lamprey occurrence were higher for cells near the river bottom and the draft tubes, and decreased for cells near the water surface and trap locations. These changes could indicate that increased water velocities from the draft tubes attracted the Sea Lampreys (Keefer et al. 2011; McLaughlin et al. 2011), pulling them away from trap sites; however, the increased flows could also be constraining movement of Sea Lampreys to locations near the river bottom (Keefer et al. 2011; Kirk et al. 2016). This seems unlikely given the evidence of Sea Lampreys entering the draft tubes. Either way, the responses of Sea Lampreys to altered discharge support Foster and Harris' (1997) observation from insect pest management; factors that serve as attractors on one spatial scale may not do so at a different spatial scale. Although the differences in occurrence may not appear striking on Figure 4,

predicted probabilities of occurrence for some cells at the bottom were 5 times higher when discharge was high versus when it was low, while the probabilities of occurrence in cells near the surface were 5 times lower.

How managers could best respond to our findings is a challenging issue. We found no evidence to advise that managers should alter the current trapping strategy of operating small numbers of fixed trap sites in areas where Sea Lampreys are likely to be from a two-dimensional perspective in favour of operating many more widely-spaced, portable traps. Our findings suggest that the space use of Sea Lamprey is heterogeneous both horizontally and vertically, and the traps are located appropriately from a horizontal perspective. It appears to be the vertical positioning of traps that results in low probabilities of encounter. We explore three possible options for managers to evaluate. One solution for overcoming the vertical mismatch would be to attract Sea Lamprey to the traps, but doing so may not be straightforward. Manipulation of discharge failed to alter space use in ways that increased encounter with traps (this study) or capture success (Rous, 2014). For the St. Marys River, experiments using pheromone to attract Sea Lampreys to the traps also resulted in little improvement in trap success (Johnson et al. 2013; see also Luehring et al. 2011). It might be possible to use electricity or alarm cues to encourage the Sea Lampreys to move away from the river bottom (Johnson et al. 2014; Wagner et al. 2011), but it is unclear whether the lampreys would move upward in the water column toward the traps or reverse back downstream. A second solution for overcoming the vertical mismatch would be to position the traps closer to the river bottom where Sea Lampreys are located. This solution would present significant engineering challenges, in terms of deployment and operation, given the nature of the hydrodynamics in the tailrace. While this change in trap placement would likely increase the rate at which Sea Lampreys encounter the traps, companion

studies suggest that trap success could still be limited by low rates of trap entry (Bravener and McLaughlin 2013; Dawson et al. 2016; McLean et al. 2015). One final solution would be to reconsider whether further investment in trapping is appropriate, or if the money and effort invested in trapping could provide a better payoff, in terms of control, if invested in other control methods (Hansen and Jones 2008; Robinson et al. 2016).

As with any study, uncertainties remain and identifying these can ensure our findings are interpreted and applied appropriately, as well as identify avenues for future research. Four limitations warrant consideration. First, our interpretation of the occupancy models has assumed that the spatial distributions of tag detections provide a representative sample of Sea Lamprey occurrence. This assumption could be biased if the detectability of tags varied spatially along the face of the generating station, possibly due to changes in background noise (e.g. boat traffic), changes in tag range associated with altered discharge and cavitation, and issues with line of sight between the tags and the hydrophones. Not all pings were detected from the tags, but inter-ping intervals were short on average and highly skewed toward short intervals (Table S4). Our preliminary analyses indicate that inter-ping intervals may differ under low and high discharge, but not in a way that could explain the vertical differences in the detections of Sea Lampreys because we found no difference in the detection probabilities for tags at the surface versus the bottom. We are not aware of any practical way to resolve this uncertainty. Second, it is unclear whether the behaviour of the tagged Sea Lampreys is representative of Sea Lampreys that were not tagged. An experiment in 2012 comparing releases of fin-clipped, PIT tagged, and acoustic and PIT tagged Sea Lampreys failed to detect any difference in catch curves for lampreys in the different marking treatments (McLaughlin et al. 2016), but comparison of Sea Lamprey behaviour across the treatments was not feasible; the opportunity to track behaviour is limited for

PIT tagged and fin-clipped individuals. Our findings regarding Sea Lampreys in front of and in the draft tubes also suggest the swimming performance of tagged lampreys was better than we had hypothesized. Third, the definition of encounter used in this analysis (occurrence in a 3 x 3 x 3m cube) is not as precise spatially as the definition used in Bravener and McLaughlin's (2013) PIT tagging study (occurrence within ~1.0 m of a trap opening). The larger spatial grain used here was based on the spatial precision of the positioning estimates and on judgment regarding how the probability of a lamprey being captured decreases with distance from the trap. Fourth, the temporal grain at which we measured space use (over 1 h) is also much larger than the temporal grain of 1-300 s that it takes individual Sea Lampreys to encounter and enter traps (Bravener and McLaughlin 2013; McLean et al. 2015). One hour was the finest temporal grain at which we could resolve differences in discharge and water temperature. The differences in spatial and temporal grain raise the possibility that much could happen in the way of trap encounter and entrance within cells containing traps, even though the occupancy models suggest that Sea Lampreys are much less likely to occur in those cells. However, the low occupancy predicted for cells containing traps (this study) is consistent with earlier findings that individual Sea Lampreys spent little time near the traps (Bravener and McLaughlin 2013; McLean et al. 2015).

Despite these limitations, two noteworthy features of our study allowed us to overcome physical features of this study system that were impeding the understanding of Sea Lamprey behaviour near traps and overall trapping success. These were the application of acoustic telemetry and experimental manipulation of discharge. In a recent review, Hussey et al. (2015) emphasized how developments in aquatic animal telemetry are enhancing opportunities to study the behaviour of aquatic animals, the types of aquatic environments considered, and scope of

questions addressed. Our study provides a demonstration of how space use can be quantified at a much finer spatial precision (~ 1 m) than the examples presented by Hussey et al (2015). It further demonstrates that this form of telemetry can be applied successfully and usefully to study movement and space use in the challenging conditions found in the tailrace of a dam, including entrained air, turbulence, and background noise from boats and any generating station. The application of acoustic telemetry to track fishes in these challenging circumstances is still new (Ingraham et al. 2014; Jung et al. 2015; Kopp et al. 2014). The manipulation of discharge also allowed us to evaluate more rigorously whether higher flows could increase encounters with traps, either through attraction or stimulation of activity. Large-scale flow experiments are valuable for supporting evidence-based changes to management policies (Johnson et al., 2012; Olden et al., 2014), but can be challenging to arrange and execute. They can be particularly valuable in situations where flow is regulated or relatively uniform, and where correlational approaches may be inconclusive or misleading.

The findings of our study have made an important contribution toward understanding why the trapping success of Sea Lampreys in large rivers is much lower than desired. They also raise questions about the adequacy of simplistic ideas suggesting that rates of encounter can be increased through manipulation of discharge, at least at larger spatial scales. Our findings help clarify the role space use can have on trap success and provide information that could guide future research directions and management decisions about trapping for control.

Acknowledgements

We thank (i) S. Filteau, D. Kelch, B. McClenaghan, and A. Brown for their daily assistance in the laboratory and field, (ii) numerous volunteers from Algoma University, Fisheries and Oceans

Canada, US Fish & Wildlife Service, and US Geological Service for assisting with the installation and removal of the hydrophone arrays and the transport of Sea Lamprey, (iii) D. Porpealia, Porpealia Repair Ltd., for dive support, his incredible insight regarding the underwater conditions at the study site, and his enthusiasm for our project, (iv) the International Joint Commission for authorizing the manipulation of discharge through the hydro-generating station, Brookfield Renewable Energy Partners for agreeing to participate, and specifically R. MacLeod and G. Labelle for their day-to-day assistance, (v) personnel, and specifically P. Nelson and S. Johnson, from HTI Sonar for their assistance with configuring the acoustic array and processing the acoustic telemetry data, and (vi) B. Robinson, J. Fryxell, T. Nudds, and three anonymous reviewers for comments on earlier drafts of the manuscript. Funding for this research was provided by grants from the Great Lakes Fishery Commission's Sea Lamprey Research Program by way of Great Lakes Restoration Initiative appropriations (GL-00E23010), Canada Foundation for Innovation, and Ontario Innovation Trust. This paper is Contribution 32 of the Great Lakes Acoustic Telemetry Observation System (GLATOS).

Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

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1 **Figures** 4 **Figure 1.**

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10 **Figure 2.**

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Figure 3.

Figure 4.

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Figure Legends

Fig. 1. The Clergue Generating Station and Sea Lamprey trap sites (closed white circles; top panel) are located approximately 23 km downstream of the outflow from Lake Superior. The traps sites from top to bottom are: north attractant water trap, north portable trap, centre portable trap, south portable trap, and south attractant water trap. Positions of the hydrophones in the acoustic telemetry array in the tailrace of the Clergue Generating Station (bottom panel). Individual hydrophone locations are shown as circles (N=16). Yellow circles denote hydrophones mounted near the water surface. Red circles denote hydrophones mounted near the river bottom.

Fig. 2. Number of Sea Lampreys caught in the five traps at the Clergue Generating Station (bars) and mean discharge (circles and dashed lines) from the generating station in 2011 (top) and 2012 (bottom). Closed circles represent nights when discharge was not reduced (high). Open circles represent nights when discharge was reduced (low).

Fig. 3. Panels depicting 2D positions for six Sea Lampreys: three from 2011 (left panels) and three from 2012 (right panels). Individual (tag) numbers appear below each panel. Yellow circles indicate individual positions. Positions on the road in front of the hydro-generating station coincide with the draft tubes where water exits the hydro-generating station.

Fig. 4. Heat maps depicting the estimated probability of occupancy during the night for each cell along the face of the Clergue Generating Station. Heat maps for low (left panels) and high (right panels) discharge are provided for 3D acoustic data from 2011 (top) and 2012 (middle), and for 2D and depth (pressure) data from 2012 (bottom). The locations of traps are indicated by small squares labeled 'T'. The locations of draft tubes where water exits the hydro-generating station are indicated by the three larger rectangles outlined in black. The south attractant water trap is not shown, because it is located about 12 m downstream of the face of the generating station on the south (left) shore of the river (see Figure 1 bottom).

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1 Tables

2 **Table 1.** Assessment of model sets for Sea Lamprey occupancy at locations (cells) along
 3 the downstream side of the face of the hydro-generating station. Model set 1 considers
 4 covariates. Model set 2 considers the effects of discharge and depth (predictors) in
 5 addition to covariates. The best approximating model from model set 1 was taken
 6 forward as the baseline model for model set 2. Separate analyses are provided for 3D
 7 positions estimated from acoustic data in X, Y, and Z spatial axes (2011 and 2012) and
 8 2D positions estimated from acoustic data in X and Y spatial axes and depth from
 9 pressure sensor.

10 2011 Acoustic 3D Data

Explanatory variables	BIC	Δ BIC	df	w_i
Model set 1 (assessment of covariates)				
Cell volume, time, temperature	3657150	0	5	0.33
Cell volume, time, date	3657150	0	5	0.33
Cell volume, temperature	3657150	0	5	0.33
Cell volume, time, temperature, date	3657162	12.4	6	<0.001
Cell volume, temperature, 1+time	3657175	24.9	7	<0.001
Model set 2 (assessment of predictors)				
Cell volume, time, temperature, discharge, depth, discharge:depth	3648790	0	8	1
Cell volume, time, temperature	3657150	8359.9	5	<0.001
Cell volume, temperature, discharge	3657162	8372.4	6	<0.001
Cell volume, temperature, discharge, depth	3657174	8384.6	7	<0.001

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12 Table 1 (cont'd)

2012 Acoustic 3D Data

Explanatory variables	BIC	Δ BIC	df	w_i
Model set 1 (assessment of covariates)				
Cell volume, time, temperature	678356.2	0	5	0.985
Cell volume, time, temperature, date	678365.1	8.9	5	0.012
Cell volume, temperature, 1+time	678367.7	11.5	6	0.003
Cell volume, time, date	678380.2	23.9	7	<0.001
Cell volume, temperature	678404.2	47.9	5	<0.001
Model set 2 (assessment of predictors)				
Cell volume, time, temperature, discharge, depth, discharge:depth	667874.6	0	8	1
Cell volume, time, temperature	678354.5	10479.9	7	<0.001
Cell volume, temperature, discharge	678356.2	10481.6	5	<0.001
Cell volume, temperature, discharge, depth	678365.9	10491.3	6	<0.001

Table 1 (cont'd)

2012 Acoustic 2-D + depth (pressure sensor) data

Explanatory variables	BIC	Δ BIC	df	w_i
Model set 1 (assessment of covariates)				
Cell volume, time, temperature	747047.2	0	5	0.33
Cell volume, time, date	747047.2	0	5	0.33
Cell volume, temperature	747047.2	0	5	0.33
Cell volume, time, temperature, date	747059.3	12	6	<0.001
Cell volume, temperature, 1+time	747071.3	24	7	<0.001
Model set 2 (assessment of predictors)				
Cell volume, time, temperature, discharge, depth, discharge:depth	744215.9	0	8	1
Cell volume, time, temperature	747047.2	2831.3	5	<0.001
Cell volume, temperature, discharge	747059.3	2843.4	6	<0.001
Cell volume, temperature, discharge, depth	747061.4	2845.5	7	<0.001

Table 2. Regression estimates of random and fixed effects from the best approximating occupancy model (mixed effects logistic regression).

2011 acoustic 3D data

random effects:	variance	standard deviation	
cell identification	5.96	2.44	
time of day individual ID	0.00	0.00	
fixed effects:	estimate	lower 95% CL	upper 95% CL
intercept	-6.92	-7.25	-6.59
discharge	-0.142	-0.147	-0.136
depth	0.21	-0.23	0.65
discharge:depth	-0.65	-0.66	-0.63
cell volume	1.04	0.60	1.47
water temperature	0.00	-0.005	0.005

Table 2 (cont'd)

2012 acoustic 3D data

random effects:	variance	standard deviation	
cell identification	4.06	2.02	
time of day individual ID	0.0064	0.080	
fixed effects:	estimate	lower 95% CL	upper 95% CL
intercept	-6.72	-7.04	-6.41
discharge	-0.38	-0.40	-0.37
depth	-1.68	-2.28	-1.09
discharge:depth	-1.64	-1.67	-1.61
cell volume	0.38	-0.21	0.97
water temperature	-0.03	-0.04	-0.02

Table 2 (cont'd)

2012 acoustic 2D + depth (pressure sensor) data

random effects:	variance	standard deviation	
cell identification	4.41	2.10	
time of day individual ID	0.00	0.00	
fixed effects:	estimate	lower 95% CL	upper 95% CL
intercept	-6.79	-7.12	-6.46
discharge	-0.28	-0.29	-0.26
depth	-1.10	-1.73	-0.46
discharge:depth	-0.90	-0.93	-0.86
cell volume	1.24	0.63	1.85
water temperature	0.00	-0.012	0.016