Behaviour and Space Use of Sea Lamprey at Traps Near a Hydroelectric Generating Station

by

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Invasive species are the focus of management concern in many ecosystems. Trapping is a potentially valuable form of control. I used telemetry to track sea lamprey immediately downstream of traps at a hydro-generating station. I tested if manipulations of discharge influenced the behaviour of lamprey in a manner that increased their susceptibility to trapping. Encounter rates with traps increased when discharge was high, but rates of departure without entering traps simultaneously increased. I further tested whether lower trapping success is a consequence of space use by lamprey immediately downstream of traps. Lamprey aggregated away from where traps were located. Differences in vertical space use with respect to discharge suggest that flows exiting the generating station attract sea lamprey to the station wall, but also away from the traps. To improve trap success, managers must make traps more attractive or place traps in locations where lamprey are most likely to aggregate.
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PRODUCTION NOTE

This thesis was written in manuscript format. As such, figures may appear more than once. In addition, there is redundancy in parts of the Introduction and Methods of each chapter. Each chapter was written in a style targeted to a specific journal. Chapter 1 will be submitted to Journal of Applied Ecology, a journal that publishes papers that apply ecological concepts and methods to inform and improve management. Chapter 2 will be submitted to Canadian Journal of Fisheries and Aquatic Sciences, a journal that reports new understanding of fisheries and aquatic sciences. Several co-investigators were involved in the conceptualization and experimental design of this project. At this time they have not been involved in the analysis and communication of this thesis. As such, Jessica Barber, Gale Bravener, Chris Holbrook, Istvan Imre, Lisa O'Connor, and Tom Pratt may be included as co-authors in the resultant publications.
PROLOGUE

Scientists are being challenged to investigate the life-history and behaviour of invasive species to develop novel and effective ways to manage their impacts (Palmer et al., 2004). Great emphasis is being placed on preventing initial invasions or limiting spread of newly established species (Hulme, 2006; Gallien et al., 2010). However, invasions continue to happen, perhaps because decision makers and the public are reluctant to spend money to prevent events that may not occur. Consequently, demand for management approaches that eliminate or control invasive species upon invasion remain. Fewer studies address how understanding the ecology of established species could reveal features that are exploitable through management (Hulme, 2006).

Management efforts to eradicate, control, or mitigate invasive species have achieved varied levels of success (da Cunha Nogueira et al., 2007; Hein et al., 2007; Bryce et al., 2011). Most successes have occurred in small isolated populations, such as islands (Veitch et al., 2011), because containment, implementation, and monitoring are all easier at a smaller spatial scale (Hulme, 2006). Of equal importance in successful control programs is the level of susceptibility of the target organism to control efforts (Myers et al., 2000). Understanding the ecology of an invasive species is fundamental in designing a program and measuring its effectiveness. Control programs that have independently developed knowledge on the ecology of the target species or can apply pre-existing knowledge often achieve the greatest success (see Myers et al., 2000 for examples).

This thesis focuses on the trapping component of an integrated management approach to controlling sea lamprey (*Petromyzon marinus*), an invasive species in the Laurentian
Great Lakes. Sea lamprey have been the target of a binational control program for over 50 years. In the Great Lakes, sea lamprey control focuses on three techniques: (i) periodic lampricide treatment of tributaries where larval sea lamprey rear for the first four to five years of their life, (ii) barriers that deny migrating adult sea lamprey access to spawning habitat in tributaries, and (iii) trapping of adult migrating sea lamprey to remove them from the population prior to reproduction.

Overall, the control program has been effective at suppressing sea lamprey populations (approximately 90% population size reduction) to levels that greatly reduce their impacts on native fishes in the Great Lakes (Vander Zanden et al., 2010). Still, population levels remain above management targets in certain regions of the Great Lakes. The St. Marys River, connecting Lakes Superior and Huron, is considered to contribute a significant portion of the sea lamprey population to Lake Huron, and as such, it is of strategic importance.

There is a desire to increase the efficiency of trapping to improve control in areas, such as large river systems, where traditional methods (i.e. lampricide treatment) are not feasible due to size and cost (Great Lakes Fishery Commission, 2008). Mark-recapture studies estimated the trapping efficiency, across all traps in the St. Marys River, to be approximately 40%, on average (Schleen et al., 2003). A recent decision analysis comparing different management options for the river revealed that the best options involved an increase in trapping efficiency to 70%, the highest efficiency that control agencies believed they could achieve, in conjunction with sterile-male release and strategic lampricide treatments (Haeseker et al., 2007). Since then, a tracking study of sea lamprey in the St. Marys River estimated that trapping efficiency for individual traps
was approximately 10%, due to low rates of encounter of sea lamprey with traps, low entrance rates upon encounter, and low rates of re-encounter with traps upon departure (Bravener and McLaughlin, 2013).

The objective of my thesis is to examine whether large-scale manipulations of discharge from the Clergue Generating Station on the St. Mary’s River, Canada influenced the behaviour and space use of migrating sea lamprey (*Petromyzon marinus*) and their vulnerability to trapping. Understanding patterns of behaviour and the underlying mechanisms that influence trapping success is of broad interest for invasive species control programs. In chapter 1, I examine if large-scale manipulations of discharge influence the behaviour of spawning-phase sea lamprey in a manner that increases their susceptibility to trapping. The experiment was set in a behavioural framework developed by Bravener and McLaughlin (2013) that quantifies encounter, entrance, and departure behaviour at traps. I tested four hypotheses and corresponding predictions of how discharge could influence sea lamprey behaviour and vulnerability to trapping. In chapter 2, I examine if sea lamprey space use can explain low trap success. I quantify i) the encounter rate of sea lamprey with traps, ii) the proportion of sea lamprey that reach the downstream face of the generating station, and iii) the probability of occupancy for locations along the face of the generating station. I use 3D acoustic telemetry and occupancy modelling to test whether sea lamprey distribute evenly in space or whether they aggregate in locations other than where traps are located. Understanding how sea lamprey use space near traps might explain lower than desired trap success if sea lamprey are unlikely to encounter traps. This analysis should provide useful insight for managers about where lamprey are located relative to traps. If lamprey are unlikely to
encounter traps in their current locations, managers could move traps to locations that could increase the likelihood of encounter.
CHAPTER 1: MANIPULATION OF DISCHARGE FAILS TO IMPROVE TRAPPING SUCCESS FOR INVASIVE SEA LAMPREY: A BEHAVIOURAL EXPLANATION

ABSTRACT

I tested if large-scale manipulations of discharge influence the behaviour of invasive migrating sea lamprey (*Petromyzon marinus*) and their vulnerability to trapping near the Clergue Generating Station on the St. Marys River, Canada. Invasive species are the focus of management concern in ecosystems across the globe. Trapping is a potentially valuable form of control. In the Laurentian Great Lakes, increased trapping success for sea lamprey in large rivers is desired to meet the objectives of a binational control program. During two seasons, 216 sea lamprey were tagged with passive integrated transponder (PIT) tags and released downstream of the generating station. Discharge through the generating station was altered nightly and sea lamprey encountering, and leaving or entering, two traps were monitored using PIT telemetry and analyzed using multi-state Markov (MSM) models. Sea lamprey altered their behaviour with changes in discharge, but with minimal improvement to trap success. Rates of encounter with traps increased when discharge was high versus when it was low, but rates of departure simultaneously increased. Rates of entrance did not change with discharge. Understanding the behavioural basis of these counteracting responses is important because it may help us understand why expected gains in trap success following a discharge manipulation were not realized.
INTRODUCTION

The frequency of species invasions and their ecological and economic impacts are compelling scientists and resource managers to develop ways of protecting and restoring natural ecosystems (Palmer et al., 2004; Pimental et al., 2005). In many impacted ecosystems, managers rely on control of invasive species as part of their restoration efforts, either because prevention was not pursued, or because prevention measures proved ineffective. Managers may also control invasive species when the potential for eradication is limited (Bonesi and Palazon, 2007; Zuberogoitia et al., 2010; Genovesi, 2011; Clark et al., 2012).

Trapping is a potentially valuable form of control providing that the proportion of the population trapped (trapping efficiency) is sufficiently high to overcome density-dependent population responses. It has been used to control a variety of invasive taxa, including species of insects (El-Sayed et al., 2006), aquatic invertebrates (Hein et al., 2007), fishes (Yavno and Corkum, 2011), amphibians and reptiles (Schwarzkopf and Alford, 2007; Clark et al, 2012), birds (Campbell et al., 2012), and mammals (Bonesi and Palazon, 2007). Trapping has proven most effective when suppressing small, isolated populations (Veitch et al., 2011); however, trapping might be applied more widely, in terms of taxa and ecological conditions, if trapping efficiencies could be improved (El-Sayed et al., 2006; Roy et al., 2006; Bryce et al., 2011).

I tested whether migrating sea lamprey (Petromyzon marinus) altered their behaviour and vulnerability to trapping in response to large-scale manipulation of discharge from the Clergue Generating Station on the St. Marys River, Canada. The sea lamprey is a parasitic fish species that feeds on the blood of large (host) fishes. It entered the Upper
Great Lakes between 1924 and 1938 (Smith and Tibbles, 1980; Christie and Goddard, 2003). Following this, sea lamprey populations increased rapidly in Lakes Erie, Huron, Michigan, and Superior and contributed to the declines of 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). The Great Lakes Fishery Commission (GLFC) was created under the Convention on Great Lakes Fisheries (1954) - a treaty between Canada and the United States - to oversee the management of sea lamprey in the Great Lakes. Field operations of the program are contracted to the Department of Fisheries and Oceans Canada (DFO) and the United States Fish and Wildlife Service (USFWS). Sea lamprey control currently relies on three methods: (i) periodic lampricide treatment of tributaries where larval sea lamprey rear for the first four to five years of the life, (ii) barriers that deny migrating adult sea lamprey access to spawning habitat in tributaries, and (iii) trapping of adult migrating sea lamprey to remove them from the population prior to reproduction. In its most recent strategic vision document, the GLFC pledged to accomplish at least 50% of sea lamprey suppression using technologies other than lampricide treatments, including enhanced use of trapping (Milestone 3, Great Lakes Fishery Commission, 2008).

Improvements in trapping success (total number of sea lamprey caught in traps) would be particularly valuable for sea lamprey control in large river systems, such as the St. Marys River. Chemical treatment of rivers with lampricides is less feasible for large than small rivers, because the size and complexity of large rivers greatly increases the amount of lampricide required and the cost and logistics of lampricide application. In the
St. Marys River connecting Lakes Superior and Huron, trapping has historically been used for population assessment and, until 2012, to collect males for a sterile-male release program that has since been discontinued (Schleen et al., 2003). Mark-recapture methods have estimated the annual trapping efficiency across the river to be approximately 40%, on average (Schleen et al., 2003). A recent decision analysis comparing different management options for the river revealed that the best options involved an increase in trapping efficiency to 70%, the highest efficiency that control agents believed they could achieve, in conjunction with sterile-male release and strategic lampricide treatments (Haeseker et al., 2007). Since then, a tracking study of sea lamprey in the St. Marys River estimated that trapping efficiency for individual traps is approximately 10%, due to low rates of sea lamprey encountering traps, low rates of entrance upon encounter, and low rates of return to traps upon departure (Bravener and McLaughlin, 2013). Trap retention was 100%.

Discharge (volume rate of water outflow) represents an environmental feature that could be altered to improve trapping success by attracting sea lamprey to and into traps. Migrating fish often search for specific cues from the hydraulic environment to identify routes past in-stream obstacles to movement (Williams et al., 2012). Traps are operated to mimic an upstream route past an obstacle. They are placed at barriers where river discharge is believed to attract the lamprey, but the barrier prevents further upstream movement, and where water flows exist, or can be provided, near the trap entrance to guide the sea lamprey into the trap. However, the specific cues that fish rely on to identify passage routes remain poorly understood and how these cues change with changes in discharge is potentially complex. Manipulation of environmental features
such as discharge can have long-distance effects that draw or repel animals to a particular location (Foster and Harris, 1997). For example, field and laboratory studies of lamprey species have indicated that fast water flows can stimulate upstream movement and general activity up to a threshold level of flow where forward progress is constrained by limits on a fish’s swimming speed and energy stores (Almeida et al., 2002; Quintella et al., 2004). Manipulation of environmental features can also have short-distance effects that influence an animal’s willingness to stay or leave once it has reached a location (Foster and Harris, 1997). Flows where sea lamprey traps are located can be highly variable in terms of water velocity. Flows varying predictably in water velocity appear to attract fish, while those that are chaotic appear to repel fish (Liao, 2007; Lacey et al., 2011). Lastly, the degree to which manipulated flows are attractive, and even detectable, can depend on the broader hydrodynamic environment. With fish passageways at dams, for example, the fish may not find or move to the fishway opening because the flows created by water discharge over the dam is more attractive than the flow from the water discharged through the fishway (Keefer et al., 2011; Johnson et al., 2012).

I used the conceptual framework of trapping developed by Bravener and McLaughlin (2013) to structure my examination of how sea lamprey alter their behaviour, and vulnerability to trapping, in response to discharge. The framework envisions trapping as a process where migrating sea lamprey can transition between four states: unavailable, available, trapped, and removed. Sea lamprey are considered unavailable when they are migrating in the river, but located far enough from any trap that it is reasonable to assume they are not vulnerable to being trapped. A sea lamprey is available when they
come close enough to the trap that there is reasonable expectation that they could be trapped (i.e. have encountered a trap). At this point, the lamprey could enter inside the trap (trapped) or leave the trap area (departure) and become unavailable again. A sea lamprey is considered removed once a trap operator has physically removed the animal from the trap and therefore the population. It is possible that trapped sea lamprey can escape from the trap before the trap operators arrive. I considered only the first three states of the framework here because, for my study traps, Bravener and McLaughlin (2013) demonstrated that all sea lamprey that enter the traps are retained and removed.

I tested four hypotheses predicting how manipulation of discharge would influence rates at which sea lamprey encounter, depart from, and enter into, traps, as well as overall trapping success (Table 1.1). One hypothesis was that increased discharge would alter hydrodynamic conditions at both long- and short-distances downstream, stimulating upstream movement and activity of sea lamprey, and increasing their encounter with and entrance into traps, while reducing departure (Full Attraction Hypothesis). A second hypothesis was that increased discharge would alter hydrodynamics downstream, stimulating upstream movement and activity, and leading to increased encounter with traps, but, at the trap location where flows are highly variable under both low and high discharge, it would have no effect on entrance and departure (Encounter Hypothesis). A third hypothesis was that increased discharge would stimulate encounter with traps, as above, but decrease entrance, and increase departure, either because increased discharge creates more chaotic flows that tend to repel fish or because high flows released from the draft tubes of the generating station become more attractive relative to the flows at the traps when discharge is high (Counteracting Responses Hypothesis).
A fourth hypothesis was that increased discharge would have no effect on rates of encounter, entrance, and departure. No change in encounter could occur if sea lamprey simply exhibit a rheotactic response that is not influenced by the magnitude of discharge. No change in entrance and departure could occur because the flows near traps are highly variable under both low and high discharge.

This hypothesis set includes the leading candidate hypotheses that can be justified based on knowledge of how migratory fishes respond to discharge, rather than an exhaustive set considering all possible changes in encounter, entrance, and departure, many of which would be hard to justify based on current knowledge. Evidence failing to support any of the candidate hypotheses would justify the development of novel hypotheses.

METHODS

DESCRIPTION OF STUDY SITE
Field tracking of sea lamprey was conducted from 26 June to 25 July 2011 and 8 June to July 7 2012 in the tailrace of the Francis H. Clergue Generating Station on the St. Marys River, connecting Lakes Huron and Superior (Fig. 1.1). The river is bounded to the south by Michigan, USA and to the north by Ontario, Canada. It 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 the four generating stations (three in US waters, one in Canadian waters) and three shipping canals (two on the US side and one on the Canadian side).
The Clergue generating station is located along the north shore of the St. Marys River, in Sault Ste Marie, Ontario, Canada (Fig. 1.2). It is a run-of-the-river hydroelectric dam with a head (height) of 6 m. The powerhouse has three turbines with capacity of 52 megawatts. Mean discharge at the Clergue generating station is approximately 1000 m³/s (Duffy et al., 1987). The tailrace of the generating station is approximately 70 m wide with water depths of approximately 16 m at the wall of the generating station, but decreasing to 12 m approximately 20 m downstream.

**SEA LAMPREY TRAPPING OPERATIONS**

Department of Fisheries and Oceans Canada operates five sea lamprey traps along the downstream face of the Clergue generating station. The north (NAWT) and south attractant water (SAWT) traps are permanent structures with two and four entrances, respectively. Both traps direct high flow out of the trap entrances to attract sea lamprey. The traps can hold thousands of lamprey. Three portable traps are installed along the downstream face of the generating station during the period of adult sea lamprey migration. Portable traps are designed like a large “minnow-trap”, with two funnel openings at opposite ends, and positioned perpendicular to the discharge from the generating station. They are placed on the face of the power plant in areas of high discharge above the draft tubes. These traps can hold up to 500 lamprey. All traps fish at depths of 1 and 3 m below water surface. The traps are checked and emptied daily by DFO. In addition to the Clergue generating station, there are four more trap locations on the St. Marys River where one to six traps are operated: the St. Marys Rapids and three other hydroelectric generating stations.
MANIPULATION OF NIGHTLY DISCHARGE

The hydro operator (Brookfield Renewable energy Partners), with the authorization from the International Joint Commission, agreed to alter discharge from night to night so that I could test how discharge affected the behaviour of sea lamprey approaching and entering traps, and trapping efficiency. Discharge was manipulated at night because that is when sea lamprey are most active (Binder and McDonald, 2007). Under normal operations, the majority of daily discharge occurs during the day (0800h-2200h; mean = 910 m³/s), when demand for electricity is higher, and decreases at night (2300h-0700h; mean = 475 m³/s), when demand for electricity is lower. During the study period, discharge from 2300-0700h was altered from the normal low for this time of year on one night to a discharge comparable to daytime discharge the next night. Every effort was made to alternate between high to low discharge on a night-to-night schedule, but infrequent exceptions were necessary due to fluctuations in demand for power generation.

ACQUISITION, TAGGING, AND TRACKING OF SEA LAMPREY

Passive integrated transponder (PIT) telemetry was used to monitor the behaviour of sea lamprey at the NAWT and SAWT. Sea lamprey for my study were obtained from the United States Fish and Wildlife Service and came from trapping operations at sites on the US side of the St. Marys River. These sea lamprey were assumed to be representative of sea lamprey lacking experience with the Clergue site. Acquiring sea lamprey from other rivers was not feasible. Sea lamprey elsewhere had already spawned; the sea lamprey migration occurs later in the St. Marys River than in other tributaries, due to the river’s large size and cold temperatures.
Upon removal from traps, the test sea lamprey were placed in aerated basins in a boat and transported by USFWS agents to the DFO Sea Lamprey Control Holding Facility adjacent to the Clergue generating station. At the holding facility, the sea lamprey were sexed and 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). The sea lamprey were held for 1-3 days prior to tagging.

Two hundred and sixteen sea lamprey (1:1 sex ratio) were surgically implanted with passive integrated transponder tags (3.4 mm x 23 mm, 0.6 g in air, Texas Instruments, Dallas, TX) and an acoustic tag (Model 795G, 4.5 g in air, Hydroacoustic Technology, Inc., Seattle, WA). PIT tags were used for tracking the encounter, entrance into, and departure from traps. Acoustic tags were used to obtain 3D positions of sea lamprey in the water column downstream of the generating station (Chapter 2). In preparation for implantation, an individual sea lamprey was netted from the holding tank, placed in an aerated bath of MS 222 (50 mg/L), observed, and removed once they reached stage 3 of anaesthesia (partial loss of equilibrium). The individual was then placed on a measuring board, measured for total length (±1mm), 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) followed by a sterile saline solution (9 g/L). A small incision (5 mm) was made near the ventral midline using a sharp scalpel and a PIT and an acoustic tag were inserted into the peritoneal cavity using forceps. The incision was closed using three independent sutures with monofilament nylon sutures (Ethicon monocryl monofilament). During the surgery, the lamprey was periodically irrigated with a maintenance dose of anaesthetic (30 mg/L) in oxygenated water. Scalpels, forceps, and tags were all
disinfected in a Virkon solution (1g/L) and rinsed with sterile saline solution (9g/L) prior to use. Scalpel blades were changed after every fifth lamprey to ensure they were sharp. Following surgery, the tagged lamprey was transferred to a recovery tank, monitored to ensure full recovery from the anaesthesia, and held for 1-4 days prior to release in the St. Marys River.

Lamprey were released at one of three sites across the river channel (south, center, north) approximately 300 m downstream from the Clergue generating station. Three release sites were chosen because I did not have knowledge of how sea lamprey normally approached the Clergue generating station from downstream. The release distance was selected to give tagged lamprey ample opportunity to select their upstream path, while ensuring that they were likely to enter our study area rather than move elsewhere in the river. Lamprey were released on six dates, separated by 48 hours, between June 26-July 6 in 2011 and June 8-June 17 in 2012. Release dates were selected to cover points before, at, and after the peak migration. On each date, six lamprey (1:1 sex ratio) were released from each release site. Releases occurred at approximately 2000h to minimize predation of tagged animals if exposed to daytime predators immediately post release and because sea lamprey are most active at night.

The activity of the tagged sea lamprey was tracked by antennas installed at each entrance of the NAWT and SAWT (Fig. 1.3). Antennas were hung in front of the entrance by braided steel cable with a steel post attached to the bottom to keep the antennas from lifting during upwells. Each antenna was made of 8 gauge multi-stranded, oxygen free, high conductivity wire placed inside rubber garden hose and attached to a 1.0 m by 0.5 m rectangular frame. The wire antenna was connected to a
tuner box (Standard Remote Tuner Box, Oregon RFID, Portland, OR) and tuned to maximize detection range (~0.5 m). Each tuner box was connected to a multiplexer (Multi-Antenna HDX Reader, Oregon RFID, Portland, OR) by twin axial cable and each multiplexer was powered through an AC to DC power converter and an AC power source. Detection range was tested weekly with the use of a test tag. When tagged sea lamprey were detected by an antenna, the date, time, antenna number, and unique tag number were recorded to a memory card in the multiplexer. Data were downloaded daily from the multiplexers. The three portable traps were not equipped with PIT antennas because a hydraulic crane is used to lift them from the water daily, creating safety risks for both the trap operators and the equipment.

**DATA ANALYSIS**

I calculated mean nightly discharge for each day of the field season based on hourly discharge data provided by the hydro operator. The distribution of mean nightly discharge was visibly bimodal. I used this separation to distinguish between high and low discharge nights, because the hydro operator adjusted discharge on some nights in response to electricity demands. For both years, nights when mean nightly discharge was greater than 775 m$^3$s were classified as high discharge nights, while nights when mean nightly discharge was less than 775 m$^3$s were classified as low discharge nights.

Multi-state Markov (MSM) models were combined with multi-model assessment to quantify rates at which sea lamprey transitioned between unavailable, available, and trapped (Fig. 1.4) and how these transition rates varied with nightly discharge and five other variables known to influence sea lamprey activity: water temperature (Binder et al., 2010), time of day (Binder and McDonald, 2007), sex, which could detect
motivational differences to migrate upstream between males and females, year, and release date, which captures sea lamprey maturity and point in the migration run (Bravener and McLaughlin, 2013). Upstream migration peaks when mean water temperature reaches approximately 11° C (Binder et al., 2010). Strong diel patterns result in most lamprey activity between dusk and dawn (2000h-0800h; Binder and McDonald, 2007). Tagged sea lamprey released earlier in the season were more likely to encounter traps than those released later in the season (Bravener and McLaughlin, 2013).

MSM models quantify how an individual moves between states (e.g., unavailable to available) in continuous time (Jackson, 2011). Movements between states are described by a transition intensity, \( q_{rs} \):

\[
q_{rs}(t, z(t)) = \lim_{\delta t \to 0} P(S(t + \delta t) = s | S(t) = r) / \delta t
\]

where \( q_{rs} \) is the instantaneous rate of an individual at time \( t \) moving from state \( r \) to state \( s \) between times \( t+\delta t \) and \( t \). This formulation assumes that movement from one state \( (r) \) to the next state \( (s) \) depends only on the current state \( (r) \). Transition intensities form a transition intensity matrix, \( Q \), that describes the allowable state transitions.

\[
Q = \begin{pmatrix}
q_{11} & q_{12} & q_{13} \\
q_{21} & q_{22} & q_{23} \\
0 & 0 & 0
\end{pmatrix}
\]
Each row of the matrix sums to zero such that:

\[ q_{rr} = - \sum_{s \neq r} q_{rs} \]

This method can further be used to evaluate whether \( q_{rs} \) varies with individual-specific or time-varying predictor variables, \( z(t) \).

For my application to sea lamprey, I developed a three state model (Fig. 1.4) where a tagged, released lamprey was considered unavailable when it was not within 0.5 m of a trap entrance, the range of the PIT tag antenna. A sea lamprey was considered available when it was within range of a PIT antenna. It was confirmed as trapped once recovered from a trap.

An objective method for determining departure and re-appearance at traps was needed, because PIT records for some individuals were interspersed by intervals where no tag detections occurred. I therefore analyzed intervals between successive detections using the method developed by Sibly et al. (1990) for dividing behaviour into bouts (bout ending criterion), which, in my application, represented periods when an individual was within the trap antenna’s field of detection and periods when the individual was outside of the field of detection. This method was applied and validated using video recordings of sea lamprey that had been tagged with both PIT and external tags (Gale Bravener, personal communication). The method entails using non-linear regression to fit the intervals between tag detections to two exponential processes. One representing the interval of time spent at a trap and the other the interval of time between trap visits. The bout ending criterion is used to separate durations spent at the trap from durations between trap visits.
Multi-model assessment was conducted using the Akaike Information Criterion (AIC) to identify the best approximating model from a set of candidate models (Burnham and Anderson, 2002). Two model sets were considered. The first model set was used to isolate the best approximating model containing covariates known to influence sea lamprey movement: water temperature, time-of-day, release date, and sex. The second model set was used to test how the sea lamprey changed their behaviour in response to nightly discharge and study year. The second set was created by adding combinations of discharge and year, predictors unique to my study, to the best approximating model from the first model set. This two-step approach was used to avoid the complexity of creating and justifying a much larger model set constructed using all six variables. For each model set, delta AIC values and Akaike weights for the models were used to identify the best approximating model in the set.

Predictions regarding how encounter, entrance, and departure changed with discharge (Table 1.1) were tested using hazard ratios from the best approximating model from set 2. The hazard ratio for each transition between states was calculated as the ratio of transition intensities estimated for high and for low discharge. A hazard ratio of 1 indicates no difference in the state transition under high and low discharge levels, while a hazard ratio greater than one indicates that the state transition is more likely under high discharge than low discharge, while a hazard ratio less than one indicates that the state transition is more likely under low discharge than high discharge. Predictions regarding vulnerability to trapping under high and low discharge were tested by comparing the cumulative distributions of daily trap catches for high and low flow nights. All sea lamprey, including tagged individuals were recorded by DFO. Trap catch was
summed for all nights when discharge was high and on nights when discharge was low. To assess trap success the percent of total catch under high discharge and low discharge was compared visually. All statistical analyses were performed using R version 2.13.1 (R Development Core Team, 2011) including the msm (Jackson, 2011) and diveMove (Luque, 2007) packages.

RESULTS

In both study years, nightly changes in discharge were alternated consistently over most of the period of sea lamprey migration and trapping (Fig. 1.5). High overnight discharge occurred for 47% and 57% of study nights in 2011 and 2012, respectively. In 2011, there was one short period (days 179-183) where the differences from night to night were smaller than usual and two periods (days 195-198 and 201-203) where discharge was low for several nights in a row. In 2012, there was a period (days 176-181) near the end of the migration where discharge was low each night, followed by a period (days 182-188) where discharge was high. Overall, nightly discharge ranged from 782 m$^3$s to 1004 m$^3$s (mean = 899 m$^3$s) on high nights and from 223 m$^3$s to 670 m$^3$s (mean = 370 m$^3$s) on low nights in 2011 and from 819 m$^3$s to 1037 m$^3$s (mean = 935 m$^3$s) on high nights and from 435 m$^3$s to 761 m$^3$s (mean = 599 m$^3$s) on low nights in 2012.

Across both study seasons, 47 (22%) of the 216 individual tagged lamprey were captured in traps located in the St. Marys River. Eighteen individuals were captured in the study traps (NAWT and SAWT), 22 individuals were caught in the portable traps at the generating station, and 7 individuals were caught in traps at other trapping sites in the river.
Rates of encounter, entrance, and departure differed with discharge, water temperature, sex, and year. The best approximating model from the first model set included water temperature and sex (Table 1.2) so all models in the second model set included these predictor variables. The best approximating model from the second set included discharge, water temperature, sex, and year as predictor variables (Table 1.2). The importance of discharge as a predictor was supported by probability for the model including discharge, water temperature, sex, and year as the best model in the model set being substantially higher than the corresponding probability for any model that did not include nightly discharge.

Examination of the hazard ratios suggested that sea lamprey were more likely to encounter traps on nights of high versus low discharge, but also more likely to depart without entering, while rates of entrance did not differ. After statistically controlling for water temperature, sex, and year, the estimated rate of tagged sea lamprey encountering traps was 1.6 times higher on nights of high discharge than on nights of low discharge (Table 1.3). However, the rate of departure was 1.9 times higher on nights of high versus low discharge (Table 1.3). The rate of entering a trap upon encounter did not differ significantly (0.94) between nights of high and low discharge (Table 1.3). The differences in encounter and departure rates appeared to be due to individual sea lamprey encountering and leaving a trap more often on nights of high discharge than on nights of low discharge. In addition to the effects of discharge, the sea lamprey were more likely to encounter a trap, but less likely to enter it, when water temperature was high than when it was low. Rates of departure did not differ with water temperature. Male sea lamprey were also more likely than females to encounter a trap,
but less likely to enter it. Rates of departure did not differ between the sexes. Encounter rate with traps was estimated to be substantially (0.14 times) lower in 2012 than 2011, while the rate of entrance was higher (6.4 times). Rates of departure did not differ between years.

Trapping success was higher on nights of high discharge compared to nights of low discharge. Under high discharge, 11 tagged individuals were trapped in each of 2011 and 2012 (Fig. 1.6). Under low discharge, 12 tagged individuals were caught in 2011 and 6 tagged individuals were caught in 2012. Of all sea lamprey trapped at the Clergue Generating Station site in 2011, 56% (1974 of 3506) were trapped during high discharge while 44% (1532 of 3506) were trapped under low discharge (Table 1.4; Fig. 1.5). In 2012, 65% (3899 of 5970) were captured on nights when discharge was high while 35% (2071 of 5970) were captured on nights when discharge was low.

DISCUSSION

My findings were most consistent with the Counteracting Responses Hypothesis (Table 1). Consistent with this hypothesis, encounter rate with traps was higher on nights of high discharge than on nights of low discharge. Further, entrance rate into traps was lower and departure rate from trap openings was higher on nights when discharge was high. My findings were less consistent with the Full Attraction and Encounter Hypotheses. For the Full Attraction Hypothesis, the prediction that encounter rate was higher on nights with high discharge was supported, but the predictions that entrance rate was higher and departure rate was lower were not supported. For the Encounter Hypothesis, the prediction that encounter rate was higher on nights of high discharge was supported, but the predictions that high discharge has no effect on entrance or
departure rate were not supported. My findings were least consistent with the No Response Hypothesis. The predictions that high discharge has no effect on encounter or departure rate were not supported.

My findings demonstrate the importance of understanding how the behaviour of a target animal changes in response to environmental cues used to improve the success of trapping it. The way in which discharge affects features of water flow, and the way in which fish in general, and sea lamprey in particular, respond to changes in flow are potentially complex. The results from my study suggest that increasing discharge had a longer-distance effect that attracted sea lamprey to traps. Results suggest that there was little difference in the proportion of individuals that encountered traps on high versus low nights, suggesting that although no more unique individuals encounter the traps under high discharge, those individuals that do encounter make more attempts to the trap entrance on nights when discharge is high. This is further supported by results from Chapter 2, where a higher proportion of tagged individuals made their first upstream movement to the wall of the generating station on nights when discharge was high compared to nights when it was low (Fig. 2.6). But manipulation of discharge also had a short-distance, counteracting effect that encouraged lamprey to depart from the trap, rather than enter. Manipulation of discharge at the Clergue generating station visibly altered the degree of turbulence immediately downstream of the outflow. Whether turbulence is exploited or avoided by fishes depends on several physical properties of the turbulence (Liao, 2007; Lacey et al., 2011). The increased departure rate on nights when flow was high could be a consequence of sea lamprey having difficulty holding position in the turbulence (Lacey et al., 2011); however, this does not
appear to be true based on evidence from video observations. Observations at trap entrances demonstrate that lamprey tend to use their oral disk for attachment coupled with burst swimming to maneuver with control around trap openings (Rob McLaughlin, unpublished data).

Understanding behaviour at traps can help identify management trade-offs that may be common across control programs. Trapping for control or monitoring purposes is widely applied by management and conservation agencies, even though trapping efficiency is often low. Understanding the behavioural basis of these trade-offs is important because it may help us understand why expected gains in trap success from a manipulation are not realized. The literature on improving efficacy of trapping programs reveals several examples of trade-offs in trapping programs that can arise because of spatial scale, population density, and trap design and operation. For spatial scale, depending of the spatial distribution of the target organism, a trade-off exists between whether to operate a small number of fixed traps versus many temporary traps. For population density trade-offs, trapping programs designed to be most effective when the target population is at high density may lose effectiveness as the program removes individuals and lowers the density (Roy et al., 2006; Hein et al., 2007). For trap design and operation, researchers and managers recognize that changes to the trap design and operation expected to improve a component of trapping may impact other components of trapping, such as a behavioural response of the organism. Switzer et al. (2009) describe the consequences of trap spillover. Japanese beetles are attracted by scent to trap locations, however, a portion of individuals do not enter the trap. Instead, they inflict substantial damage to plants immediately surrounding the trap location. Attracting
individuals to concentrate near trap locations with less than perfect trap efficiency could have even more substantial consequences for control programs. In cases where animals are reproductively active during the trapping period, such as the sea lamprey, managers could be unintentionally assisting mate searching, leading to population growth especially if there are compensatory reproductive mechanisms.

There is considerable and broad value in this study because it provides a unique experimental field test of the effects of discharge on the behaviour of migrating fish. Despite the inherent difficulty in a large-scale manipulation, there is considerable interest in evaluating biological responses in altered flows (Lancaster and Downes, 2010; Poff and Zimmerman, 2010; Poff et al., 2010). My study is valuable for three reasons. First, information on how fish respond to altered flows gained from flume studies have been helpful (Quintella et al., 2009; Kemp et al., 2011; Russon and Kemp, 2011; Vowles and Kemp, 2012), but limited in spatial scale making it uncertain whether results can apply to the field. My study is designed to demonstrate how sea lamprey respond to altered flow, within the context of improving trap efficiency at a scale relevant to field implementation and program operation. Second, larger-scale observational studies have revealed correlations between discharge and fish response, but the cause and effect often remains unclear (see Poff and Zimmerman, 2010 Supplemental Material; Noonan et al., 2012). My study applies a manipulative experimental approach that provides a more direct evaluation of the response of fishes to altered discharge. Third, this study has empirically eliminated simple explanations that sea lamprey encounter traps simply because of a positive rheotactic response, irrespective of the discharge. Evidence that sea lamprey change their behaviour with the magnitude of
discharge provides continued justification for the current management approach of using attractant flow from traps.

For sea lamprey, the behavioural basis of the trade-off is of value because it helps identify the limiting component in the trapping process. If management agencies hope to reach a trapping efficiency of 70% across the St. Marys River (Haeseker et al., 2007), entrance rates must be improved. Such an increase, when the trapping efficiency of individual traps appears to be lower than 40%, such as in this study and Bravener and Mclaughlin (2013), is a considerable task. My results provide a clear indication that increased overnight discharge resulted in increased encounter rate. However, an observed change in departure from trap openings in response to altered discharge limited the potential increase in trap success via higher encounter rate. This influence on sea lamprey trap behaviour is not substantial enough to improve trapping efficiency to desired control levels on the St. Marys River. Without a thorough understanding of behaviour, and specifically potential behavioural changes in response to manipulations, improvements to trapping efficiency are unlikely (Foster and Harris, 1997). Furthermore, it is important to understand that environmental features that have long-distance effects may not only be different from features that have short-distance effects, but could elicit a response entirely opposite at each scale (Foster and Harris, 1997). The information provided by this study on the space use of sea lamprey could help direct future trapping strategies for a wide variety of taxa.
**Fig. 1.1:** A map depicting the St. Marys River connecting Lakes Superior and Huron. Sea lamprey trapping sites are approximately 23 km downstream of Lake Superior outflow. QGIS base layer courtesy of Bing aerial photography layer.
**Fig. 1.2:** An aerial view of the Francis H. Clergue Generating Station on the north side of the St. Marys River. The river flows from left to right. Sea lamprey control traps are located along the downstream face of the dam. There are five traps at the Clergue Dam: the north attractant water trap (NAWT), south attractant water trap (SAWT), and three portable traps (depicted by white circles) placed between the NAWT and SAWT. QGIS base layer courtesy of Bing aerial photography layer.
**Fig. 1.3:** A schematic drawing of the south attractant water trap, SAWT (left) and north attractant water trap, NAWT (right). Entrances are depicted by triangles. PIT antennas, depicted by black rectangles, were placed at each entrance, Single arrows indicate the direction of entrance by sea lamprey (Adapted from Bravener, 2011).

**Fig. 1.4:** A depiction of the three state Markov model used to quantify transition intensities (q’s) for encounter (q_{12}), entrance into (q_{23}) or departure from (q_{21}) the study traps, and combined encounter and entrance into non-study traps (q_{13}). The dashed line separates the spatial scale at which behavioural responses occur. Trap success is the total number of sea lamprey captured in traps.
Fig. 1.5: Numbers of sea lamprey caught in the five traps at the Clergue Generating Station (bars) and mean daily discharge (circles and doashed lines) from the generating station in 2011 (top) and 2012 (bottom). Closed circles represent dates when nightly discharge was high. Open circles represent dates when nightly discharge was low.
Fig. 1.6: Numbers of PIT tagged sea lamprey caught in the five traps at the Clergue Generating Station (bars) and mean daily discharge (circles and doashed lines) from the generating station in 2011 (top) and 2012 (bottom). Closed circles represent dates when nightly discharge was high. Open circles represent dates when nightly discharge was low.
**Table 1.1.** Prediction matrix summarizing how behaviour was expected to differ between nights of high and low discharge.

<table>
<thead>
<tr>
<th>Hypothesis</th>
<th>Predictions</th>
<th>(high discharge/low discharge)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>encounter</td>
<td>entrance</td>
</tr>
<tr>
<td>Full Attraction</td>
<td>high</td>
<td>high</td>
</tr>
<tr>
<td>Encounter</td>
<td>high</td>
<td>no response</td>
</tr>
<tr>
<td>Counteracting Responses</td>
<td>high</td>
<td>low</td>
</tr>
<tr>
<td>No Response</td>
<td>no response</td>
<td>no response</td>
</tr>
</tbody>
</table>

† trap success will depend on the relative importance of changes in encounter, entrance, and departure rates
**Table 1.2.** Two-step multi-model assessment using the Akaike Information Criterion (AIC). The best approximating model from model set 1 was taken forward to the second model set.

<table>
<thead>
<tr>
<th>Variables</th>
<th>AIC</th>
<th>ΔAIC</th>
<th>df</th>
<th>wi</th>
</tr>
</thead>
<tbody>
<tr>
<td>Model set 1 (Selection of important covariates)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>temperature, sex</td>
<td>-1291.8</td>
<td>0.0</td>
<td>12</td>
<td>1</td>
</tr>
<tr>
<td>temperature</td>
<td>-1214.3</td>
<td>77.6</td>
<td>8</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>release date, sex</td>
<td>-1108.0</td>
<td>183.8</td>
<td>16</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>sex</td>
<td>-1058.4</td>
<td>233.4</td>
<td>8</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>release date</td>
<td>-1032.5</td>
<td>259.3</td>
<td>12</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>(none)</td>
<td>-961.1</td>
<td>330.7</td>
<td>4</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Model set 2 (Evaluation of the importance of discharge)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>temperature, sex, year, discharge</td>
<td>-1438.9</td>
<td>0.0</td>
<td>20</td>
<td>1</td>
</tr>
<tr>
<td>temperature, sex, year</td>
<td>-1405.5</td>
<td>33.4</td>
<td>16</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>temperature, sex, discharge</td>
<td>-1339.5</td>
<td>99.4</td>
<td>16</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>temperature, sex</td>
<td>-1291.8</td>
<td>147.1</td>
<td>12</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>
Table 1.3. Hazard ratios and 95% confidence intervals (CI’s) summarizing the relative change in transition intensities for trap encounter, entrance, departure, and for encounter and entrance of non-study traps, under high and low discharge. Values presented are for the best approximating model from set 2 of Table 2. Labels in parentheses for predictors indicate the level for categorical variables.

<table>
<thead>
<tr>
<th>Predictor</th>
<th>Treatment effect</th>
<th>Encounter (q₁₂)</th>
<th>Entrance into study traps (q₂₃)</th>
<th>Departure (q₂₁)</th>
<th>Entrance into non-study traps (q₁₃)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Discharge (high)</td>
<td></td>
<td>1.63 (1.26, 2.11)</td>
<td>0.94 (0.47, 1.85)</td>
<td>1.87 (1.36, 2.59)</td>
<td>18119 (0.00, Inf)</td>
</tr>
<tr>
<td>Covariates</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Temperature</td>
<td></td>
<td>2.10 (1.99, 2.22)</td>
<td>0.37 (0.17, 0.73)</td>
<td>0.94 (0.80, 1.10)</td>
<td>0.49 (0.00, Inf)</td>
</tr>
<tr>
<td>Sex (male)</td>
<td></td>
<td>2.66 (2.02, 3.51)</td>
<td>0.36 (0.17, 0.74)</td>
<td>0.81 (0.53, 1.25)</td>
<td>8866 (0.00, Inf)</td>
</tr>
<tr>
<td>Year (2012)</td>
<td></td>
<td>0.14 (0.10, 0.18)</td>
<td>6.37 (2.18, 18.59)</td>
<td>0.96 (0.59, 1.56)</td>
<td>5.16 (0.00, Inf)</td>
</tr>
</tbody>
</table>
Table 1.4. Numbers of sea lamprey trapped (percent of total) in five Sea Lamprey Control Traps at the Clergue Generating Station on nights when discharge was high compared to nights when discharge was low in 2011 and 2012.

<table>
<thead>
<tr>
<th>Year</th>
<th>Trap Success</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>High discharge</td>
<td>Low discharge</td>
<td></td>
</tr>
<tr>
<td>2011</td>
<td>1974 (56%)</td>
<td>1532 (44%)</td>
<td></td>
</tr>
<tr>
<td>2012</td>
<td>3899 (65%)</td>
<td>2071 (35%)</td>
<td></td>
</tr>
</tbody>
</table>
CHAPTER 2: UNDERSTANDING SPACE USE TO SUPPORT TRAPPING OF INVASIVE SEA LAMPREY

ABSTRACT

Trapping is a potentially valuable form of control for invasive sea lamprey (*Petromyzon marinus*) migrating in the St. Marys River, Canada, but encounter rates with traps are low. To understand why, I used acoustic telemetry and occupancy modelling to quantify the space use of 108 approaching sea lamprey. Invasive species are the focus of management concern in ecosystems across the globe. Trapping is a potentially valuable form of control. In the Laurentian Great Lakes, increased trap success in large rivers is desired to meet the management objectives of a binational control program for sea lamprey. Discharge through a hydro-generating station was manipulated nightly to alter flows attracting sea lamprey to traps at the station wall. Eighty-four of 108 tagged sea lamprey (78%) reached the wall of the generating station. The lamprey spent their time at the river bottom near the draft tubes exiting the generating station and away from the traps near the water surface, consistent with previous observations that the proportion of lamprey that encountered traps was low regardless of discharge. To improve trap success, managers must make traps more attractive or place traps in locations where sea lamprey are most likely to aggregate.
INTRODUCTION

The frequency of species invasions and their ecological and economic impacts are compelling scientists and resource managers to develop ways of protecting and restoring natural ecosystems (Palmer et al., 2004; Pimental et al., 2005). In many impacted ecosystems, managers rely on control of invasive species as part of their restoration efforts, either because prevention was not pursued, or because prevention measures proved ineffective. Managers may also control invasive species when the potential for eradication is limited (Bonesi and Palazon, 2007; Zuberogoitia et al., 2010; Genovesi, 2011; Clark et al., 2012).

Trapping is a potentially valuable form of control providing that the proportion of the population trapped (trapping efficiency) is sufficiently high to overcome density-dependent population responses. It has been used to control a variety of invasive taxa, including species of insects (El-Sayed et al., 2006), aquatic invertebrates (Hein et al., 2007), fishes (Yavno and Corkum, 2011), amphibians and reptiles (Schwarzkopf and Alford, 2007; Clark et al., 2012), birds (Campbell et al., 2012), and mammals (Bonesi and Palazon, 2007). Trapping has proven most effective when suppressing small, isolated populations (Veitch et al., 2011); however, trapping could be applied more widely, in terms of taxa and ecological conditions, if trapping efficiencies could be improved (El-Sayed et al., 2006; Roy et al., 2006; Bryce et al., 2011).

I tested how the space use of invasive sea lamprey (*Petromyzon marinus*) migrating in the St. Marys River, Canada, could explain low encounter rates with traps used for control and whether experimental manipulation of discharge from a hydro-generating station could improve encounter rates. The sea lamprey is a parasitic fish species that
feeds on the blood of large (host) fishes. It entered the Upper Great Lakes between 1924 and 1938 (Smith and Tibbles, 1980; Christie and Goddard, 2003). Following this, 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). The Great Lakes Fishery Commission (GLFC) was created under the Convention on Great Lakes Fisheries (1954)—a treaty between Canada and the United States – to oversee the management of sea lamprey in the Great Lakes. Field operations of the program are contracted to the Department of Fisheries and Oceans Canada (DFO) and the United States Fish and Wildlife Service (USFWS). Sea lamprey control currently relies on three methods: (i) periodic lampricide treatment of tributaries where larval sea lamprey rear for the first four to five years of the life, (ii) barriers that deny migrating adult sea lamprey access to spawning habitat in tributaries, and (iii) trapping of adult migrating sea lamprey to remove them from the population prior to reproduction. In its most recent strategic vision document, the GLFC pledged to accomplish at least 50% of sea lamprey suppression using technologies other than lampricide treatments, including enhanced use of trapping (Milestone 3, Great Lakes Fishery Commission, 2008).

Improvements in trapping success (total number of sea lamprey caught in traps) would be particularly valuable for sea lamprey control in large river systems, such as the St. Marys River. Chemical treatment of rivers with lampricides is less feasible for large than small rivers, because the size and complexity of large rivers greatly increases the amount of lampricide required and the cost and logistics of lampricide application. In the
St. Marys River connecting Lakes Superior and Huron, trapping has historically been used for population assessment and, until 2012, to collect males for a sterile-male release program that has since been discontinued (Schleen et al., 2003). Mark-recapture methods have estimated the annual trapping efficiency across the river to be approximately 40%, on average (Schleen et al., 2003). A recent decision analysis comparing different management options for the river revealed that the best options involved an increase in trapping efficiency to 70%, the highest efficiency that control agents believed they could achieve, in conjunction with sterile-male release and strategic lampricide treatments (Haeseker et al., 2007). Since then, a tracking study of sea lamprey in the St. Marys River estimated that trapping efficiency for individual traps is approximately 10%, due to low rates of sea lamprey encountering traps, low rates of entrance upon encounter, and low rates of return to traps upon leaving (Bravener and McLaughlin, 2013). Trap retention was 100%.

Understanding the space use of invasive animals could be crucial to increasing encounter rates with traps, and ultimately trapping efficiency. Space use is recognized as fundamentally important to improving trapping success for brown tree snakes (Engeman and Vice, 2001), American mink (Bonesi and Palazon, 2007; Zuberogoitia et al., 2010; Roy, 2011), coypu (Kendrot, 2011), and ferrets (King et al., 2011). For sea lamprey, the current trapping strategy involves positioning a relatively small number of traps in locations where many lamprey are known to migrate past, usually near barriers that impede upstream migratory movements and create flows that are believed to be attractive to the lamprey. The success of this approach relies upon a high proportion of sea lamprey occurring near, and therefore encountering, traps. If trapping efficiency is
low because sufficiently high numbers of sea lamprey do not encounter traps, reliably knowing where sea lamprey are using space could help increase trap encounter in one of two ways. Either, traps could be moved to areas where sea lamprey would be more likely to encounter them, or alternatively, the behaviour of sea lamprey could be manipulated in a manner that could greatly increase the likelihood of more sea lamprey coming into contact with traps. Actual measurement of space use at spatial scales relevant to trapping has been limited because the fast flows, entrained air, and low light at trap sites makes it difficult to quantify sea lamprey behaviour.

Understanding environmental features that affect the space use of sea lamprey can create further opportunities to improve trapping success, either by attracting the lamprey to trap locations (attractants) or deterring them from going to areas where trapping is difficult (distractors). Water flow represents one feature that could be manipulated. Fast flows are known to be attractive to fishes in general (Liao, 2007; Williams et al., 2012). For Pacific (Lampetra tridentate), river (Lampetra fluviatilis), and sea lampreys, laboratory and field studies have demonstrated that high discharge stimulates upstream movement (Almeida et al., 2002; Lucas et al., 2009; Keefer et al., 2011). At barriers to movement, increased flow can also increase general activity (Almeida et al., 2002) near barriers (Quintella et al., 2004) and fishways (Moser et al., 2011). When Pacific lamprey encounter competing attraction flows, discharge from the power house of a hydro-generating station versus discharge from a fishway, the lamprey approach the generating station before approaching the fishway entrances (Keefer et al., 2011; Johnson et al., 2012). Fast flows can also deter upstream movement, due to limits on swimming capacity and added energetic costs (Almeida et al., 2002; Russon and Kemp,
Exploiting the rheotactic behaviour during upstream migration in a manner that would increase the likelihood of sea lamprey encountering traps might significantly improve sea lamprey control.

I used a two-step approach to investigate why low proportions of sea lamprey encounter traps in the St. Marys River. In the first step, I tested whether the proportion of sea lamprey encountering traps is low because the lamprey stop moving upstream before reaching the wall of the generating station. Sea lamprey could stop short of the wall 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 habitat (e.g. spawning sites) downstream of the station. I further expected that numbers of sea lamprey reaching the wall would be higher on nights of high discharge than on nights of low discharge, if the sea lamprey were attracted by water flow. I expected the reverse, or that numbers would not differ between discharge levels, if sea lamprey were deterred by high water flow. In the second step, for sea lamprey reaching the wall of the generating station, I tested whether the proportion of sea lamprey encountering traps is low because the sea lamprey occur at locations away from traps. This could happen in two ways. The sea lamprey could aggregate at locations away from the trap sites, possibly in response to attraction flows created by the discharge from the draft tubes of the generating station or due to the need to attach to surfaces (using their oral disc; Kelso and Gardner, 2000) in the strong flows. Alternatively, the sea lamprey could be overdispersed, and attached (immobile) for long periods of time across the wall of the generating station, so that relatively few individuals encounter traps. I further expected that sea lamprey would be more likely to
occur near traps on nights of high discharge than on nights of low discharge, if sea lamprey were stimulated to be more active and drawn off the river bottom by water flow.

METHODS

DESCRIPTION OF STUDY SITE

My research was conducted between 26 June to 25 July 2011 in the tailrace of the Francis H. Clergue Generating Station on the St. Marys River, connecting Lakes Huron and Superior (Fig. 2.1). The river is bounded to the south by Michigan, USA and to the north by Ontario, Canada. It 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 the four generating stations (three in US waters, one in Canadian waters) and three shipping canals (two on the US side and one on the Canadian side).

The Clergue generating station is located along the north shore of the St. Marys River, in Sault Ste Marie, Ontario, Canada (Fig. 2.2). It is a run-of-the-river hydroelectric dam with a head (height) of 6 m. The powerhouse has three turbines with capacity of 52 megawatts. Mean discharge at the Clergue generating station is approximately 1000 m³/s (Duffy et al., 1987). The tailrace of the generating station is approximately 70 m wide with water depths of approximately 16 m at the plant exit, but decreasing to a depth of 12 m approximately 20 m downstream.
SEA LAMPREY TRAPPING OPERATIONS

Department of Fisheries and Oceans Canada operates five sea lamprey traps along the downstream face of the generating station. The North (NAWT) and South Attractant Water Traps (SAWT) are permanent structures with two and four entrances, respectively. Both of these traps direct attraction flow out of the trap entrances. They can hold thousands of lamprey. Three portable traps are installed along the downstream face of the generating station during the period of adult sea lamprey migration. Portable traps are designed like a large “minnow-trap”, with two funnel openings at opposite ends, and positioned perpendicular to the discharge from the generating station. They are placed along the power plant wall in areas of high discharge above the draft tubes. These traps can hold up to 500 lamprey. All traps fish at depths of 1 and 3 m below water surface. The traps are checked and emptied daily by DFO. In addition to the Clergue generating station, there are four more trap locations on the St. Marys River where one to six traps are operated: the St. Marys Rapids and three other hydroelectric generating stations.

MANIPULATION OF NIGHTLY DISCHARGE

The hydro operator (Brookfield Renewable Energy Partners), with authorization from the International Joint Commission, agreed to alter discharge from night to night so that I could test how discharge affected the space use of sea lamprey approaching the wall of the generating station. Discharge was manipulated at night because that is when sea lamprey are most active (Binder and McDonald, 2007). Further, under normal operations, the majority of daily discharge occurs during the day (0800h-2200h; mean = 910 m³/s), when demand for electricity is higher, and decreases overnight (2300h-
0700h; mean = 475 m³/s), when demand for electricity is lower. During the study period, discharge from 2300-0700h was altered from the normal low for this time of year on one night to a discharge comparable to daytime discharge the next night. Every effort was made to alternate between high to low discharge on a night-to-night schedule, but infrequent exceptions were necessary due to fluctuations in demand for power generation.

ACQUISITION, TAGGING, AND RELEASE OF SEA LAMPREY

Sea lamprey were obtained from the United States Fish and Wildlife Service and came from trapping operations at sites on the US side of St. Marys River. These sea lamprey were assumed to be representative of sea lamprey lacking experience with the Clergue site. Acquiring naïve sea lamprey from other rivers was not feasible because they had already spawned. Sea lamprey migration in the St. Marys River occurs later than for other tributaries, due to the river’s large size and cold water temperatures.

Upon removal from traps, the test sea lamprey were placed in aerated basins in a boat and transported by USFWS agents to the DFO Sea Lamprey Control Holding Facility adjacent to the Clergue generating station. At the holding facility, the sea lamprey were sexed and 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). The sea lamprey were held for 1-3 days prior to tagging. The incision was closed using three independent sutures with monofilament nylon sutures (Ethicon monocryl monofilament). One hundred and eight sea lamprey (1:1 sex ratio) were surgically implanted with an acoustic tag (Model 795G, 4.5 g in air, Hydroacoustic Technology, Inc., Seattle, WA) and a passive integrated transponder (PIT) tag (3.4 mm x 23 mm, 0.6 g in air, Texas
Instruments, Dallas, TX). Acoustic tags were used to obtain 3-D positions of sea lamprey in the water column downstream of the generating station. PIT tags were used for tracking the encounter, entrance into, and departure from, traps (Chapter 1). In preparation for tag implantation, an individual sea lamprey was netted from the holding tank, placed in an aerated bath of MS 222 (50 mg/L), observed, and removed once it reached stage 3 of anaesthesia (partial loss of equilibrium). The individual was then placed on a measuring board, measured for total length (±1mm), 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) followed by a sterile saline solution (9 g/L). A small incision (5 mm) was made near the ventral midline using a sharp scalpel and acoustic and PIT tags were inserted into the peritoneal cavity using forceps.

During surgery, the lamprey was periodically irrigated with a maintenance dose of anaesthetic (30 mg/L) in oxygenated water. Scalpels, forceps, and tags were all disinfected in a Virkon solution (1g/L) and rinsed with sterile saline solution (9g/L) prior to each surgery. Scalpel blades were changed after every fifth lamprey. Following surgery, the tagged lamprey was transferred to a recovery tank, monitored to ensure full recovery from the anaesthesia, and held for 1-4 days prior to release in the St. Marys River.

Lamprey were released at one of three sites across the river channel (south, center, north) approximately 300 m downstream from the Clergue generating station. Three release sites were chosen because I did not have knowledge of how sea lamprey normally approach the Clergue generating station from downstream. The release distance was selected to give tagged lamprey ample opportunity to select their
upstream path, while ensuring that they were likely to enter our study area rather than move elsewhere in the river. Lamprey were released on six dates, separated by 48 hours, between 26 June – 6 July. Release dates were selected to cover points before, at, and after the peak in migration. On each date, six lamprey (1:1 sex ratio) were released from each release site. Releases occurred at approximately 2000h to minimize predation of tagged animals immediately post release and because sea lamprey are most active at night.

3D TRACKING OF SPACE USE
The tagged sea lamprey were tracked using an acoustic telemetry system consisting of acoustic tags, 16 omni-directional hydrophones, an acoustic telemetry receiver (ATR; Model 290, Hydroacoustic Technology, Inc., Seattle, WA), and cables that connected the hydrophones to the acoustic receiver. Each acoustic tag transmitted a repetitive signal. Arrival times of the emitted signals are received by the hydrophones, synchronized and stored by the receiver, and used to determine the position of the tag.

The 16 hydrophone array was positioned in a river section extending 70 m across the downstream face of the generating station and approximately 70 m downstream of the station (Fig. 2.3). Eight hydrophones were mounted on the wall of the generating station (Fig. 2.3) and fastened to 2.5 cm diameter stainless steel pipes anchored into the wall (#’s 1-8: Fig. 2.3). Four of these were mounted near the surface (approximately 1 m below the water level) and four were mounted near the river bottom (15 m deep). Eight more hydrophones were positioned downstream of the wall. Four (#’s 9-12) were positioned roughly 20 m downstream of the generating station. Two (9 and 12) were mounted from the shore (one on each side of the river) by attaching them to 2.5 cm
stainless steel pipes secured in position by piled rock and braided steel cable and extending horizontally into the water column. Two others (#’s 10 and 11) were attached to pyramid shaped metal frames (1 m high with a 1 m x 1 m base) that were weighted and placed on the river bottom. The final four hydrophones (#’s 13-16) were positioned approximately 50 m downstream. Two of these (#’s 13 and 16) were also attached to pipe extending from shore. The last two water column hydrophones (14 and 15) were attached to vertical underwater pipes (diffusers) from an effluent system extending across the river in a north-south direction. The array geometry was determined based on tests conducted in 2010 and consultation with personnel from HTI and professional divers familiar with conditions in the draft tubes and the tailrace. Spacing of hydrophones was selected 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 position of each hydrophone was determined by professional land surveyors. Speed of sound in water was estimated each day using mean daily water temperatures calculated using values from temperature loggers operated by DFO at the traps.

**DATA PROCESSING AND POSITIONING**

The data processing required to estimate 3D positions involved (i) identifying tag signals from background noise, (ii) geo-positioning the study site and hydrophone array on a map, and (iii) geo-positioning the tag positions within the study site. The first step involved separating true tag signals from background noise, based on the period of each tag signal. Each tag emitted a signal sufficiently unique in period to allow
identification of individuals. This period ranged from 2003 ms to 4571 ms depending on the tag (individual). In the second step, the geospatial coordinates of the hydrophones were inputted into the HTI software package and the speed of sound for each day was estimated. In the third step, a proprietary algorithm was used to estimate 3D positions based on the differential time of arrival of signals emitted from a tag. Calculation of a 3D position requires a tag signal be detected on at least four hydrophones. Two-dimensional (XY) positions were then overlaid on an aerial map of the study site using GIS software (QGIS Development Team) and the NAD83 / UTM zone 16N coordinate system. Processing and positioning was done in consultation with experts at HTI. All processing and positioning of tag data was performed using the HTI AcousticTag software package (v.5.10).

**POSITION ACCURACY**

Accuracy estimates were made using telemetry records for 14 fish caught across the three portable traps and for a test tag positioned at the NAWT. Average Euclidean distances between the estimated tag position (via telemetry) and true position (via GPS and depth measurements) were estimated to be 0.84 m, 0.73 m, and 1.01 m in the X, Y, and Z directions. From these estimates, I calculated that 50% of the estimated tag positions were within 1.15 - 1.23 m of the true tag position, depending on whether the data were for fish in a trap or for the test tag. Sixty-one percent of the tag positions estimated via telemetry were within 1.34 - 1.40 m of the true tag position, 90% were within 1.87 - 2.01 m, and 99% were within 2.52 - 2.71 m (Appendix 1).
DATA ANALYSIS

The proportion of sea lamprey that encountered a trap was estimated as the number of sea lamprey released that came within 3 m of a trap divided by the total number of lamprey released. A value of 3 m was considered reasonable as a practical fishing distance for a trap and was greater than the positioning error for this study. Encounter was determined using QGIS.

I tested whether the proportion of sea lamprey encountering traps is low because the lamprey stop moving upstream before reaching the wall of the generating station by determining the furthest upstream position reached by each tagged individual. The distance from the wall to the downstream extent of the telemetry array was divided into a sequence of twenty-four 3m zones running parallel to the wall of the generating station. I then calculated the proportion of fish that reached each zone.

I tested whether the proportion of sea lamprey encountering traps is low because sea lamprey aggregate away from trap locations or because sea lamprey are widely distributed across the wall in four steps: i) I assigned each tag position into cells comprising a vertical grid along the wall of the generating station, ii) developed a set of occupancy models describing the spatial distribution of sea lamprey along the wall, iii) used the conditional modes and predictions from the best occupancy model to evaluate whether the sea lamprey were aggregated or over dispersed, and iv) determined where the sea lamprey were aggregating based on the probability of occupancy for each cell.

The grid along the wall of the generating station was created using QGIS tools and 3D drawing software. Each cell in the grid was approximately 3 m x 3 m x 3 m (9 m³). Cells
along the top and edges were less than 9m$^3$ because of the irregular shape of the dam wall. The Spatial Query tool in QGIS was then used to assign all tag positions along the wall into one of the 118 cells.

Mixed effect logistic regression models (occupancy models) were used to estimate the probability of a lamprey occupying each of the cells during a specified hour. The dependent variable was the proportion of positions in each unique cell relative to the total number of positions in all cells for each hour that an individual was present along the generating station wall. The independent variables considered were cell identification number, fish identification number, cell volume, time of day, time of season (day of study), water temperature, discharge, water depth, and a discharge by depth interaction. Cell identification number and fish identification number were included in the model as random effects. Random effects are parameters that represent a sample of all the possible levels (Pinheiro and Bates, 2000). Cell volume, time of day, time of season (day of study), water temperature, discharge, water depth, and a discharge by depth interaction were included as fixed effects. Fixed effects are parameters that are reproducible (Pinheiro and Bates, 2000). I standardised (z-transformation) cell volume, water temperature, discharge, and depth to facilitate more meaningful comparisons among these variables (Schielzeth, 2010). 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.

Observations of occurrence together with environmental covariates can help predict the space use of individuals (Elith and Leathwick, 2009). If lamprey aggregate in space and there is competition for positioning along the dam face, the cell volume may influence cell occupancy where lamprey are less likely to occupy small cells. Time of day is
included because lamprey are known to be more active during the night and tend to seek refuge during the day (Kelso and Gardner, 2000; Quintella et al., 2004; Binder and McDonald, 2007; Vrieze et al., 2011). Time of season is included because lamprey motivation and hence activity and space use differ across the migration and spawning season. Lamprey are expected to initiate migration when water temperature reaches approximately 11°C and temperature increase could detect differences in motivation to migrate over the course of the season (Binder et al. 2010). Discharge is included because discharge stimulates upstream migration and can signal upstream passage routes (Almeida et al., 2002; Andrade et al., 2007; Lucas et al., 2009). Depth is included because lamprey spend the majority of time along the river bottom (Bravener, 2011) and there are differences in the physical features of the dam at the bottom relative to the top. Lastly, a discharge by depth interaction was included because there are differences in the hydraulic environment with depth that may influence where the lamprey use space along the dam face.

I used a two-step approach of multimodel assessment using the Bayesian Information Criterion (BIC) to determine the best approximating model from a set of candidate models (Burnham and Anderson, 2002). BIC was chosen because it has been shown to perform best with large sample sizes (Burnham and Anderson, 2002). The first model set assessed the best approximating model that contained covariates that are known to influence sea lamprey space use: cell volume, time of day, water temperature, time of season. The best approximating model from the first model set was taken forward to the second model set. I added the fixed effects: discharge, depth, and a discharge by depth interaction in the second model set. The difference in BIC values ($\Delta$BIC) and BIC
weights \((w_i)\) for the models were compared to evaluate the best approximating model from each set. I estimated the conditional mode for each cell, which represents the variation that remains after accounting all covariates in the model (Bates et al., 2011). Last, I estimated the probability of occupancy, \(P\), for each cell:

\[
P = \frac{e^{(b_0 + b_1 x_1 + b_2 x_2 + \ldots + B_i)}}{1 + e^{(b_0 + b_1 x_1 + b_2 x_2 + \ldots + B_i)}}
\]

Where \(b_n\) are the fixed effects parameter estimates, \(x_n\) are the observed values, and \(B_i\) is the conditional mode from the random effect of each unique cell. I used the predicted probabilities to compare whether there were cells where sea lamprey were more likely to occur than others, as well, where sea lamprey were occupying relative to traps. All statistical analyses were performed using R version 2.13.1 (R Development Core Team, 2011) including the lme4 (Bates et al., 2011) package.

RESULTS

Nightly discharges were alternated consistently over most of the period of sea lamprey migration and trapping (Fig. 2.4). High overnight discharge occurred for 47% of study nights. There was one short period (days 179 -183) where the differences from night to night were smaller than usual and two periods (days 195 -198 and 201- 203) where discharge was low for several nights in a row. Overall, nightly discharge ranged from 782 m\(^3\)s to 1004 m\(^3\)s (mean = 899 m\(^3\)s ± 63 m\(^3\)s) on high nights and from 223 m\(^3\)s to 670 m\(^3\)s (mean = 370 m\(^3\)s ± 118 m\(^3\)s) on low nights in 2011.

Ninety one of 108 (84%) individuals moved upstream into the hydrophone array. Twenty six (24%) and 16 (15%) encountered the SAWT and NAWT, respectively. Fifty
(46%), 52 (48%), and 53 (49%) lamprey encountered the three portable traps, respectively. Of the 17 sea lamprey that did not enter the array, 3 were captured at traps located elsewhere in the St. Marys River and 14 were never detected following release.

There was little evidence that encounter rate with traps is low because sea lamprey stop moving upstream before reaching the generating station wall. Eighty-four (78%) of the 108 tagged individuals swam all the way to the wall of the generating station (Fig. 2.5). Total time spent along the wall was highly variable among individuals (range = 0–196h, mean = 56h). On average, fish had positions along the wall during at least one hour of a given day for 7 days during the study (range = 1day – 16days). Further, the flows from the generating station appeared to attract, rather than deter, sea lamprey from reaching the wall of the generating station. A higher proportion of individuals made their first upstream movement to the wall on nights when discharge from the generating station was high compared to nights when it was low (Fig. 2.6).

There was much stronger evidence suggesting that encounter rate with traps is low because sea lamprey aggregate away from the trap locations. The model set examining factors already known to influence sea lamprey behaviour and trapping revealed that time-of-day was the only significant predictor of space use. The second model set specifically testing the effects of depth and discharge revealed that the best approximating model of space use included time of day, discharge, depth, and a discharge by depth interaction (Table 2.1). The hypothesis that sea lamprey aggregate, rather than spread out, was supported by the conditional modes for cell identification number being highly variable, with occupancy being relatively high in certain cells and
much lower in others (Fig. 2.7). Further, the hypothesis that sea lamprey aggregate away from traps was supported by the predictions from the best approximating occupancy model from the model set (Fig. 2.8). The predictions from the occupancy model indicated that sea lamprey occurred in cells at the bottom of the wall of the generating station, especially cells located along pillars separating the draft tubes (Fig. 2.8a). Conversely, the sea lamprey were much less likely to occur near the water surface, where traps are located, and especially at the top corners of the wall near the shore.

The expectation that high discharge would increase the likelihood of sea lamprey being near traps was not supported (Fig. 2.8b, 2.8c). The probability of sea lamprey occurring in specific cells varied with discharge; the model including a term for the depth by discharge interaction was the best approximating model in the model set. However, on nights of high discharge, the probabilities of sea lamprey occurring in cells including, and adjacent to, traps were predicted to be lower than the probabilities predicted for nights of low discharge. Regardless of discharge, sea lamprey were more spread out on the dam face during the night and were more likely to concentrate into few cells during the day (Fig. 2.8d, 2.8e).

DISCUSSION
My findings support two main conclusions. First, encounter with traps is low because sea lamprey aggregate near the bottom of the water column away from traps near the water surface at the wall of the generating station. Second, sea lamprey altered their behaviour in response to experimental manipulation of discharge, but in a manner that was unsuitable for improving trapping efficiency overall. More sea lamprey arrived at the
wall of the generating station on nights of high versus low discharge, but the sea lamprey were less likely to move toward the water surface where traps are located when discharge was high than when it was low.

My conclusion that encounter with traps is low because sea lamprey aggregate at locations away from the traps was supported by three pieces of evidence. First, my analysis of occupancy demonstrated that sea lamprey were aggregated near the river bottom. In fact, the telemetry tracks suggested that many sea lamprey were entering the draft tubes exiting the generating station, where they would also be unavailable to encounter traps at the surface (Appendix 2). Second, the alternative that sea lamprey were evenly dispersed was not supported by analysis of conditional modes or by evidence that many sea lamprey moved horizontally across the face of the generating station, which would have made them susceptible to traps had they been using the water column more thoroughly. Third, there was little support for the possibility that sea lamprey were not reaching the wall of the generating station, either because of limitations on swimming capability or because they stop at attractive features downstream of the generating station wall. Twenty-two percent of the tagged sea lamprey did not reach the wall, but on its own this percentage was not sufficient in magnitude to explain the low encounter observed by Bravener and McLaughlin (2013). Of those sea lamprey that entered the tailrace of the generating station, there was also little evidence suggesting that upstream progress was deterred by limits on swimming ability, given that many of the tagged lamprey reached the wall and even entered the draft tubes where water velocities were highest. In addition, most sea lamprey were
reaching the wall of the generating station even though spawning was observed in the
tailrace by contract divers (Jessica Barber, personal communication).

My conclusion that sea lamprey respond to discharge in a manner unsuitable for
improving trap efficiency was supported by predictions from the occupancy model. Sea
lamprey responded to discharge at a large distance as more sea lamprey moved
upstream to the generating station wall on nights when discharge was high. However, at
a closer scale, high discharge from the draft tubes was more attractive to sea lamprey
than attractant flow from the traps and as such lamprey spent more of their time near
the draft tubes, making repeated forays into them. Even though lamprey were
concentrating space use near the draft tubes, they were rarely drawn up to the surface
where the portable traps are located, just above the draft tubes. Trade-offs, such as the
one here, where the positive gain at a large spatial scale is negated by the negative loss
at a small spatial scale, have been recognized for several trapping programs (Foster
and Harris, 1997; Roy et al., 2006; Hein et al., 2007; Switzer et al., 2009).

The current trapping strategy for sea lamprey that relies on a small number of traps is
appropriate. Sea lamprey are clumping horizontally and vertically in space. Control
agents are therefore faced with either moving the traps to locations where the sea
lamprey aggregate or improving the attraction for sea lamprey to encounter traps. The
former is more practical biologically because alteration of discharge does not appear to
improve efficiency. Additionally, attraction using pheromones may be limited at sites like
generating stations. The spatial configuration of the tailrace, combined with traps
located at the surface, suggest that pheromone released from traps could quickly pass
over the sea lamprey. Experiments with pheromone in the St. Marys and other rivers
also achieved little improvement (Luehring et al., 2011; Johnson et al., 2013). Further, moving traps to the bottom of the river would present significant engineering challenges, in terms of deployment and operation, given the nature of the hydrodynamics in the tailrace. Alternatively, sea lamprey aggregate to a greater degree during the day. At times, nearly all lamprey were in one of three locations along the bottom of the generating station wall. Lamprey are relatively stationary during the day (Almeida et al., 2002; Andrade et al., 2007; Binder and McDonald, 2007; 2008) once they have found refuge. This could provide a unique opportunity for control agents to target animals with traps that exploit refuge behaviour as opposed to migratory behaviour.

This large-scale manipulation experiment provided a unique opportunity to test how sea lamprey responded to altered flows in the field and could offer insights into the biology of lamprey that could be useful in other circumstances (e.g. upstream passage). Based on the pattern of space use, I suspect that sea lamprey were responding to discharge from the draft tubes more than the comparatively weaker attractant flow from the trap entrances. Many individuals entered all three draft tubes, either in an attempt to pass the barrier or to gather information from the flow through the draft tubes. Managers that operate fishways used to pass lamprey, along with other fishes, could manipulate flow from both the generating station and the fishway entrance to try to increase the likelihood of lamprey being attracted to, and subsequently entering the fishways. Lamprey have been considered poor swimmers (Beamish, 1978) but recent tracking evidence from Russon and Kemp (2011) and this study suggest that lamprey are more capable at swimming in fast flows than previously held. It is important to note, however, that much of their movement in high discharge at the generating station is along the
bottom of the river, where flows are lowest. It is likely that sea lamprey are exploiting attachment surfaces to maintain and gain position in fast flows (Quintella et al., 2004) along the dam face and in the draft tubes.

Large scale ecological studies are tremendously difficult to perform and as such often present a set of limitations for their interpretability. I recognize four limitations in this study. First, it is unclear whether the behaviour of the tagged sea lamprey is representative of sea lamprey that were not tagged. Close et al. (2003) suggested that tagging did not influence the swimming ability of tagged Pacific lamprey, however little is known about how tags affect the motivation and decision-making of sea lamprey. I note, however, that my findings suggest the swimming performance of tagged sea lamprey was better than I had hypothesized. Second, the definition of encounter used in this analysis is more spatially coarse than the definition used in the PIT tagging studies conducted by me (chapter 1) and by Bravener and McLaughlin (2013). The definition of encounter used in this analysis based on acoustic telemetry represents a fish that is near (within 3m) of a trap, whereas the definition of encounter used in the PIT telemetry study in the preceding chapter represents a fish that is near (within 0.5 m) the physical entrance to the trap. As such, sea lamprey could be considered to encounter a trap based on the expectation that at 3 m they are able to perceive the trap. Third, there is uncertainty whether space use at the spatial scale of the grid cells can be used to predict behaviour at the scale of the trap opening in terms of encounter with, and departure or entrance into the trap. The grid cell size of 3 m x 3 m x 3 m was selected for two reasons. It encompasses the ‘trapable’ area we have operationally defined that includes both the physical size of the trap itself as well as the sensory field of the
lamprey when in the vicinity of the trap. In addition, this cell size is greater than the estimated positioning error such that it minimizes the frequency of fish being assigned to the wrong cell. Fourth, there is uncertainty that cell occupancy at the temporal scale we use in this study is able to predict encounter with, and entrance into traps, which typically lasts between 1-300 seconds (Gale Bravener, personal communication). The probability of occupancy was estimated for each hour of the study season because this was the finest temporal scale that we could resolve discharge and water temperature.

Despite these limitations, this study provides a set of novel, significant aspects. First, using large-scale experimental manipulation of discharge to examine whether sea lamprey actually respond and how that response influences trapping efficiency (cause and effect) provides more useful information than correlational studies of environmental features and trap catch. Testing an environmental feature at a scale which is relevant to what management agencies can control is crucial to developing improvements for management strategies. Bravener (2011) was unable to detect an influence of discharge on the movement of sea lamprey further downstream of the Clergue generating station. This inability to detect a response could be due to two reasons. Discharge from the generating station was not manipulated resulting in little night to night variation in discharge. Alternatively, we do not know the downstream spatial extent for which the discharge may be perceived by sea lamprey. The area where sea lamprey were tracked in Bravener (2011) may have been beyond where sea lamprey gather and respond to the discharge. Second, the 3D positions recorded with acoustic telemetry are more precise than what could be achieved with any other technology. It has allowed us to examine space use at a scale larger than achieved previously. Examination of
space use along the entire 3D movement track for these sea lamprey is warranted to
determine whether sea lamprey tend to use the river bottom in the entire tailrace or
whether there are locations where sea lamprey tend to use the water column more
thoroughly. Third, information on the space use of sea lamprey gained from this study
should allow managers to use evidence-based decision making to improve trapping
efficiency, trap placement, and overall trapping strategy. Managers may decide to
explore novel trap options including targeting lamprey at their daytime refuge locations
or limit further reliance on more challenging options like pheromone manipulations.

The information provided by this study on the space use of sea lamprey should help
direct future trapping strategies. This study provides evidence of a trade-off for
behavioural manipulation where increased discharge at a large spatial scale attracts
sea lamprey to the generating station but once they reach the source at a close spatial
scale, it inhibits their ability to perceive a comparatively weaker attraction discharge
from traps. In addition, it provides basic information on where sea lamprey occur along
the face of the generating station. Although each barrier provides a unique physical and
hydrological environment, the findings presented here should transfer well to trap
locations at other barriers for sea lamprey.
**Fig. 2.1:** A map depicting the St. Marys River connecting Lakes Superior and Huron. Sea lamprey trapping sites are approximately 23 km downstream of Lake Superior outflow. QGIS base layer courtesy of Bing aerial photography layer.
**Fig. 2.2:** An aerial view of the Francis H. Clergue Generating Station on the north side of the St. Marys River. The river flows from left to right. Sea lamprey control traps are located along the downstream face of the dam. There are five traps at the Clergue Dam: the north attractant water trap (NAWT), south attractant water trap (SAWT), and three portable traps (depicted by white circles) placed between the NAWT and SAWT. QGIS base layer courtesy of Bing aerial photography layer.
Fig. 2.3: Acoustic telemetry array in the tailrace of the Clergue generating station. Individual hydrophone locations are shown as circles (N=16). Yellow circles denote surface mounts and red circles denote bottom mounts. QGIS base layer courtesy of Bing aerial photography layer.
Fig. 2.4: Mean daily discharge (m³/s) from the Clergue Generating Station. Closed circles represent dates when overnight discharge from the generating station remained high. Open circles represent dates when overnight discharge from the generating station was low.
**Fig. 2.5:** Distance from the dam reached by the proportion of tagged sea lamprey that entered the acoustic telemetry array (N=91) immediately downstream of the Clergue Generating Station.
Fig. 2.6: Proportion of tagged sea lamprey that make their first upstream movement to reach the wall of the Clergue Generating Station (N=83) per night on nights when discharge was high (N=14) compared to nights when discharge was low (N=16).
Fig. 2.7: Conditional modes of the random effect for each cell along the face of the Clergue Generating Station (n=118 cells). Horizontal lines are 95% prediction intervals. Individual cells are ranked and plotted from lowest to highest.
Fig.2.8: Estimated probability of occupancy for each cell along the face of the Clergue Generating Station. (A) is the mean probability for each hour across the entire study (N=29 days). (B) is the mean probability for each hour on dates when overnight discharge was high across the entire study (N=13 days). (C) is the mean probability for each hour on dates when overnight discharge was low across the entire study (N=16 days). (D) is the mean probability for each hour during the night (2300h-0700h), and (E) is the mean probability for each hour during the day (0800h-2200h). Black outlines represent the draft tubes. Black stars denote location of traps.
**Table 2.1:** Two-step multimodel assessment using the Bayesian Information Criterion (BIC). The best approximating model from model set 1 was taken forward to the second model set.

<table>
<thead>
<tr>
<th>Covariates</th>
<th>BIC</th>
<th>ΔBIC</th>
<th>df</th>
<th>wi</th>
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<tr>
<td><strong>Model set 1</strong></td>
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<td>time</td>
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<td>cell volume, time</td>
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<td>13</td>
<td>5</td>
<td>0.0014</td>
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<tr>
<td>time, temperature</td>
<td>13917711</td>
<td>13</td>
<td>5</td>
<td>0.0014</td>
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<tr>
<td>time, date</td>
<td>13917711</td>
<td>13</td>
<td>5</td>
<td>0.0014</td>
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<tr>
<td>cell volume, time, temperature</td>
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<td>26</td>
<td>6</td>
<td>&lt;0.001</td>
</tr>
<tr>
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<td>13917724</td>
<td>26</td>
<td>6</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>cell volume, time, date, temperature</td>
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<tr>
<td>time</td>
<td>13917698</td>
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<td>time, discharge, depth</td>
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Table 2.2: Regression estimates of random and fixed effects from the best approximating occupancy model (mixed effects logistic regression).

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<th>Random effects:</th>
<th>Variance</th>
<th>Standard deviation</th>
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<tr>
<td>cell identification</td>
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<tr>
<td>fish identification</td>
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<td>0.0000</td>
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</table>

<table>
<thead>
<tr>
<th>Fixed effects:</th>
<th>Estimate</th>
<th>Lower estimate</th>
<th>Upper estimate</th>
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<tbody>
<tr>
<td>intercept</td>
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<td>-7.1882495</td>
<td>-6.2974601</td>
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<tr>
<td>time of day</td>
<td>0.0027297</td>
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<td>discharge</td>
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<td>depth</td>
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<tr>
<td>discharge:depth</td>
<td>-0.7689075</td>
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EPILOGUE

My thesis provides important insight into the behaviour and space use of sea lamprey near traps that could help management agencies improve trap efficiency. Results from chapter 1 suggest that trapping efficiency at the Clergue Generating Station was low, even though encounter was high, because the entrance rate was low and the departure rate was high (Counteracting Responses Hypothesis). A discharge regime that stimulates upstream movement in the early evening to bring lamprey towards the barrier but lowers discharge after midnight so as to not compete with the attractant trap discharge could offer the most effective compromise between increasing trapping success and balancing the hydroelectric needs. Results from chapter 2 suggest that most sea lamprey make it all the way up to the Clergue Generating Station wall. Sea lamprey responded to discharge at a large distance as more sea lamprey moved upstream to the generating station wall on nights when discharge was high. However, at a closer scale, high discharge from the draft tubes was more attractive to sea lamprey than attractant flow from the traps and as such lamprey spent more of their time near the draft tubes. To increase encounter rate with traps, control agents should operate traps in a way that places them at the bottom of the dam face along the concrete pillars that separate the draft tubes or current trap locations must be manipulated so as to make them highly attractive to sea lamprey.

This thesis also provides examples of how to apply sophisticated statistical models to assess largely applied management questions. The multistate Markov analysis offers the ability to track individual sea lamprey behaviour through the trapping process. This method reveals important differences compared to simple catch enumeration. It is
important to assess each component of trapping individually to appropriately evaluate the influence of external factors on sea lamprey trapping efficiency. The occupancy model approach from chapter 2 reveals important understanding of where sea lamprey are aggregating. Some agency managers and scientists have hypothesized that sea lamprey are aggregating along the bottom of the dam because of unique hydraulic and physical features, however, they were not validated until this thesis applied acoustic telemetry and occupancy models to examine sea lamprey space use.

A theme emerging from this thesis is one of the trade-offs that exist for behavioural manipulations. In both studies in this thesis, the results suggest that at a large spatial scale, sea lamprey respond to discharge due to increased attraction which increases the likelihood of encountering traps and improving trap efficiency. However, as the sea lamprey reach a smaller scale (closer to the traps), the increased discharge elicits behaviour that reduces trapping efficiency. Explicit recognition of these trade-offs is important because it may help us understand why expected gains in trap success from a manipulation are not realized.

To improve trap efficiency for sea lamprey, the next step is to investigate the reasons for low entrance efficiency at traps. To improve efficiency, we must elucidate why sea lamprey enter or depart, upon encountering a trap. Although this study focuses on sea lamprey in the St. Marys River and suggests management options that can be specific to that system, there are elements that could inform both other invasive species control programs and species conservation programs related to upstream passage at barriers via fishways. Of ultimate importance, would be to elucidate the patterns of behavioural
responses to discharge and link these responses to the hydrological conditions to inform management.
REFERENCES


Appendix 1. 3D positioning accuracy estimates obtained using telemetry records for 14 fish across 3 portable traps (N=2, 7, and 5, respectively) and for a test tag located at the NAWT. Methods for error calculation were based on Connolly (2012). Spherical Error Probable (SEP), Mean Radial Spherical Error (MRSE), and Standard Accuracy Standards (SAS90 and SAS99) estimate that a sphere with the calculated radius will contain the true position of the tag 50, 61, 90, and 99% of the time, respectively.

<table>
<thead>
<tr>
<th></th>
<th>Spherical Error Probable (SEP)</th>
<th>Mean Radial Spherical Error (MRSE)</th>
<th>Spherical Accuracy Standard (SAS90)</th>
<th>Spherical Accuracy Standard (SAS99)</th>
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<tr>
<td>Test tag</td>
<td>1.22 m</td>
<td>1.39 m</td>
<td>1.99 m</td>
<td>2.69 m</td>
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<td>Trap 1</td>
<td>1.20 m</td>
<td>1.38 m</td>
<td>1.96 m</td>
<td>2.64 m</td>
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<td>Trap 2</td>
<td>1.23 m</td>
<td>1.40 m</td>
<td>2.01 m</td>
<td>2.71 m</td>
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<tr>
<td>Trap 3</td>
<td>1.15 m</td>
<td>1.34 m</td>
<td>1.87 m</td>
<td>2.52 m</td>
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</table>
Appendix 2. 3D tracks for sea lamprey that entered the telemetry array downstream of the Clergue Generating Station (N=91 individuals). Red indicates the start of the track (the first detected position) and blue represents the end of the track (the last detected position). Fish identification number (tag period; milliseconds) is listed in the upper left corner of each map. QGIS base layer courtesy of Bing aerial photography layer.