Telemetry narrows the search for sea lamprey spawning locations in the St. Clair-Detroit River System

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Abstract

Adult sea lamprey (*Petromyzon marinus*) abundance in Lake Erie has remained above targets set by fishery managers since 2005, possibly due to increased recruitment in the St. Clair-Detroit River System (SCDRS). Sea lamprey recruitment in the SCDRS poses an enormous challenge to sea lamprey control and assessment in Lake Erie because the SCDRS contains no dams to facilitate capture and discharge is at least an order of magnitude larger in the SCDRS than most other sea lamprey-producing tributaries in the Great Lakes. As a first step toward understanding population size, spatial distribution, and spawning habitat of adult sea lampreys in the SCDRS, we used acoustic telemetry to determine where sea lampreys ceased migration (due to spawning, death, or both) among major regions of the SCDRS. All tagged sea lampreys released in the lower Detroit River (N=27) moved upstream through the Detroit River and entered Lake St. Clair. After entering Lake St. Clair, sea lampreys entered the St. Clair River (N=22), Thames River (N=1), or were not detected again (N=4). Many sea lampreys (10 of 27) were last observed moving downstream ("fallback") but we were unable to determine if those movements occurred before or after spawning, or while sea lampreys were dead or alive. Regardless of whether estimates of locations where sea lampreys ceased migration were based on the most upstream region occupied or final region occupied, most sea lampreys ceased migration in the St. Clair River or Lake St. Clair. Results suggest that spawning and rearing in the St. Clair River could be an important determinant of sea lamprey recruitment in the SCDRS and may direct future assessment and control activities in that system.

Keywords: sea lamprey; Petromyzon; telemetry; spawning; migration; St. Clair Detroit-River
System

Introduction

Sea lamprey (*Petromyzon marinus*) entered the Laurentian Great Lakes through shipping canals in the early 1900s and contributed to the decimation of native fish populations (Smith and Tibbles 1980). Since the 1950s, sea lamprey control has facilitated recovery and promoted sustainability of many native and economically valuable fishes (Cornelius et al. 1995; Hansen 1999). Until recently, sea lamprey control in Lake Erie supported restoration of lake trout (*Salvelinus namaycush*), lake whitefish (*Coregonus clupeaformis*), burbot (*Lota lota*), and other fishes by maintaining sea lamprey abundance below targets set by fishery managers (Adair and Sullivan 2015). However, estimates of adult sea lamprey abundance in Lake Erie have remained above the target since 2005 despite increased effort to control sea lamprey in known producing streams and to identify new sources (Adair and Sullivan 2013).

Success of the sea lamprey control program in the Great Lakes has been attributed to knowledge of sea lamprey life history and ecology during the earliest (larval) and latest (adult) stream-dwelling life stages. The sea lamprey is an anadromous, parasitic fish, native to the Atlantic Ocean that depends on both streams for spawning and rearing and on oceans or lakes for somatic growth. Spawning occurs on nests with gravel substrate and steady flow, beginning when water temperatures reach about 10 °C and ending at water temperatures below 26 °C, typically June–July in Great Lakes tributaries (Applegate 1950; Manion and Hanson 1980). Sea lampreys are nocturnal during stream entry and initial migration, but become more active during the daytime as they approach spawning (Applegate 1950). During maturation, adults also experience irreversible degeneration of visual and digestive systems and die shortly after spawning (Beamish 1980). Unsuccessful spawners also die during the same time period

(Applegate 1950). Larval sea lampreys hatch in mid- to late summer, drift downstream, and burrow into soft sediment, where they filter-feed on drifting algae and plankton. After three to eight years in the stream, larvae undergo a physiological transformation and migrate into lakes where they will either find and parasitize a host fish or die. Parasitic sea lampreys remain in the lake for 12 to 18 months before entering streams to spawn. Timing of stream entry is largely unknown but adults have been seen arriving in Great Lakes tributaries between April and July (Applegate 1950). Unlike other anadromous fishes, sea lampreys do not home to their natal streams (Bergstedt and Seelye 1995; Waldman et al. 2008), but use chemical cues emitted by larvae to locate suitable streams for spawning and rearing (Bjerselius et al. 2000; Sorenson and Vrieze 2003). Despite rich understanding of sea lamprey ecology, cost-effective control and assessment strategies remain elusive in large rivers, particularly those lacking migration barriers (Jones 2007; McLaughlin et al. 2007).

Sea lamprey abundance may have increased in Lake Erie if sea lamprey recruitment, survival, or both, increased in the St. Clair-Detroit River System (SCDRS) that flows into Lake Erie from Lake Huron (Figure 1). The SCDRS, which includes the Detroit River, Lake St. Clair, St. Clair River, and (for the purposes of this study) their tributaries, had historically not been considered an appreciable source of sea lampreys to Lake Erie based on previous surveys (Sullivan et al. 2003) and because Lake Erie tributary treatments during the 1990s were highly effective and did not include treatment of the SCDRS (Jeff Slade, USFWS, personal communication). Therefore, increased recruitment of sea lampreys to Lake Erie from the SCDRS may be a recent phenomenon and important new source. Indeed, assessments during 2011–2015 showed that larval sea lampreys were broadly distributed in the St. Clair River and the St. Clair River delta

(Adair and Sullivan 2013, 2015). Coded-wire-tagged juvenile sea lampreys released in the St. Clair River were also caught in traps in eastern Lake Erie (Barber et al. 2015), confirming that juvenile sea lampreys released in the St. Clair River survived downstream migration through Lake St. Clair, the Detroit River, and western Lake Erie to contribute to the population in Lake Erie.

Widespread sea lamprey infestation and recruitment in the SCDRS poses an enormous challenge to sea lamprey control and assessment in Lake Erie. Among rivers targeted by sea lamprey control, the SCDRS is most similar to the St. Marys River, where specialized control strategies were developed to provide cost-effective control in deep, high-flow environments. Since the late 1990s, sea lampreys in the St. Marys River have been targeted with an integrated program of trapping, release of sterilized male sea lampreys, and application of granular Bayluscide (gB), a selective lampricide for deep water (Fodale et al. 2003; Schleen et al. 2003). However, effective gB treatment and rigorous larval surveys required to direct treatment effort would be far more costly in the SCDRS than in the St. Marys River due to lower larval densities, larger potential treatment area, and greater discharge (e.g., 5200 m³/s in the St. Clair River versus 2100 m³/s in the St. Marys River). Therefore, alternative (non-lampricide) control strategies, especially those that would target adult sea lampreys in the SCDRS, may be important to the future of sea lamprey control in Lake Erie.

Unlike the St. Marys River, where barrier-integrated sea lamprey traps provided population assessment data since the 1970s (Mullett et al. 2003), the Detroit and St. Clair rivers contain no dams to facilitate trapping for assessment or control. Traps also provided critical data to guide release of sterile-male sea lampreys (Twohey et al. 2003). Therefore, new

methods that do not require barrier-integrated traps may be needed to design population assessments and sterile-male release strategies in the SCDRS.

As a first step toward understanding population size, migration routes, spawning locations, and habitat use of adult sea lampreys in the SCDRS, we used acoustic telemetry to estimate the proportion of tagged adult sea lampreys that ceased migration (assumed spawning, death, or both) within each major region of the SCDRS (e.g., Detroit River and its tributaries, St. Clair River and its tributaries, Lake St. Clair tributaries, other Lake Erie tributaries, other Lake Huron tributaries). Acoustic telemetry is a popular tool for spatial fish population assessment (Cooke et al. 2014), including sea lampreys and other fishes in the Great Lakes (Altenritter et al. 2013; Hayden et al. 2014; Holbrook et al. 2014). However, neither spawning nor death can be directly observed from telemetry data, requiring that the location where each sea lamprey ceased migration be inferred from observed changes in behavior (e.g., timing and direction of final movements). To test the assumptions required of those inferences, we compared concurrent changes in sea lamprey behavior and environment (e.g., water temperature) as evidence that sea lampreys ceased migration in the area last detected or most upstream area occupied. Results were expected to direct future assessment and control activities in the SCDRS and other large rivers.

Methods

Sea lamprey collection and tagging

Adult sea lampreys were collected from a sea lamprey trap at the Harpersfield Dam in the Grand River near Geneva, Ohio, USA. Those individuals were not collected from within the

SCDRS because it was not possible to collect enough sea lampreys from that system. Fifteen female and fifteen male sea lampreys were collected between 11 May and 13 May 2014. Three female sea lampreys died from hypoxia during transport but all others appeared healthy when tagged the next day. The remaining individuals were surgically implanted with acoustic transmitters (model V8-4H, Vemco; Halifax, Nova Scotia, Canada) on 14 May 2014 using methods described by Holbrook et al. (2014). Sex was confirmed by visual examination of the gonads through the incision. Body mass ranged 188–353 g (mean 285 g) among tagged females and 148–296 g (mean 237 g) among tagged males. Total length ranged 45.4–58.0 cm (mean 51.8 cm) among tagged females and 43.0–53.7 cm (mean 49.6 cm) among tagged males. Transmitters were 0.8 cm in diameter, 2.1 cm long, and weighed 2.0 g in air (0.9 g in water). Transmitter mass represented 0.6–1.4 % (mean 0.8 %) of sea lamprey body mass. Each transmitter emitted a uniquely encoded burst of acoustic pulses (sound pressure level 147 dB re 1 μ Pa at 1 m) every 60–180 s and was expected to operate for at least 112 days. All tagged sea lampreys were released into the Amherstburg Channel of the lower Detroit River (Figure 1) about 7 km upstream of Lake Erie and about 40 km downstream of Lake St. Clair on 16 May 2014 at 0943 hours (UTC - 0400).

Acoustic telemetry receivers

Autonomous acoustic telemetry receivers (N=72; model VR2W; Vemco) were used to listen for acoustic-tagged sea lampreys at 12 locations within the SCDRS (Figure 1), including 13 in the lower Detroit River (site DRL), 6 in the middle Detroit River (site DRM), 11 in the upper Detroit River (site DRU), 1 in Lake St. Clair (site LSC), 2 in each of the Clinton and Thames rivers

(site CLN and THA; tributaries to Lake St. Clair), 22 in the lower St. Clair River and its delta (site SCL), 2 in the middle St. Clair River (site SCM), 2 in each of the Belle, Pine, and Black rivers (sites BLE, PNE, and BLK; tributaries to St. Clair River), and 11 at the head of the St. Clair River (site SCU). The Great Lakes Acoustic Telemetry Observation System (GLATOS; www.data.glos.us/glatos) also provided data from 462 other receiver locations in Lake Erie and Lake Huron (Figure 1).

Assumptions

We assumed that (1) behavior and survival of tagged sea lampreys from the Grand River was representative of untagged sea lampreys in the SCDRS; (2) all transmitters were retained and functioned properly during the study period; (3) all sea lampreys ceased migration (due to spawning, death, or both) during the study period (14 May 2014 to 03 September 2014); and (4) no tagged sea lampreys passed any group of receivers undetected. Assumption 1 was not tested but could have been violated if behavior or survival were affected by prior experience (e.g., in the Grand River), physiological state (e.g., maturation, available energy), or handling (e.g., transmitter implantation, transport stress). Previous research has not revealed any evidence that transport of adult sea lampreys among streams influence their behavior (Kelso et al. 2001). To minimize possible violations of Assumption 1, we used the earliest-caught (i.e., least mature) lampreys from Lake Erie tributaries and used smaller transmitters than have been used on sea lampreys (Kelso and Gardner 2000; Holbrook et al. *In Press*). Transmitter retention rates (Assumption 2) were perfect and failure rates were low (<3 %) in a recent study that used transmitters from the same manufacturer over a similar time period (Holbrook et al. *In Press*), suggesting that violations of Assumption 2 were negligible. Violations of Assumption 3 were not

expected because live adult sea lampreys have been rarely caught or seen in any Great Lakes tributary during September or later (Applegate 1950). Nonetheless, we summarized the number, direction, and timing of final movements during the study period to identify changes in behavior that might be indicative of pre- or post-spawn behavior. Detection data were analyzed to determine if Assumption 4 was violated. In situ detection range tests were also conducted at three receiver locations in the St. Clair River (see Electronic Supplementary Material (ESM) Appendix S1).

Data analysis

Each telemetry receiver stored the date, time, and unique transmitter ID code when a tagged sea lamprey was detected in its vicinity (see ESM Appendix S1 for detection range analysis). Detection data from all receivers, sea lamprey release data (e.g., location, date, time), and biological data (e.g., sex, length, mass) were used to create a geo-referenced detection history for each tagged sea lamprey among all receivers. To remove the effects of potential false positive detections (Simpfendorfer et al. 2015) on conclusions, we removed detections that were not within 60 minutes of another detection of the same tag ID on each receiver. Discrete passage events (passage of a receiver station by a tagged sea lamprey) were defined by arrival and departure events at each receiver station. When two adjacent detections were logged on different receivers, the first was deemed a departure from the first station and the second was deemed an arrival at the second station. When two adjacent detections were logged on the same receiver, but the interval between them was greater than 12 hours, then those were also considered two separate passage events. Direction of movement between

passage events was determined visually (see ESM kmz file 2). Movement (1) between Lake Erie and the Detroit River, (2) between the Detroit River and Lake St. Clair, (3) between Lake St. Clair and the St. Clair, Thames, and Clinton rivers, and (4) between the St. Clair River and the Belle, Pine, Black rivers, and Lake Huron were determined from movement among receiver locations. All waterways among those transitions contained acoustic receivers, except there were no receivers in two narrow channels around Walpole Island in the lower St. Clair River (Figure 1). Thus, tagged sea lampreys could have moved between Lake St. Clair and the St. Clair River through those channels with no opportunity for detection.

Cessation of migration. — Spawning and death were not directly observed, so the location (i.e., major region of study area) where each tagged sea lamprey ceased migration was inferred from the movement history of each tagged sea lamprey. Unexpectedly, 37 % (10/27) of tagged sea lampreys were last observed moving downstream into Lake St. Clair from the St. Clair (n=9) and Thames (n=1) Rivers. We were not able to determine if those movements occurred before spawning, after spawning, or even if those tagged sea lampreys were alive or dead when those downstream movements occurred. Therefore, we estimated the location (major region of the study area) where each sea lamprey ceased migration based on two separate models. In the first model (hereafter, ‘most upstream model’), we assumed that each tagged sea lamprey ceased migration in the most upstream reach (area bounded by two groups of receivers) occupied (i.e., where it ceased upstream movement). In the second model (hereafter, ‘final location model’) we assumed that each tagged sea lamprey ceased migration in the final reach occupied (i.e., where it ceased all movement). For each model, the proportions of tagged sea lampreys that ceased migration (ϕ_k) within each major region of the

SCDRS (k) were estimated by assuming that the number of sea lampreys that ceased migration within each region, $\mathbf{R}_k$, were the outcome of a multinomial process, such that $\mathbf{R}_k \sim \text{multinomial}(\varphi_k, \mathbf{N}_{\text{REL}})$, where $\mathbf{N}_{\text{REL}}$ was the number of fish released. Models were fit to the data using Markov chain Monte Carlo (MCMC) simulation with the software program OpenBUGS (Lunn et al. 2009). “Flat” Dirichlet prior distributions (i.e., all parameters equal to one) were used for all φ_k . Maximum likelihood estimates (MLEs; analytical solution) were used as point estimates of φ_k and uncertainty was estimated using 95% highest posterior density (HPD) intervals.

Testing Assumptions.—To check Assumption 3 (all sea lampreys ceased migration during the study period), daily frequencies of final movements were summarized and compared to hourly water temperature in the St. Clair River to determine if final movements were coincident with water temperatures that have been associated with spawning in other tributaries. Direction of final observed movement and time of day were described to determine if behaviors were consistent with behaviors associated with spawning. To check Assumption 4 (no tagged sea lamprey passed a group of receivers undetected), we estimated the probability that a tagged sea lamprey was detected at each location, given that it passed that site. Site-specific detection probabilities were estimated by first identifying all possible first-order transitions (e.g., movement from one site to another) based on the spatial arrangement of receivers within the SCDRS under the assumption of perfect detectability at each site. If an observed transition was not a first-order transition, then a tagged sea lamprey must have passed one or more sites undetected. Locations of missed detections were inferred from the set of possible first-order transitions. Detection probabilities (p) were estimated by assuming that the number of sea

lampreys detected at each site, $\mathbf{D}_k$, was the outcome of a binomial process, such that $\mathbf{D}_k \sim \text{binomial}(p_k, \mathbf{N}_k)$, where p_k was the probability of detection and $\mathbf{N}_k$ was the number of tagged sea lampreys known to have passed the k th site. The model was fit and parameters were summarized using methods described for cessation of movement except that “flat” uniform prior distributions (i.e., $\text{uniform}(0, 1)$) were used for all p_k .

Results

Cessation of migration

All tagged individuals moved upstream to the upper Detroit River after release and entered Lake St. Clair based on direction and location of last detection in the upper Detroit River (see ESM kmz file 2). No sea lampreys were detected on any receivers at the head of the St. Clair River, in Lake Erie, in Lake Huron, or in the Clinton, Belle, Pine, or Black rivers. After entering Lake St. Clair, 4 % (1 of 27) entered the Thames River, 81 % (22 of 27) entered the St. Clair River, and 15 % (4 of 27) were not detected elsewhere. The sea lamprey that ascended the Thames River was detected leaving the Thames River (i.e., moving downstream) three days later (May 28) and was not detected again. Among sea lampreys that ascended the St. Clair River, 41 % (9 of 22) fell back to Lake St. Clair and 59 % (13 of 22) ceased movement in the St. Clair River, based on location and direction of last observed movements (see ESM kmz file 2). Among all tagged sea lampreys, 48 % (13 of 27) were last observed moving upstream (Figure 2), so we concluded that those individuals ceased migration in the reach they were last observed entering. Direction of last observed movement was not determined for three sea lampreys, but the St. Clair River was the most upstream and final location occupied in all three cases. If

downstream movements of the other 11 sea lampreys (Figure 2) occurred after spawning (i.e., ‘most upstream model’ was true) then 22 tagged sea lampreys would have ceased migration in the St. Clair River, four would have ceased migration in Lake St. Clair, and one would have ceased migration in the Thames River (Table 1). However, if all observed “fallback” occurred before spawning (i.e., ‘final location model’ was true), then 13 tagged sea lampreys would have ceased migration in the St. Clair River and 14 tagged sea lampreys would have ceased migration in Lake St. Clair (Table 1; Figure 2). Under both models, most successful spawning would have occurred in the St. Clair River because there was not believed to be any spawning habitat in the lentic region defined as Lake St. Clair (Leach 1991; Anderson et al. 2010; see Discussion) or in the narrow, transitional zones between lake and river habitats.

Testing assumptions

Assumption 3.—No movement was observed after 29 June 2014 (Figure 3), suggesting that all tagged sea lampreys ceased migration at least 66 days before the end of the study (03 September 2014). Among sea lampreys that were last observed moving upstream, 77 % (10 of 13) were last observed moving before 10 June when water temperature in the St. Clair River ranged 9–15 °C. Among sea lampreys that were last observed moving downstream, 91 % (10 of 11) were last observed moving between 10 June and 29 June, when water temperature in the St. Clair River ranged 15–19 °C. The only sea lamprey last observed moving downstream prior to 10 June was the sea lamprey that was observed moving from the Thames River into Lake St. Clair. We did not monitor water temperature in the Thames River, but it was likely greater than

the St. Clair River. All 11 final movements observed before 10 June occurred during night; five of 13 final movements observed after 10 June occurred during night (Figure 4).

Assumption 4.—Estimates of detection probabilities suggested that any violations of Assumption 4 were small. Groups of receivers in the lower Detroit River (site DRL; Figure 1) detected 93 % (25 of 27; 95% HPD interval: 79–99 %) of tagged sea lampreys that were known to have passed that site (because they were detected farther upstream). Groups of receivers in the middle Detroit River (site DRM) detected 96 % (26 of 27; 95% HPD interval: 79–99 %) of tagged sea lampreys that were known to have passed that site. Groups of receivers in the upper Detroit River (site DRU) and lower St. Clair River (site SCL) detected all tagged sea lampreys that were known to have passed those sites: 23 at DRU (95% HPD interval: 88–100 %) and eight at SCL (95% HPD interval: 71–100 %). Detection probabilities could not be estimated for receivers that detected no sea lampreys or in the middle St. Clair River (site SCM) or Thames River (site THA) because no sea lampreys were detected upstream of those locations. Detection probability estimates were conditional only on fish that were known to have passed, so they did not use information from tagged sea lampreys that were last detected at each site. Detection range tests conducted over two days at three sites in the St. Clair River suggested that the probability of detecting each unique transmission was about 50 % at 225 m, 10 % at 388 m, and was relatively consistent among locations (see Appendix S1).

Discussion

Despite small sample size and inability to determine precisely where sea lampreys spawned or died, results from this study suggest that among regions of the SCDRS with

potential spawning habitat, most sea lampreys ceased migration in the St. Clair River rather than the Detroit River or any of the five tributaries in which larval sea lampreys have been found in recent years. These results are consistent with recent surveys in which larval sea lampreys were found throughout the St. Clair River and St. Clair River delta but not the Detroit River (Adair and Sullivan 2013; Adair and Sullivan 2015). Although several tagged sea lampreys may have ceased migration in Lake St. Clair, we assumed that no successful spawning occurred in Lake St. Clair because there have been no reports of sea lampreys spawning in lentic habitats elsewhere (Applegate 1950; Manion and Hanson 1980). Current speed and direction in Lake St. Clair can be highly variable, even near the bottom (Anderson et al. 2010). Although never observed for sea lampreys, lentic spawning has been identified as an uncommon life history for Pacific Lampreys (*Entosphenus tridentatus*; Russell et al. 1987). Although unexpected, future attempts to identify lentic spawning habitats in Lake St. Clair might best be directed along the south shore and near the head of the Detroit River, where some gravel may be present (Leach 1991). Current knowledge of sea lamprey habitat requirements, however, would suggest that most spawning occurred in the St. Clair River. Future research may seek to determine the number of adult sea lampreys that spawn in the St. Clair River, where spawning occurs, and physical variables that are associated with cessation of migration and spawning. For example, artificial spawning reefs have been constructed in the Detroit and St. Clair rivers since 2004 to promote restoration and recovery of native fishes (Roseman et al. 2011; Hondorp et al. 2014), but the extent to which those reefs are used by sea lampreys has not been evaluated.

Fallback, to the extent observed in this study, has not been previously described and presents a new challenge in use of telemetry data to understand sea lamprey behavior.

Increased prevalence of downstream and nocturnal movements suggested that a change in behavior coincided with water temperature changes that have been associated with spawning behavior in other systems (Applegate 1950). While shifts to diurnal behavior prior to spawning have been described for sea lamprey (Applegate 1950; Binder and MacDonald 2008), it remains unknown if fallback behavior marked the end of active migration (e.g., search for spawning grounds or mate) or passive post-spawn drifting (e.g., dead or alive). Applegate (1950) observed sea lampreys downstream of their spawning locations in the Ocqueoc River, but the total distance moved was small because negatively-buoyant sea lampreys were impinged on debris or settled to the bottom of pools. Perhaps post-spawn, passively-drifting sea lampreys can travel farther in the St. Clair River than in the Ocqueoc River because the St. Clair River is largely void of woody debris and pools. Several other detailed descriptions of movements of radio-tagged sea lampreys have not described fallback behavior after spawning (Kelso and Gardner 2000; Kelso et al. 2001; Almeida et al. 2002). Given the broad distribution of larval sea lampreys in the St. Clair River, and that many tagged sea lampreys in this study did not return to the St. Clair River or ascend any other tributary after fallback, we hypothesize that most of the fallback observed in this study was post-spawn, passive drift. Testing that hypothesis might require combining telemetry with nest and carcass surveys, as has been done with Pacific Lamprey (Starcevich et al. 2014). While that information may not have changed the main conclusion of this study, mortality of adult sea lampreys in Lake St. Clair could affect inferences from future research or population assessments by decreasing sample size, especially for research focused on spawning behavior or habitat use. Understanding precisely when and where sea lampreys spawn, die, or seek refuge during migration, will require further research, almost certainly

combining telemetry with other tools (e.g., sensor tags) and techniques (e.g., nest surveys, carcass surveys, video monitoring).

Minimal use of tributaries is consistent with earlier observations that treatment of tributaries in the SCDRS was not critical to sea lamprey control in Lake Erie and the emerging hypothesis that spawning in the main stem of the St. Clair River contributed to recent recruitment to Lake Erie. Indeed, relatively little spawning or rearing habitat exists for sea lampreys in those streams, which are mostly low-gradient, high-turbidity streams whose watersheds are dominated by residential, industrial, or agricultural use. Recent research suggests that migratory pathways might be manipulated with synthetic attractants (Sorensen and Vrieze 2003) or repellents (Imre et al. 2010; Wagner et al. 2011). Minimal use (i.e., low pheromone concentrations) and apparent low quality of rearing habitat (i.e., high natural mortality) in tributaries may offer ideal conditions to determine if population sinks or ecological traps (Battin 2004) can be created by increasing the number of adult sea lampreys that enter tributaries where spawning success or recruitment are much lower than in main channel habitats or where larvae can be more effectively targeted with lampricides.

Without dams (a requisite for effective sea lamprey traps) and with discharge at least an order of magnitude larger than most other sea lamprey-producing tributaries in the Great Lakes, the SCDRS is a new frontier in sea lamprey control and assessment. Despite the small sample size, all tagged sea lampreys moved upstream at least 40 km after release, but remained in the SCDRS even though no barriers prevented upstream movement into Lake Huron. Consistent with recent larval assessments, these results suggest that spawning and rearing in the St. Clair River could be an important determinant of sea lamprey recruitment in

the SCDRS. Although we caution against population-level inferences from results of this study, results show clear patterns that, if substantiated with larger sample sizes, more rigorous tracking, and integration with other methods (e.g., nest surveys, mark-recapture) over multiple years, may direct future assessment and control activities toward the St. Clair River in the SCDRS. The insights from this study would not have been possible with traditional sampling techniques (e.g., nets, traps) and show the value of telemetry in narrowing the search area for critical habitats in large rivers.

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Tables

Table 1. Observed number and proportion (95% HPD regions in parentheses) of acoustic-tagged adult sea lampreys that ceased migration in each region of the SCDRS during 2014 based on most upstream reach occupied (most upstream model) and final reach occupied (final location model).

Model	Location	#of Tagged sea lampreys			% of sea lampreys
		Female	Male	Total	
Most upstream	Lake St. Clair	1	3	4	15 % (4–28 %)
-	St. Clair River	11	11	22	81 % (58–88 %)
-	Thames River	0	1	1	4 % (0–15 %)
-	Other ¹	0	0	0	0 % (0–10 %)
Final location	Lake St. Clair	5	9	14	52 % (32–67 %)
-	St. Clair River	7	6	13	48 % (29–64 %)
-	Other ²	0	0	0	0 % (0–10 %)

¹Includes lakes Erie and Huron, Detroit, Clinton, Belle, Pine, and Black rivers.

²Includes lakes Erie and Huron, Detroit, Thames, Clinton, Belle, Pine, and Black rivers.

Figure Captions

Figure 1: Map of the St. Clair-Detroit River System (SCDRS) with release site of acoustic-tagged sea lampreys (N=27) and locations of acoustic telemetry receivers (red symbols), grouped by location (rectangles), used to track sea lamprey during May–July 2014. ESM file kmz-1 also shows these locations on Google Earth. Inset shows location of the study site (rectangle) in the Great Lakes basin and locations of acoustic telemetry receivers outside the SCDRS during the study.

Figure 2: Location and direction (upstream or downstream) of last observed movement (determined from sequences of detections at last two stations where each sea lamprey was observed) of each tagged sea lamprey (N=27) in the SCDRS in 2014. Diamonds represent sea lampreys for which direction could not be determined (see Methods). Symbols show general direction of movement; not specific path used.

Figure 3: Daily number of tagged sea lampreys that were last detected moving upstream (n=13), downstream (n=11), or in an unknown direction (n=3), in the SCDRS in 2014 with hourly water temperature of the St. Clair River near Algonac, MI. Water temperature data were obtained from NOAA station 9014070 (<http://tidesandcurrents.noaa.gov>; accessed 23 December 2014).

Figure 4. Time of day (UTC – 0400) when sea lampreys were last observed moving upstream before (A) and after (B) 10 June, 2014 and downstream before (C) and after (B) 10 June, 2014. Symbol shading shows movements observed during day (light grey) and night (dark grey) based

on mean civil twilight at Algonac, Michigan, USA. Civil twilight data were obtained from the U.S. Naval Observatory (http://aa.usno.navy.mil/data/docs/RS_OneDay.php; accessed 18 March 2016).

A - Upstream; before 10 June 2014

B - Upstream; on/after 10 June 2014

C - Downstream; before 10 June 2014

D - Downstream; on/after 10 June 2014