DYNAMICS OF SEA LAMPREY, *PETROMYZON MARINUS*, SPAWNING MIGRATIONS IN LARGE RIVERS, WITH APPLICATION TO POPULATION ASSESSMENT AND CONTROL IN THE GREAT LAKES

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ABSTRACT

DYNAMICS OF SEA LAMPREY, *PETROMYZON MARINUS*, SPAWNING MIGRATIONS IN LARGE RIVERS, WITH APPLICATION TO POPULATION ASSESSMENT AND CONTROL IN THE GREAT LAKES

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Knowledge of the spatial and temporal migration dynamics of adult Sea Lamprey (*Petromyzon marinus*) is needed to improve population assessment and control in the Great Lakes. In Chapter 1 of this dissertation, a Bayesian state-space model provided reach-specific probabilities of movement, including trap capture and dam passage, for 148 acoustic-tagged adult Sea Lamprey in the lower Cheboygan River, Michigan, a tributary to Lake Huron. Reach-specific movement probabilities were combined to obtain estimates of spatial distribution and abundance needed to evaluate a barrier and trap complex for Sea Lamprey control and assessment. Of an estimated 21,828 – 29,300 adult Sea Lampreys in the river, 0-2%, or 0-514 untagged Sea Lampreys, could have passed upstream of the dam, and 46-61% were caught in the trap. Although no tagged Sea Lampreys passed above the dam (0/148), the sample size was not sufficient to adequately evaluate barrier effectiveness for large populations as in the Cheboygan River. For example, more than 1 643 tagged Sea Lampreys would have been needed to conclude (with 95% probability) that fewer than 50 tagged Sea Lampreys could have passed above the dam when no passage of tagged fish was observed. Results also showed that existing traps are in good locations because 83-96% of the population was available to existing traps. However, only 52-69% of Sea Lampreys available to traps were caught, suggesting that traps can be improved. In Chapter 2, I explored the current and possible future role of traps to control and assess Sea Lamprey in the St. Marys River, the connecting channel between lakes Superior and Huron.

Exploitation rates (i.e., fractions of the adult Sea Lamprey population removed by traps) at two upstream locations were compared among three years and two points of entry to the system. Telemetry receivers throughout the drainage allowed trap performance (exploitation rate) to be partitioned into two components: proportion of migrating Sea Lampreys that visited traps (availability) and proportion of available Sea Lampreys that were caught by traps (local trap efficiency). Estimated exploitation rates were well below those needed to provide population control in the absence of lampricides. Local trap efficiency and availability estimates suggested that substantial increases in catch would require major changes to Sea Lamprey trapping systems, including improvements to existing traps, installation of new traps, or modifications to attract more Sea Lampreys toward and into traps. Lower-than-expected local trap efficiency estimates also suggested that traditional assessment methods underestimated abundance of spawning-phase Sea Lampreys in the St. Marys River and highlighted the need to evaluate the equal catchability assumption of mark-recapture models when a single trap is used for capture and recapture. In Chapter 3, I determined if migration behavior of adult Sea Lampreys in the St. Marys River was consistent with the current conceptual model of spawning migration. As expected, most adult Sea Lampreys made directed upstream movements until they encountered a barrier or entered a tributary. Results suggested that most Sea Lampreys spawned in the upper reaches of the St. Marys River near Sault St. Marie or in the three tributaries to the upper North Channel. The proportion of Sea Lampreys that presumably spawned at each location differed between release sites and among years due to differences in route selection probabilities at downstream bifurcations of the channel. The approaches used in this study may have broader applications, including evaluation of barriers and traps for other invasive species (e.g., Asian carp *Hypophthalmichthys spp.*) and fish passage structures for other diadromous fishes.

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PREFACE

The Laurentian Great Lakes were severely disrupted by the arrival of invasive Sea Lamprey (*Petromyzon marinus*) through shipping canals in the early 1900s. Like other anadromous fish, Sea Lampreys depend on streams for spawning and rearing and on oceans or lakes for somatic growth and maturation. In the Great Lakes, Sea Lamprey predation contributed to extirpation of several native fish species, including the top predator, Lake Trout, *Salvelinus namaycush*, from three of the five lakes. Since the 1950s, Sea Lamprey populations have been suppressed in the Great Lakes with selective pesticides (lampricides) that target larvae in streams, barriers that block access to spawning habitat, traps that remove adults prior to spawning, and from 1997 to 2011, releases of sterilized males to compete with fertile males. Sea Lamprey populations have been maintained at about 10% of their maximum levels since the 1960s, but their continued control is costly.

Knowledge of the spatial and temporal migration dynamics of adult Sea Lamprey is needed to improve population assessment and control in the Great Lakes. Despite decades of research, our knowledge of the Sea Lamprey spawning migration (from host detachment to initiation of spawning) remains inadequate. Most of the current knowledge of Sea Lamprey ecology has come from those habitats where animals are easily observed—namely in small (wade-able) streams or at barriers within streams. However, emerging technologies (e.g., telemetry, sonar imaging) are increasingly providing the ability to observe fish in environments where conventional methods cannot be used.

In this dissertation, I used data from acoustic telemetry studies in two large tributaries to Lake Huron to evaluate Sea Lamprey movement in association with traps and barriers for assessment and control. Compared to conventional methods, acoustic telemetry provides greater detection probabilities due to large ranges of signals from acoustic transmitters and ability to sample concurrently at many locations with autonomous underwater receivers. Movement histories from individual tagged fish not only provided detailed information about spatial and temporal movements of individuals, but were combined to provide estimates of population-level parameters.

Barrier-integrated Sea Lamprey traps have been used to provide estimates of stream-specific adult Sea Lamprey abundance that have formed the basis of lake-wide adult Sea Lamprey abundance estimates—one of three metrics used to evaluate success of the Sea Lamprey control program. Typically, a sample of Sea Lampreys caught in barrier-integrated traps have been marked and released downstream of traps each day for possible recapture in that same set of traps. Release and recovery data have been used in a time-stratified mark-recapture model to estimate adult Sea Lamprey abundance (hereafter, ‘traditional’ estimates) at the release site. Trap efficiency, a measure of trap performance, has also been estimated as the proportion of the adult population that was caught in traps. However, two critical assumptions of the method have not been rigorously tested. First, it must be assumed that marked and unmarked Sea Lampreys are equally likely to be captured in traps. The use of the same traps for capture and recapture has raised some concern that traditional estimates of abundance and trap efficiency could be biased if some Sea Lampreys in the population are behaviorally predisposed to trap capture. Second, it must be assumed that all Sea Lampreys in the population pass the release point.

In chapters 1 and 2, I tested those assumptions during one year in the Cheboygan River and three years in the St. Marys River. The two river systems represented model systems at two ends of a spectrum. In the Cheboygan River, traps were located at a barrier only 2.5 km from Lake Huron and no spawning habitat was available in tributaries between the river mouth and the barrier. In the St. Marys River, traps in the upper St. Marys River and Echo River were located at least 80 km from Lake Huron or the North Channel and spawning habitat was known to exist in the main stem downstream of the barrier and in at least three tributaries (Root, Garden, and Echo rivers).

Telemetry-based estimates of local trap efficiency were similar to traditional estimates in the Cheboygan River but lower than traditional estimates in the upper St. Marys River. Consequently, telemetry-based estimates of adult Sea Lamprey abundance at traditional mark-recapture release sites were similar to traditional abundance estimates in the Cheboygan River, but larger than traditional abundance estimates in the upper St. Marys River. However, traditional estimates of abundance were smaller than telemetry-derived estimates of stream-wide abundance in both rivers because some Sea Lampreys in each river did not reach traditional release sites. Results suggest that accuracy of adult Sea Lamprey abundance estimates could be improved if marked Sea Lampreys could be released closer to river mouths. In some systems (e.g., St. Marys River) accuracy could also be improved by capturing Sea Lampreys with a method that is independent of barrier-integrated traps.

A recent goal of the Sea Lamprey control program has been to increase the effectiveness of traps and barriers for Sea Lamprey control, ideally to the point that they could replace lampricide treatments. In chapters 1 and 2, I described a conceptual framework for evaluating barrier-integrated traps for Sea Lamprey control and then applied that framework to the Cheboygan and St. Marys rivers. Specifically, the proportion of an adult Sea Lamprey population removed by traps (i.e., exploitation rate) was separated into two underlying processes: the proportion of the stream-wide population available to traps (i.e., availability) and the portion of those available that were caught (i.e., local trap efficiency).

In both rivers, exploitation rates were lower than what has been considered necessary for trap-based Sea Lamprey control in the absence of lampricides. In the Cheboygan River, exploitation rates were more limited by local trap efficiency than by availability. Therefore, improvements to existing traps in the Cheboygan River have greater potential to increase catches than installation of new traps in new locations or efforts to attract more Sea Lamprey toward traps. In the St. Marys River, exploitation rates seemed to be severely limited by both availability to traps and local trap efficiencies. In the St. Marys River, improvements to existing traps and either trapping in new locations or development of methods to attract more Sea Lampreys toward traps may be needed to increases catches to levels that would be expected to provide population control in the absence of lampricides.

In Chapter 3, I described movements of Sea Lampreys among reaches in the St. Marys River to better understand what processes influence spatial distribution of spawners, including availability to traps. Consistent with expectations, most Sea Lampreys moved quickly up to the barriers or entered tributaries, suggesting that most spawning habitat was located in those locations. However, many Sea Lampreys ceased migration before reaching barriers or tributaries and many were last detected in a tributary or at least 5 km downstream of the barrier, suggesting that use of spawning habitat downstream of barriers limits exploitation. The fate of Sea Lampreys also differed between two release locations. Sea Lampreys released in the shipping channel in Munuscong Lake (outlet to northern Lake Huron main basin) tended to remain in the shipping channel and were more likely to arrive at traps in the upper St. Marys River or cease migration in the main stem more than 5 km downstream of the traps than Sea Lampreys released in the North Channel. A small proportion of Sea Lampreys released in the North Channel entered the shipping channel. Consequently, Sea Lampreys released in the North Channel were much more likely to enter the Root, Garden, or Echo rivers than Sea Lampreys released in Munuscong Lake. In lieu of new traps, substantial improvements to existing traps, or both, results suggest that Sea Lamprey control in systems like the St. Marys River could be improved if migration pathways could be manipulated to increase the proportion of the adult Sea Lamprey population that enters tributaries where offspring would be susceptible to relatively inexpensive lampricide treatments.

This study addressed questions that are critical for understanding effectiveness of existing barriers and traps to assess and control Sea Lamprey and for predicting benefits of control strategies that are alternative to lampricides. The approaches used in this study may have broader applications, including evaluation of barriers for other invasive species (e.g., Asian carp) and fish passage structures for other diadromous fishes.

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CHAPTER 1

ESTIMATING REACH-SPECIFIC FISH MOVEMENT PROBABILITIES IN RIVERS WITH A BAYESIAN STATE-SPACE MODEL: APPLICATION TO SEA LAMPREY PASSAGE AND CAPTURE AT DAMS

Abstract

Improved methods are needed to evaluate barriers and traps for control and assessment of invasive Sea Lamprey (*Petromyzon marinus*) in the Great Lakes. A Bayesian state-space model provided reach-specific probabilities of movement, including trap capture and dam passage, for 148 acoustic tagged Sea Lamprey in the lower Cheboygan River, Michigan, a tributary to Lake Huron. Reach-specific movement probabilities were combined to obtain estimates of spatial distribution and abundance needed to evaluate a barrier and trap complex for Sea Lamprey control and assessment. Of an estimated 21,828 – 29,300 adult Sea Lampreys in the river, 0-2%, or 0-514 untagged lampreys, could have passed upstream of the dam, and 46-61% were caught in the trap. Although no tagged lampreys passed above the dam (0/148), the sample size was not sufficient to consider the lock-and-dam an effective Sea Lamprey barrier. Results also showed that existing traps are in good locations because 83-96% of the population was vulnerable to existing traps. However, only 52-69% of lampreys available to traps were caught, suggesting that traps can be improved. The approach used in this study was a novel use of Bayesian state-space models that may have broader applications, including evaluation of barriers for other invasive species (e.g., Asian carp (*Hypophthalmichthys spp.*)) and fish passage structures for other diadromous fishes.

Introduction

The Laurentian Great Lakes were severely disrupted by the arrival of invasive Sea Lamprey (*Petromyzon marinus*) through the Welland Canal in the early 1900s (Smith and Tibbles 1980; Hansen 1999). After hatching, non-parasitic, filter-feeding larvae remain in streams for one to seven years and then transform into parasitic juveniles (Applegate 1950). After transformation, juveniles migrate downstream and enter lakes where they grow rapidly by feeding on the body fluid of other fishes. After 12-18 months in the lake, semelparous adults cease feeding and ascend tributaries to spawn during spring and early summer. Like other anadromous fishes, Sea Lampreys have been most vulnerable to life cycle interruptions during their larval stream-resident and stream migratory adult stages, and control strategies have been developed to target those stages.

In the Great Lakes, Sea Lamprey populations have been suppressed with selective pesticides (lampricide) that target larvae in streams, barriers that block access to spawning habitat, and traps that remove adults prior to spawning (Christie and Goddard 2003). Improving effectiveness of traps and barriers, which target Sea Lampreys during the adult stage, has been a priority of the Sea Lamprey research program (Jones et al. 2007; McLaughlin et al. 2007). However, empirical evaluations of traps and barriers have been limited to indirect evidence of upstream passage (e.g., presence of larval Sea Lampreys upstream of a barrier), direct observation in shallow water (Applegate 1950), or mark-recapture methods for which critical assumptions have not been rigorously tested.

Barrier construction was among the earliest efforts used to control Sea Lampreys in the Great Lakes and a need exists to both evaluate current barriers and establish new ones (Swink 1999; Lavis et al. 2003; Johnson et al. 2014). The fraction of a population blocked by a barrier provides an intuitive basis to compare barriers, but does not represent the effectiveness of any single barrier because upstream recruitment dynamics (e.g., stock-recruitment) often depend on the number of mature individuals above the barrier (i.e., stock size), not the proportion passing. Thus, the passage proportion is not sufficient to determine effectiveness of a barrier as a Sea Lamprey control device. Instead, the number of individuals that escape above a dam should be estimated.

Although the primary function of a barrier is to block access of adults to upstream spawning habitat, barriers also facilitate removal of individuals prior to spawning via barrier-integrated traps. Little is known about the fate of Sea Lampreys that encounter an impassable barrier, though it is generally assumed they spawn downstream of the barrier if suitable habitat is available. Barrier-integrated traps remove some of these individuals prior to spawning, but like barriers, the efficacy of a trap for Sea Lamprey control depends on the fraction of the population removed (i.e., exploitation rate) and the number of mature individuals that are left to spawn. Primary challenges in evaluating a trap for Sea Lamprey control are estimating the fraction of a population available for capture at a trap location (i.e., availability), the proportion of those that are caught (i.e., local trap efficiency), and the size of adult population. Understanding availability and trap efficiency are critical to increasing exploitation because they allow comparison of the potential benefits of improving existing traps (to increase efficiency) versus adding traps in new locations (to increase availability; Bravener and McLaughlin 2013).

Traps are also used to obtain mark-recapture estimates of adult abundance and exploitation rates; these estimates serve as the basis for lake-wide adult population estimates (Mullet et al. 2003). Within tributaries, adult Sea Lamprey abundance has been estimated using a mark-recapture method in which trap-caught lampreys are marked and released downstream for recapture in the same trap (or set of traps). Abundance has been estimated using a modification of Schaefer's (1951) mark-recapture model (Mullet et al. 2003), which requires the assumption that marked and unmarked individuals are equally-likely to be captured in the second sample (Pollock et al. 1990). Potential violation of the "equal catchability" assumption is a critical uncertainty in trap operations because it could bias estimates of trap efficiency and exploitation. Finally, these abundance estimates may not be indicative of entire river populations because the marked lampreys are released at a single location near each barrier.

My goal was to evaluate a Sea Lamprey trap and barrier complex in the Cheboygan River (Figure 1.1) using a multi-state capture-recapture model with observations from acoustic telemetry and traps. Recent advances in telemetry (Hockersmith and Beeman 2012; Cooke et al. 2014) and capture-recapture modeling (Perry et al. 2012; Royle et al. 2014) have allowed estimation of population-level fish movement probabilities (e.g., passage, survival, collection, and space use) while accounting for observation error (i.e., imperfect detection; Skalski et al. 2009; Buchanan and Skalski 2010; Perry et al. 2010; Holbrook et al. 2011; Raabe et al. 2013). Although models of this class have been most commonly fit using maximum likelihood estimation (Perry et al. 2012), I used a Bayesian state-space model (BSSM) fit to the data using Markov Chain Monte Carlo (MCMC) simulation (Giminez et al. 2007; Calvert et al. 2009). Bayesian methods have recently become popular in ecology (see Buckland et al. 2004; King et al. 2010; Kery and Schaub 2012) because they allow incorporation of information beyond the data (e.g., prior knowledge), facilitate estimation of the marginal distribution of higher-level parameters in hierarchical models, and do not require asymptotic (i.e., large sample) assumptions (Brooks et al. 2000; Ellison 2004; Kery 2010). State-space models provide a flexible and intuitive framework for building and fitting complex models because they explicitly separate ecological processes (e.g., movement, mortality) from sampling or observation processes (e.g., detection, capture; Buckland et al. 2004; Giminez et al. 2007; Calvert et al. 2009). Specifically, the model used individual movement data derived from acoustic telemetry and trapping to estimate reach-specific fish movement probabilities (including dam passage and trap capture probabilities) and to describe the spatial distribution and abundance of adult Sea Lampreys above and below the barrier during riverine spawning migration.

The Cheboygan River, MI, a tributary to Lake Huron, has consistently experienced some of the largest catches of adult Sea Lampreys in the Great Lakes. Despite a seemingly impassable barrier (consisting of a powerhouse, vessel passage lock, and separate spillway) near the river mouth (Figure 1.1A), the watershed above the lock and dam has remained infested with Sea Lampreys and has been treated with lampricide every three years at a cost ranging from $400,000 to $600,000 USD. Although some evidence also exists that lakes in the upper Cheboygan River system support a landlocked population of Sea Lampreys upstream of the lock and dam (Applegate 1950), it is not known what fraction of the lower river population passes into the upper river, how many individuals escape above the dam, or which routes (e.g., vessel lock, turbine units, spill gates), if any, are used for upstream passage. Further, exploitation rate estimates for the Cheboygan River trap may be biased because marked lampreys are released in the spill basin, so abundance estimates may not have included lampreys that ceased migration farther downstream or passed upstream through the powerhouse or lock before reaching the spill basin.

To address these uncertainties, I estimated (1) the proportion of the population that passed the dam (i.e., upstream escapement rate); (2) the number of individuals that passed the dam (i.e., escapement); (3) the proportion of the lower river spawning population that was available to the trap (i.e., proportion that reached the spill basin near the trap); (4) local trap efficiency (i.e., number of lamprey caught as a proportion of those present in the spill basin); and (5) the exploitation rate due to trapping. My objectives addressed questions critical for understanding effectiveness of barriers and traps to control Sea Lamprey and for predicting benefits of control strategies that are alternative to lampricides. The approach used in this study was also a novel application of BSSMs that may have broader applications, including evaluation of barriers for other invasive species (e.g., Asian carp (*Hypophthalmichthys spp.*)) and fish passage structures for other diadromous fishes (e.g., Pacific salmon (*Oncorhynchus spp*.), American Eel (*Anguilla rostrata*)).

Methods

Sea Lamprey tagging and release

Acoustic-tagged adult Sea Lampreys (N=148) were released into the lower Cheboygan River during spring 2011. Sea Lampreys for tag implantation were collected from Carp Lake Outlet, a nearby tributary to Lake Michigan, and were 405-576 mm in length (median 491 mm) and weighed 150-381 g (median 240 g). The Sea Lamprey trap in Carp Lake Outlet was located about 500 m from the stream mouth, so Sea Lampreys captured in the trap were early in their migration and usually not sexually mature. Acoustic tags (model V8-4L; Vemco, Halifax, Nova Scotia, Canada) were 8 x 21 mm (diameter x length), weighed 2.0 g in air (0.9 g in water), had an expected minimum tag life of 84 d, and were programmed to transmit a uniquely encoded signal with a power level of 146 dB (re 1 μPa at 1 m) every 15-45 s for 4 d and then every 30-90 s for 80 d. Prior to surgery, each lamprey was anesthetized by immersion in 0.2 $ml \cdot L^{-1}$ clove-oil solution. Tags were surgically implanted through a 2-cm ventral incision near the midpoint between the posterior gill pore and the anterior dorsal fin. Each incision was closed with two interrupted surgeon knots using a size 3-0 polydioxanone monofilament suture (PDSII, Ethicon) and glue (Vetbond, 3M) was applied to each knot. Sea Lampreys were allowed to recover in an aerated tank for at least 48 h prior to release. Every 1-2 days between May 5 and June 13, 2011, four tagged Sea Lampreys (two male, two female) were placed in a holding cage in the Cheboygan River about 1.3 km upstream from Lake Huron and about 1.2 km downstream of the lock and dam. The cage door was opened at dusk for volitional release during the night.

Acoustic telemetry receivers

A network of 21 autonomous acoustic telemetry receivers (VR2W; Vemco) recorded a time-stamped movement history for each tagged fish during upstream migration (Figure 1.1A). Receivers were placed at locations to document approach to the lock and dam (5 receivers at site 2A), presence near the trap (5 receivers at site 3B) and escapement upstream of the dam (5 receivers each at sites 3A and 4A; one receiver at site 5A). Several receivers were placed at some sites for redundancy and for determination of routes used to pass the dam. Sentinel transmitters (model V13-1L and model V13T-1L; output power 147 dB and 150 dB respectively; Vemco) were also placed in the river above (sites 2A, 3B; V13-1L) and below the barrier (sites 3A, 4A; V13T-1L) to evaluate receiver performance.

Trap catch data

The Sea Lamprey trap (site 4B; Figure 1.1A) at the Cheboygan Lock and Dam was operated once daily by the U.S. Fish and Wildlife Service between April 17 and June 18, 2011. The trap, a mesh box with two funnel entrances leading to holding cages, was attached to the face of the dam below the spill gates so that attractant water flowed through each holding cage. Each Sea Lamprey collected was scanned for presence of an acoustic tag using a metal detector

(R-8000 tunnel detector; Northwest Marine Technology Inc., Shaw Island, Washington, USA) designed for detecting coded-wire tags and visually inspected for evidence of tagging (i.e., incision or sutures). All acoustic tags were removed and implanted into another Sea Lamprey for release downstream. The elapsed time between release and recovery ranged 1 – 35 d (median 9 d) among recovered lampreys and all tags were still pinging when recovered.

Data analysis

Parameter estimates were obtained with a three-step process. First, a BSSM was used to estimate probabilities of movement among river reaches and into the trap while accounting for site-specific probabilities of detection. Second, spatial distribution of the spawning population (i.e., fraction of the population that reached each sampling location) was estimated as a function of individual movement probabilities among reaches. Third, the number of untagged lampreys caught in the trap was expanded by spatial distribution estimates to estimate abundance at each telemetry station and release location.

Estimating movement probabilities

The BSSM included transition parameters that represented probabilities of upstream movement among contiguous river reaches (delineated by telemetry receivers) and trap capture (Figure 1.1B). Each river channel was considered a separate state in the model. For example, state A was assigned to the main river channel that extended from the mouth through the vessel passage lock and into the upper river. State B was assigned to the route that extended around the island toward the spillway outfall and trap, so a fish could only have entered the trap after moving from state A to state B. Although the trap could have been assigned a separate state, I treated the trap as the last monitoring site in state B. Finally, state C represented cessation of upstream migration (e.g., due to death, spawning, or fallback) within a reach.

A tagged fish that entered any river reach could have either ceased migration within that reach, continued migration upstream, or have been captured in the trap. Each of those processes was estimated as a transition probability. Transition probabilities ($\varphi_{t,h,k}$) estimated the probability that a fish moved from state h at the t^{th} upstream site (t=1 at the release site and increments at each telemetry station or trap upstream) to state k at t+1. In most cases, transition probabilities were considered movement probabilities and estimated the probability that a fish moved between any two sites. Alternatively, transition probabilities represented trap capture probabilities (i.e., $\varphi_{3,B,B}$ was the probability that a fish moved from the river at site 3B into the trap at site 4B) or dam passage probabilities (i.e., $\varphi_{2,A,A}$ was the probability that a fish moved from site 2A below the dam to 3A above the dam).

Simply calculating the proportion of all fish that were detected at each location would not provide unbiased estimates of fish distribution because a tagged fish may have passed a telemetry receiver undetected. Therefore, the model included detection probabilities to prevent biased transition probability estimates caused by observation error. Detection probabilities ($p_{t,h}$) estimated the probability that a tagged fish was detected in state h at the t^{th} site, given that the fish reached that site.

The BSSM was a modification of models presented by Giminez et al. (2007) and Calvert et al. (2009) and was fit to data using MCMC (Gibbs sampling) with the software program WinBUGS (Spiegelhalter et al. 2003; Giminez et al. 2009; Ntzoufras 2009) using the R package R2WinBUGS (Sturtz et al. 2005; R Development Core Team 2012). Input data were matrices $w_{\mathrm{i,t}}$ and $z_{\mathrm{i,t}}$: $w_{\mathrm{i,t}}$ were the data that indicated that individual i was either observed ($w_{\mathrm{i,t}}$ =1) or not observed ($w_{\mathrm{i,t}}$ =0) at the t^{th} site; $z_{i,t}$ was the partially-observable state matrix that provided the true state of individual i at the t^{th} site. The true state was known where an individual was observed, but was inferred where an individual was not observed. For example, corresponding rows $\mathrm{z}_{i,\cdot}$ = [A A 0 B 0] and $\mathrm{w}_{i,\cdot}$ = [1 1 0 1 0] represented a fish that was released in state A, detected again in state A at t=2 (i.e., first telemetry station upstream from release), not detected in any state at t=3 (i.e., true state was unknown), caught in the trap at t=4, and not detected at t=5. Each row z_i described the encounter history of a single lamprey, analogous to the encounter histories (often called capture histories) of time-based capture-recapture models. However, the encounter histories used in this model were spatial rather than temporal.

Posterior distributions of parameters were estimated by simulating draws from the joint posterior probability distribution

(1) $\pi(\varphi, p \mid z, w) \propto \pi(z, w \mid \varphi, p)\,\pi(\varphi)\,\pi(p)$.

Thus, posterior probabilities ($\pi(\varphi, p \mid z, w)$) of the parameters were proportional to the product of the likelihood of the data given the parameters ($\pi(z, w \mid \varphi, p)$) and the prior probabilities of movement ($\pi(\varphi)$) and detection ($\pi(p)$). The median and mode of the posterior distribution of each parameter were used as measures of central tendency. Uncertainty was quantified using credible intervals calculated by determining the smallest interval for each parameter that contained 95% of posterior samples. These highest posterior density (HPD) intervals (Gelman et al. 2003; King et al. 2010) do not require distributional assumptions, incorporate all uncertainty regarding information of other parameters, and were especially convenient in this study because the shape of posterior distributions varied among parameters. HPD intervals were calculated using the HPDinterval function in the R package coda (Plummer et al. 2006).

The full likelihood,

(2) $\pi(z, w \mid \varphi, p) = \prod_{i=1}^{N} \prod_{t=2}^{T} (\pi(\mathrm{z}_{i,t} \mid \mathrm{z}_{i,t-1}, \varphi_{t-1,j,k})\pi(w_{i,t} \mid z_{i,t}, p_{t,k}))$

included a process likelihood (i.e. the probability of each state $z_{i,t}$ given the previous state $z_{i,t-1}$ and the probability of transitioning between those states, $\varphi_{t-1,h,k}$) and an observation likelihood (i.e., the probability that an individual was observed ($w_{i,t}$) in state $z_{i,t}$ given that it was present at that site and that the detection probability at that site was $p_{t,k}$), where $h=z_{i,t-1}$, $k=z_{i,t}$, N was the number of tagged lamprey released, and T was the number of encounter occasions, including release.

Process likelihood.—The true state $z_{i,t}$ was considered a categorical variable with probabilities:

$$(3)\quad \pi(z_{i,t}=k \mid z_{i,t-1}=h)=\left\{\begin{array}{ccc} \varphi_{t-1,h,k} & h=\mathrm{A,B}; & k=\mathrm{A,B,C} \\ 0 & h=\mathrm{C}; & k=\mathrm{A,B} \\ 1 & h=\mathrm{C}; & k=\mathrm{C} \end{array}\right\}$$

For example, after release, a fish may have moved from state A to state k with probability $\varphi_{1,A,k}$. Note that if a fish had ceased migration (h=C), it must have remained in the non-migratory state ($\varphi_{t,C,C} = 1$), so could not later have been observed in any other state. Similarly, a fish could not have been observed in another state after being caught in the trap. The general form of the process likelihood (Eq. 3) was further modified because some transitions could not have occurred given the structure of the study system. For example, $\varphi_{1,A,B} = 0$ because a fish could not have moved directly from release to the trapped state (Figure 1.1B). Further, I assumed that upstream passage through spill gates was impossible ($\varphi_{3,B,A} = 0$). By applying these constraints, I assumed perfect prior knowledge about these parameters. Consequently, four transition parameters were estimated by the model. Only one transition ($\varphi_{2,A,k}$) remained multinomial because the river split within that reach, allowing two possible migratory states (one for each pathway) and a third possible non-migratory state. Other transition parameters became binomial because they represented movement through single, unbranched river reaches with only two possible underlying states (i.e., migratory and non-migratory). For binomial and multinomial transitions, flat beta and dirichlet prior probability distributions were used, respectively, because no prior information was available about those parameters and because they are proper conjugate distributions for binomial and multinomial distributions (Gelman et al. 2003).

Observation likelihood.—The observation of each tagged fish at each site was considered a Bernoulli random variable arising from the binominal detection probability $p_{t,k}$ and was conditional on presence at that location:

$$(4)\quad \pi(w_{i,t}=1 \mid z_{i,t}=k) = \begin{Bmatrix} p_{t,k} & k = \mathrm{A,B} \\ 0 & k = \mathrm{C} \end{Bmatrix}$$

Therefore, each fish was only observable in states A and B and never observable in state C. Further constraints were applied based on the structure of the study system and availability of data. For example, I set $p_{1,B} = 0$ because site 1B did not exist and $p_{4,B} = 1$ because all acoustic-tagged fish were assumed to be identified by trap personnel using a metal detector that was designed to detect much smaller coded-wire tags.

Detection probabilities were not estimable without some detection information farther upstream. Therefore, under the general model, detection and transition parameters were confounded at sites 4B and 5A, so only $\lambda_{4,B} = \varphi_{3,B,B}p_{4,B}$ and $\lambda_{5,A} = \varphi_{4,A,A}p_{5,A}$, the joint probabilities of moving and being detected, were estimable at those locations. However, I was able to estimate $\varphi_{3,B,B}$ (i.e. trap capture probability) because I assumed $p_{4,B} = 1$. Similarly, no fish were detected above the dam (see Results), but I was able to estimate $\varphi_{2,A,A}$ (i.e., dam passage probability) because I assumed $p_{3,A} = 1$based on auxiliary data (i.e. sentinel tag detections). After these constraints were applied, only two detection probabilities ($p_{2,A}$ and $p_{3,B}$) were estimable. Flat beta prior distributions (i.e., beta(1,1)) were assumed for $p_{2,A}$ and $p_{3,B}$ because no prior information was available and because the beta distribution is a proper conjugate distribution for binomial and Bernoulli distributions.

MCMC convergence diagnostics.—Inferences were based on 10 000 posterior samples for each parameter. I discarded the first 10 000 samples (i.e., burn-in) from an initial chain of 110 000, and then retained every tenth sample (i.e. thinning) from the remaining chain. Burn-in was determined from three short chains using Gelman and Rubin's (1992) potential scale reduction factor (i.e., shrink factor). Total chain length and thinning interval were determined using methods described by Raftery and Lewis (1992). Convergence was confirmed by examining autocorrelation, trace, and posterior density plots for each parameter, including the deviance (Appendix A).

Assessing prior sensitivity.—To determine if inferences were sensitive to assumptions of perfect prior information about $p_{3,A}$ and $p_{4,B}$, I compared results from the BSSM to results obtained using two alternative prior probability distributions for each of those parameters (Appendix B). For each parameter, a "less informative" prior probability distribution was chosen to represent hypothetical, but conservative, information that could have been obtained if auxiliary field tests had been conducted during the study. A flat prior probability distribution was also chosen to determine how inferences would have changed if no prior information had existed about $p_{3,A}$ and $p_{4,B}$.

Assessing model fit.—To assess fit of the model to data, the observed frequency of each unique encounter history was compared to the distribution of frequencies predicted by the model. The predicted frequency of each encounter history was calculated from parameter estimates and compared to the corresponding observed frequency at each MCMC iteration. A posterior predictive p-value was calculated for each encounter history as the proportion of expected frequencies that were greater than the observed frequency, plus one half of the expected frequencies that were equal to the observed frequency. A predictive p-value of 0.5 was considered evidence that the parameter estimates provided by the model were a perfect fit to the data and fit was considered to decline as the p-value approached 0 and 1.

Inferring the spatial distribution of the population

The proportion of the stream spawning population that reached ($\Phi_{t,k}$) the t^{th} monitoring site in state k was estimated as a function of all possible transition probabilities that traced all possible routes leading up to that site. Some spatial distribution parameters were further defined in a management context (i.e., availability, exploitation, and escapement probabilities). Availability to the trap was defined as the fraction of the population present in the spillway outfall at site 3B and was estimated as $\Phi_{3,B} = \varphi_{1,A,A}\, \varphi_{2,A,B}$. The exploitation rate was defined as the fraction of the population harvested in the trap at site 4B and was estimated as $\Phi_{4,B} = \varphi_{1,A,A}\, \varphi_{2,A,B}\, \varphi_{3,B,B}$. The escapement rate was defined as the fraction of the population present above the barrier at site 3A and was estimated as $\Phi_{3,A} = \varphi_{1,A,A}\, \varphi_{2,A,A}$. A posterior probability distribution was obtained for each derived parameter by calculating the value of each parameter for each MCMC iteration and then summarized as described for transition and detection parameters.

Estimating abundance at release, receiver, and trap locations

Adult Sea Lamprey abundance was estimated at each sample location (i.e., release site and telemetry station) using a modification of the Peterson estimator (Seber 1982):

$$(5)\quad \hat{N}_{t,k} = \frac{c\Phi_{t,k}}{\Phi_{4,\mathrm{B}}}$$

where $\Phi_{t,k}$ was the fraction of the population present at site tk, c is the number of unmarked lamprey caught in the trap, and $\Phi_{4,B}$ was the fraction of the population caught in the trap. All potential spawners were assumed to have passed the release site (i.e., $\Phi_{1,A} = 1$) because no spawning habitat was known between the river mouth and release site. Therefore, $N_{1,A}$ was defined as the total population size and $N_{3,A}$ as the number of Sea Lampreys that passed upstream of the barrier (i.e., escapement).

Model assumptions.— Model assumptions included: (1) All tags were correctly identified, no tags were lost, and no tags failed during the study period; (2) Tagged and untagged lampreys had equal transition (i.e., movement, dam passage) and trap capture probabilities; (3) At each sampling location, every tagged lamprey had the same probability of detection and transition; and (4) For each tagged lamprey, detection and transition probabilities were independent among sampling locations. Violation of Assumption 1 would result in biased transition probability estimates because incorrect tag identification, tag loss, or premature tag failure (e.g., battery failure during the study) would be incorrectly interpreted as cessation of upstream migration. I assumed that such violations were rare because all recovered tags were functional and because no tag loss was observed from recoveries of Sea Lampreys that were double-tagged with acoustic and coded-wire tags (CMH, unpublished data). Assumption 2 could have been violated if tagged lampreys were not a representative sample of the untagged population in this study, or if fate of tagged fish was affected by tagging. For this study, Sea Lampreys were purposely collected from a source outside of the study stream so that tagged fish were “naïve” to the study system to reduce the likelihood of bias caused by previous experience or capture heterogeneity (Pollock et al 1990). Use of animals captured in other streams should not have affected their migration patterns because Sea Lampreys do not home to natal streams (Bergstedt and Seelye 1995). Although I did not expect tagging to affect behavior, timing of releases may not have matched timing of migration through the lower Cheboygan River. The implications of this assumption were further explored by testing the hypothesis that trap capture probability was related to release date. Assumptions 3 and 4 could have been violated if detection, movement, or trap capture probabilities varied among individuals (e.g., due to differences in sex, weight, or maturity) or over time (e.g., due to changes discharge or water temperature). Violations of assumptions 3 and 4 were expected to be evident as lack of fit in posterior predictive checks (see *Assessing model fit*).

Testing the assumption of constant capture probability

To test the hypothesis that the probability of trap capture was constant during the trapping season, I modified the likelihood to define $\varphi_{3,B,B}$ as a function of release date. Specifically, the logit link function (logistic regression) was used to estimate $logit(\varphi_{3,B,B,i})$ as a linear combination of parameters β_1 (intercept), β_2 (slope) and release date (e.g. $logit(\varphi_{3,B,B,i}) = \beta_1 + \beta_2 x_i$), where x_i and $\varphi_{3,B,B,i}$ represented release date and trap capture probability for the i^{th} tagged fish. I used a normal distribution with mean of 0 and variance of 2.72 (i.e., precision = 0.368) as prior probability distributions for β_1 and β_2 because that distribution is essentially flat on the logit scale (see Lunn et al. 2012). Posterior samples were obtained using MCMC simulation as described above. Estimates of $\varphi_{3,B,B}$ for a specific release date were back-calculated using the inverse logit function. To test the hypothesis that $\varphi_{3,B,B}$ was constant over time, I calculated the proportion of posterior samples where $\beta_2 < 0$ (i.e., decreasing over time) and, separately, where $\beta_2 > 0$ (i.e., increasing over time).

Results

Assessing model fit

All observed encounter history frequencies were contained in 95% HPD intervals for expected frequencies (Figure 1.2). Observed and expected (posterior median) frequencies differed by less than three fish among all encounter histories and one fish for the most "poorly-predicted" encounter history (Table 1.1).

Movement and detection probabilities

In the lower river, 144 of 148 tagged Sea Lampreys released were detected at telemetry receivers, but no tagged Sea Lampreys were detected at telemetry stations above the dam. Although detection probabilities could not be estimated upstream of the dam, sentinel tag detections indicated that conditions were more favorable for detection at sites upstream of the dam (sites 3A and 4A) than below the dam where detection probability estimates ranged 88-98% (Table 1.2). Of adult Sea Lampreys that entered the river, 94-100% moved upstream to the powerhouse ($\varphi_{1,A,A}$; Table 1.2; Figure 1.3). From the powerhouse tailrace, 0-2% of the population passed the dam into the upper river ($\varphi_{2,A,A}$) and 86-98% approached the spillway outfall containing the trap ($\varphi_{2,A,B}$). Of Sea Lampreys that were present in the spillway outfall, 52-69% were caught in the trap ($\varphi_{3,B,B}$).

Spatial distribution and abundance

The trap caught 13,580 unmarked and 81 acoustic-tagged Sea Lampreys. Based on transition probability estimates, 83-96% (Table 1.3) of the spawning population reached the trap site (i.e., availability, $\Phi_{3,B}$), 46-61% were caught in the trap (i.e., exploitation, $\Phi_{4,B}$), and 0-2% passed upstream through the lock and dam facility (i.e., escapement rate, $\Phi_{3,A}$). Based on spatial distribution estimates, 21,828 to 29,300 Sea Lampreys (95% HPD interval) entered the river from Lake Huron (i.e., passed the release site; $N_{1,A}$) and 0 to 514 passed above the dam ($N_{3,A}$) during 2011. Posterior distributions for derived parameters deviated from normality, especially near the boundaries of the binomial distribution (Figure 1.4).

Testing the assumption of constant capture probability

Trap capture probability decreased during the trapping season (Figure 1.5). I estimated (95% HPD intervals) that β_1 ranged from 0.249 to 1.734 (median = 0.979), β_2 ranged from -0.061 to -0.004 (median = -0.029), 96.0% of β_2 posterior samples were less than zero, and 4.0% of β_2 posterior samples were greater than zero. Back-calculated estimates of the trap capture probability ($\varphi_{3,B,B}$) ranged from 72% (posterior median) for lampreys released at the beginning of the study on 6 May to 46% at the end of the study on 13 June.

Discussion

Implications for Sea Lamprey control and assessment

Evaluating the lock and dam as a Sea Lamprey barrier.— Although the Cheboygan Dam allowed no tagged fish to pass above the barrier, I estimated (based on my sample of 148 tagged lampreys in a population of about 25,000 lampreys) that 0-2% of the untagged population could have escaped upstream above the dam without passage of a single acoustic-tagged lamprey. Although data from this study did not reveal any upstream passage routes at the barrier, I concluded, after further inspection of the powerhouse, spillway, and lock, that the vessel lock would have provided the most plausible route of upstream passage.

To ensure low recruitment in Sea Lamprey populations, Dawson and Jones (2009) recommended that Sea Lamprey control agents should aim for stream-specific spawner abundances less than 0.2 females $\cdot 100\ \mathrm{m}^{-2}$ of larval habitat. Applying that criterion to roughly 425,000 m^2 of preferred larval habitat upstream of the Cheboygan Dam (A. Jubar, United States Fish and Wildlife Service, Ludington, Michigan, personal communication, 2013) yields a target threshold of 1,700 adult Sea Lampreys (assuming equal sex ratio). My best inference (with 95% probability) was that the number of Sea Lampreys passing the dam was between 0 and 514, so I conclude that the Cheboygan Dam was an effective Sea Lamprey barrier under the criterion proposed by Dawson and Jones (2009). Alternatively, an effective Sea Lamprey barrier has been defined by control agents as one that prevents or delays upstream lampricide treatments by limiting passage to a sufficiently small number of individuals. I do not know precisely how many Sea Lampreys would be necessary to colonize the upper river to produce sufficient recruitment to trigger a lampricide treatment, but I reason that my sample size was insufficient to adequately evaluate barrier effectiveness for large populations as in the Cheboygan River. For example, I would have needed to release more than 1,643 tagged lampreys to conclude (with 95% probability) that fewer than 50 tagged lampreys could have passed above the dam when no passage of tagged fish was observed.

Although the estimated Sea Lamprey population escaping upstream of the dam was less than 514, the upper river has required regular lampricide treatment since the 1960s and Sea Lamprey reproduction and recruitment was observed above the dam during the year of this investigation (J. Slade, United States Fish and Wildlife Service, Ludington, Michigan, personal communication, 2013). Evidently, Sea Lamprey are not prone to recruitment failures even when population density is low, consistent with their history of rapid colonization of the Great Lakes (Smith and Tibbles 1980). While the presence of a landlocked Sea Lamprey population above the dam has been supported by accounts from anglers of parasitic lamprey in upstream lakes of the Cheboygan River system and by Applegate (1950), results from this study do not rule out the possibility that spawners from Lake Huron have contributed to recruitment in the upper river. Prior to taking expensive management actions to eliminate possible Sea Lamprey passage at the lock and dam, confirmation of lamprey passage at the lock and additional information on Sea Lamprey ecology and life history in the upper river should be obtained.

Evaluating the Sea Lamprey trap: Availability and exploitation—Results suggest that improved trapping at the current location has greater potential to increase exploitation (46-61% were removed) than installation of traps at new locations because 83-96% of the population ($\Phi_{3,B}$) was availability to existing traps (because they used route B and approached the spillway) while only 52-69% of those were caught ($\varphi_{3,B,B}$). Although results suggest that catch is limited more by trap performance than trap location, previous mark-recapture studies have shown that the Cheboygan River trap is one of the most efficient in the Great Lakes. Good performance has been attributed to the trap being located in a small basin with circular flow pattern below an impassable spillway. Recent studies of Sea Lamprey behavior around similar traps in the St. Marys River have suggested that many lampreys remain close to the river bottom near traps and do not encounter entrances to surface-oriented traps (R. L. McLaughlin, personal communication). Future studies should aim to determine if similar dynamics are limiting efficiency of traps in the Cheboygan River.

Implications of decreasing capture probability on population assessment—Decreasing trap capture probability during the trapping season (Figure 1.5) supports the use of a time-stratified model for adult assessment because lampreys that were released earlier in the season were more likely to be captured than lampreys released later in the season. Interestingly, the non-stratified BSSM and the modified Schaeffer model yielded similar point estimates of trap capture probability (BSSM: 0.60; modified Schaeffer: 0.62) and abundance near the trap site (BSSM: 22 257; modified Schaeffer: 21 986), which suggested that they may have been affected similarly by temporal variation in capture probability. Although my estimate of trap capture probability when $\varphi_{3,B,B}$ was assumed constant (52-69%) and was close to the capture probability for Sea Lamprey released during the middle of the trapping season (Figure 1.5), more accurate estimation of population spatial distribution and abundance may require further assumptions about the timing of river entry. For example, if more Sea Lampreys entered the river early in the season than late in the season, then greater weight would need to be applied to encounter histories of early-released fish. Although declining capture probability may confirm the need for a time-stratified model, it also supports concern that use of a single capture method at a single location may violate the assumption of equal catchability in the abundance estimator. Future research should be directed toward understanding the timing of entry into streams and the relation between trap capture probability and environmental covariates. Such information could guide the development of improved assessment methods.

Advantages, limitations, and challenges of the Bayesian state-space approach

State-space approaches are conceptually well-suited to estimation of reach-specific transition and site-specific detection probabilities from telemetry data because of the conditional nature of fish movement through river systems and the potential for imperfect detection at any site. Indeed, the goodness of fit test showed that observed encounter histories were not improbable under the model (Figure 1.2), suggesting that any violations of assumptions 3 and 4 were small. For example, if tagged lampreys that migrated during high river discharge were less likely to be detected at sites 2A and 3B than lampreys migrating during lower discharge, I might have observed more encounter histories like “A00B0” and fewer encounter histories like “AA0B0” and “A0BB0” than expected under the model. Similar processes likely contributed to minor deviations from perfect fit (Figure 1.2), as expected for any model.

Quantifying uncertainty.—Accurate accounting of uncertainty is a basic element of inference (Royle and Dorazio 2008) and can be especially important in telemetry studies because small sample sizes are common (caused by the high cost of tags) and because telemetry data are often used to evaluate structures or strategies that are considered critical for invasive species control (in this case a barrier for Sea Lamprey control), or native species conservation or restoration. In many applications, individual parameters of a mark-recapture model are of less interest or use than parameters that are estimated as combinations of individual model parameters. In Bayesian models, derived parameters can be calculated for each MCMC iteration to yield a posterior distribution for each parameter that can be summarized using percentiles or HPD regions. In my experience, credible interval construction is easy with MCMC and more intuitive than analogous methods for maximum-likelihood estimates (e.g., Delta method; Seber 1982) that rely on asympototic (e.g., large sample) assumptions.

Accurate estimation of uncertainty can be challenging when an estimate is on the boundary of the binomial distribution (i.e., no successes or failures were observed). This situation has received much more attention in medicine (e.g., for estimating risk of complications after a procedure when none have been observed; Hanley and Lipman-Hand 1983; Eypasch et al. 1995) than in ecology. In such cases, confidence intervals can be approximated with an "exact confidence interval" (Clopper and Pearson 1934) or by the simple "rule of three" (i.e., 3/n, where n is the number of trials; Hanley and Lipman-Hand 1983), but these methods do not allow uncertainty to be included in the model. Bayesian models can accurately characterize uncertainty in these instances by using information from the prior probability distribution in addition to the likelihood function. For example, the BSSM produced a posterior distribution for dam passage with a nominal estimate (posterior mode) matching the observed proportion (e.g., $\varphi_{2,A,A} = 0.00$) and a 95% HPD interval (0.00-0.02) representing uncertainty due to my sample size. These results are similar to those that could have been obtained with profile likelihood confidence intervals if I had fit the model using maximum likelihood estimation.

Sensitivity to prior distributions.—Prior probability distributions were used for three purposes in this study. First, I used priors to apply structural constraints when transition or detection was physically impossible. Second, “flat” priors were used when I had no prior information about the value of a parameter (i.e., all values within the parameter space were equally plausible a priori). Use of a flat prior is not free of criticism because it implies that all values within the parameter space were equally plausible a priori. This was my choice, however, due to lack of better information. Third, I used priors to specify assumptions needed to estimate parameters that were confounded with other parameters. Based on conservative estimates, inferences would not have changed if I had used “less informative” priors, such as those that might have been obtained from auxiliary field tests, for the probabilities of detection in the trap and upstream of the dam (Appendix B). Use of a flat prior for the probability of detection upstream of the dam would have increased uncertainty about the proportion of the population that passed the dam and the number of individuals that escaped upstream, but would not have affected any other parameter estimate. Use of a flat prior for probability of detection in the trap would have produced a larger estimate of trap efficiency and smaller estimate of abundance, but the trend still would have suggested, albeit with greater uncertainty, that catch was limited by trap efficiency more than location. Although Bayesian models are often criticized for use of subjective prior distributions (Efron 1986; Dennis 1996), I view prior distributions as valuable tools that provide formal mechanisms to specify and test assumptions.

Despite many perceived advantages, several limitations and challenges may prevent widespread use of Bayesian state-space models for fish movement analysis. First, more user-friendly software applications may be needed for wide-spread adoption of Bayesian approaches. The recent addition of Bayesian estimation to the popular software program MARK (White et al.

2006) is one example. Second, I am not aware of any widely accepted model selection procedures for Bayesian state-space models (see Kery and Schaub 2012), although one might emerge from recent progress on Bayesian variable selection methods (O'Hara and Sillanpaa 2009; King et al. 2010). Finally, although the unidirectional (e.g., upstream-only) structure of the model in this study was useful for estimating upstream passage probabilities, a model that allows for movement in both directions could be useful or needed in future fish passage evaluations. For example, if any lampreys had passed upstream of the dam, then I would have desired an estimate of the proportion of those that later "fell back" over the dam. The need for such models may not be limited to measuring fallback over dams (see Frank et al. 2009), but could also be used to identify locations where migrants show reversals or other behavioral changes that could increase exposure to predators or other risks. To some degree, I suspect that the tendency to use unidirectional models in fish passage studies (Skalski et al. 2009; Perry et al. 2010; Holbrook et al. 2011) can be attributed to the historical use of capture-recapture models to estimate demographic parameters through time (Arnason 1972; Seber 1982; Lebreton et al. 1992; Brownie et al. 1993) rather than space. A primary difference between time-based models and space-based models is that movement through time is unidirectional, and therefore conditional, but movement through space may be unconstrained. A primary challenge in developing multi-state capture recapture models that allow for reversals is state-specific estimation of detection probabilities. Promising new approaches have recently emerged (Buchanan and Skalski 2010; Raabe et al. 2013) but there remains a need to better define and distinguish spatial capture recapture models (in this case discrete-space) from their time-based analogs (see Royle et al. 2014).

APPENDICES

APPENDIX 1A

Main Tables and Figures

Table 1.1.— Observed encounter history frequencies from detections of tagged Sea Lampreys in the Cheboygan River during 2011, with expected frequencies (posterior median) predicted from the Bayesian state-space model and the proportion of posterior expected frequencies that were more extreme than the observed frequency (P-value).

Encounter History	Observed Frequency	Expected Frequency	P-value
A0000	4	5	0.625
A00B0	1	0	0.025
A0A00	0	0	0.500
A0B00	0	1	0.914
A0BB0	1	1	0.708
AA000	16	16	0.535
AA0B0	8	9	0.651
AAA00	0	1	0.794
AAB00	47	45	0.355
AABB0	71	68	0.312

Table 1.2.— Transition and detection probability estimates (posterior mode and median) with 95% highest posterior density intervals (HPDI) for Sea Lampreys in the Cheboygan River during 2011 (see Figure 1.1).

Parameter	Posterior Mode	Posterior Median	95% HPDI
$\varphi_{1,A,A}$	0.978	0.971	0.940-0.995
$\varphi_{1,A,C} = 1 - \varphi_{1,A,A}$	0.022	0.029	0.008-0.065
$\varphi_{2,A,A}$	0.001	0.005	0.000-0.020
$\varphi_{2,A,B}$	0.919	0.920	0.857-0.982
$\varphi_{2,A,C} = 1 - \varphi_{2,A,A} - \varphi_{2,A,B}$	0.073	0.073	0.013-0.135
$\varphi_{3,B,B}$	0.602	0.602	0.516-0.685
$\varphi_{3,B,C} = 1 - \varphi_{3,B,B}$	0.398	0.398	0.316-0.486
$p_{2,A}$	0.983	0.979	0.951-0.998
$p_{3,B}$	0.884	0.883	0.811-0.944

Table 1.3.— Estimates (posterior median with 95% highest posterior density intervals, HPDI, in parentheses) of adult Sea Lamprey abundance ($N_{t,k}$) and proportion of the population ($\Phi_{t,k}$) that reached each acoustic monitoring site in the Cheboygan River during 2011 (see Fig. 1).

[1] No HPDI is available because I assumed $\Phi_{1,A}=1$ (i.e., all individuals in the population passed the release site).

[2] $N_{4,B}$ is the number of unmarked Sea Lampreys caught in the trap.

Site (*tk*)	$\Phi_{t,k}$	$N_{t,k}$
1A	1.000 [1]	24,958 (21,828, 29,299)
2A	0.978 (0.940-0.995)	24,331 (21,250, 28,375)
3A	0.001 (0.000-0.020)	34 (0, 514)
3B	0.891 (0.826-0.956)	22,257 (19,698, 26,166)
4B	0.542 (0.457-0.613)	13,580[2]

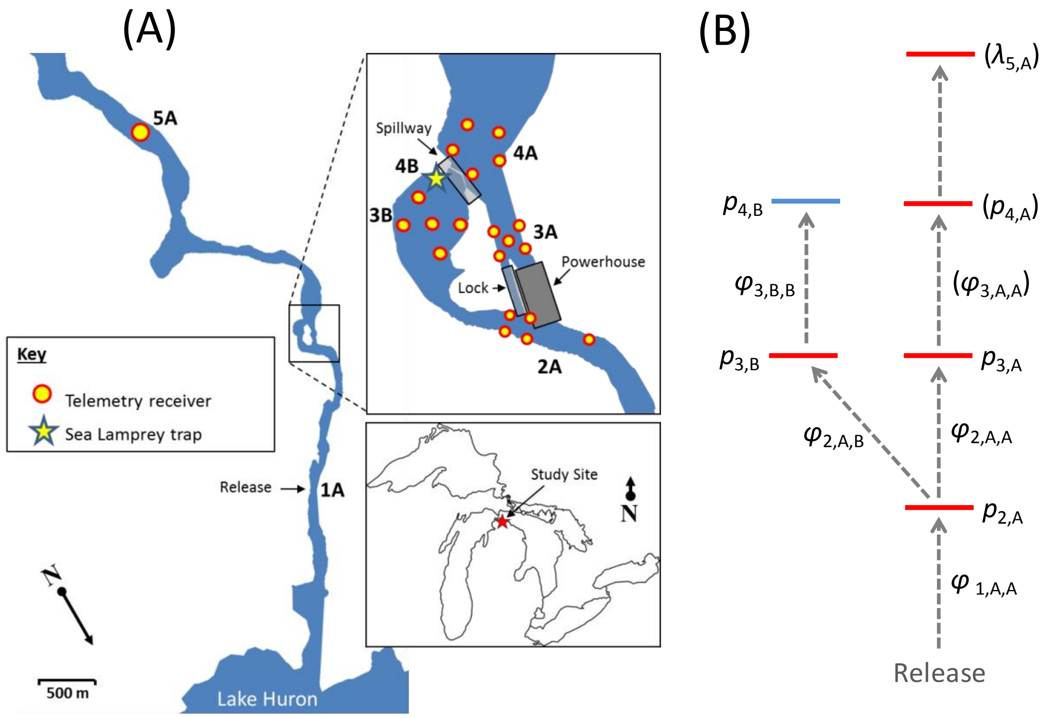

Figure 1.1.—Schematics of (A) the lower Cheboygan River (bottom inset shows general location of study site in the Great Lakes Basin) with telemetry receiver, Sea Lamprey release, and adult Sea Lamprey trapping sites; and (B) multi-state mark-recapture model used to estimate transition ($\varphi_{t-1,h,k}$) and detection ($p_{t,k}$) probabilities for acoustic-tagged Sea Lamprey during 2011. Parameters in parentheses were not estimated due to insufficient data.

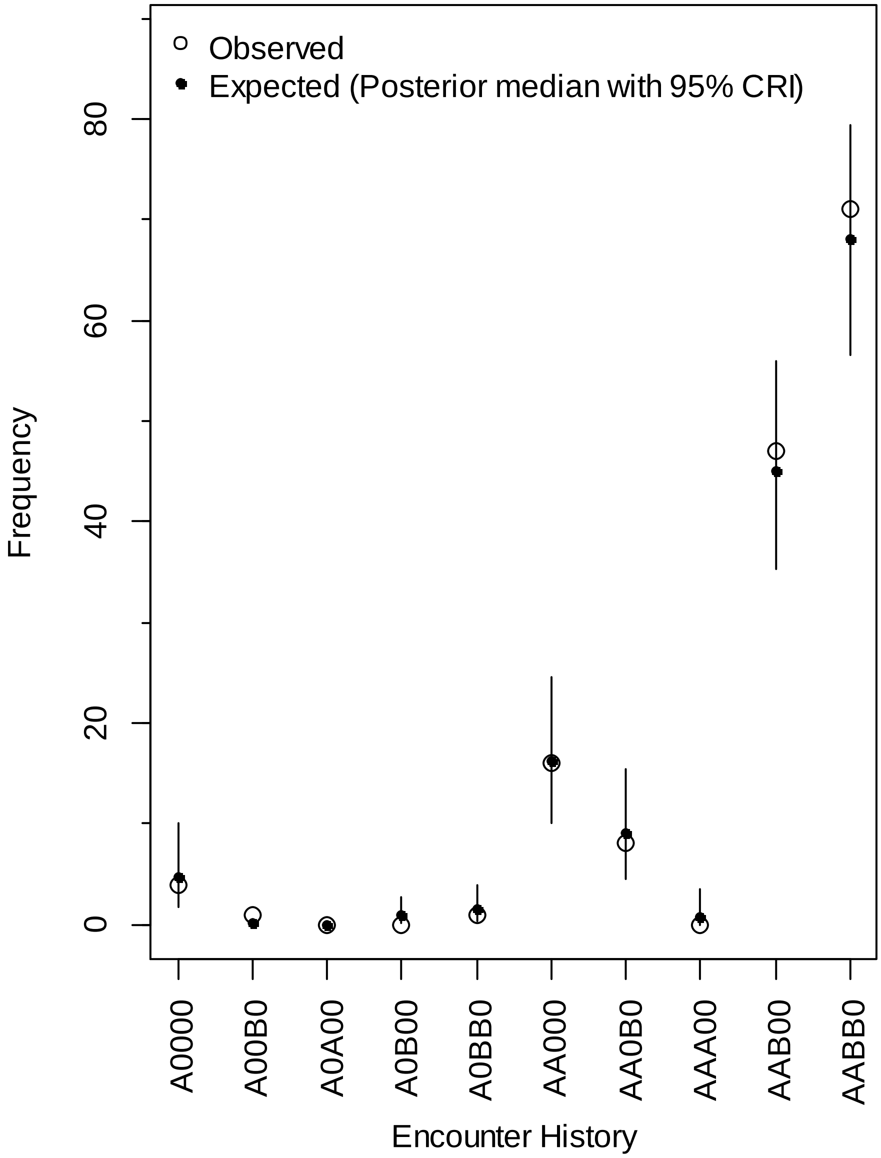

Figure 1.2.—Observed frequencies of unique encounter histories against expected frequencies (posterior median) under the Bayesian state-space model.

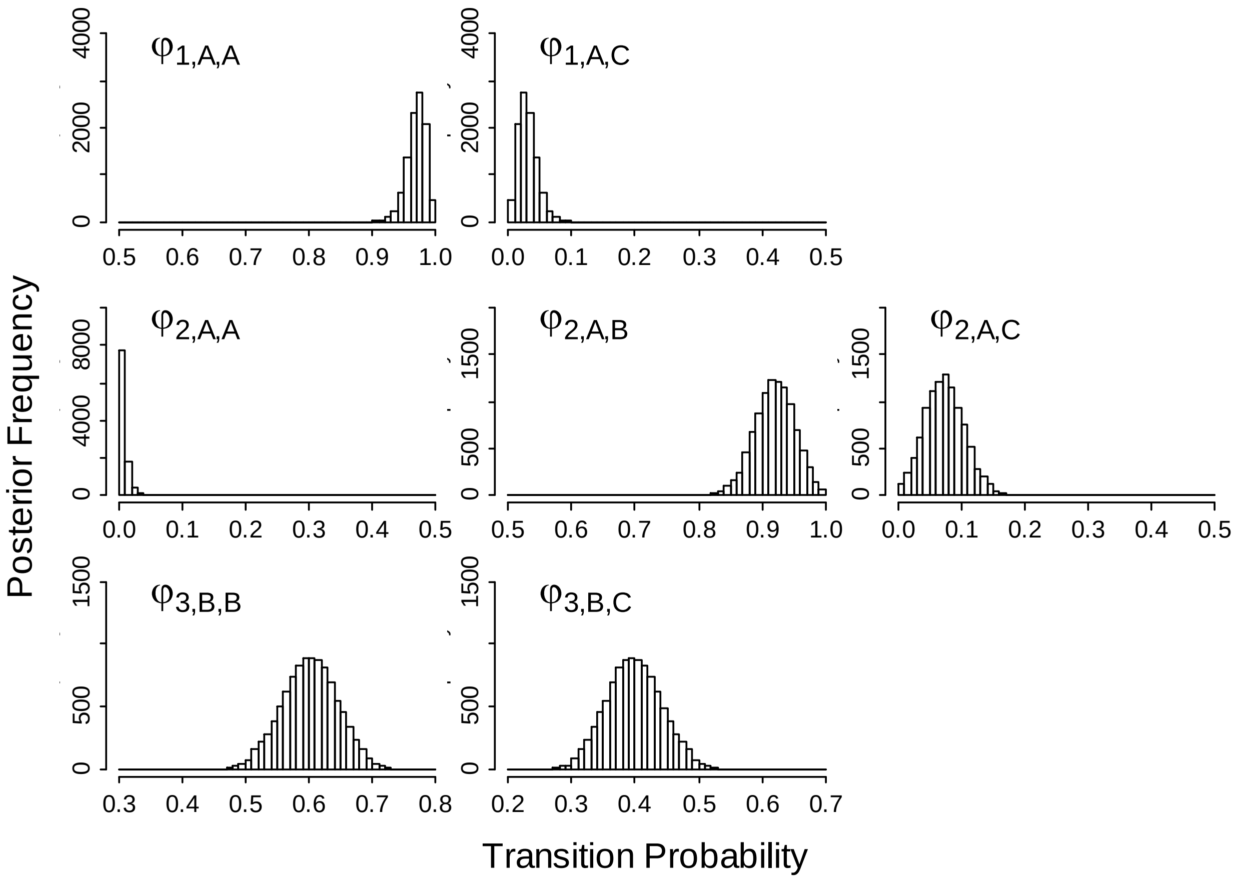

Figure 1.3.—Posterior distributions of transition parameters (see Figure 1.1) representing movement, dam passage, and trap capture probabilities for acoustic-tagged Sea Lampreys in the lower Cheboygan River.

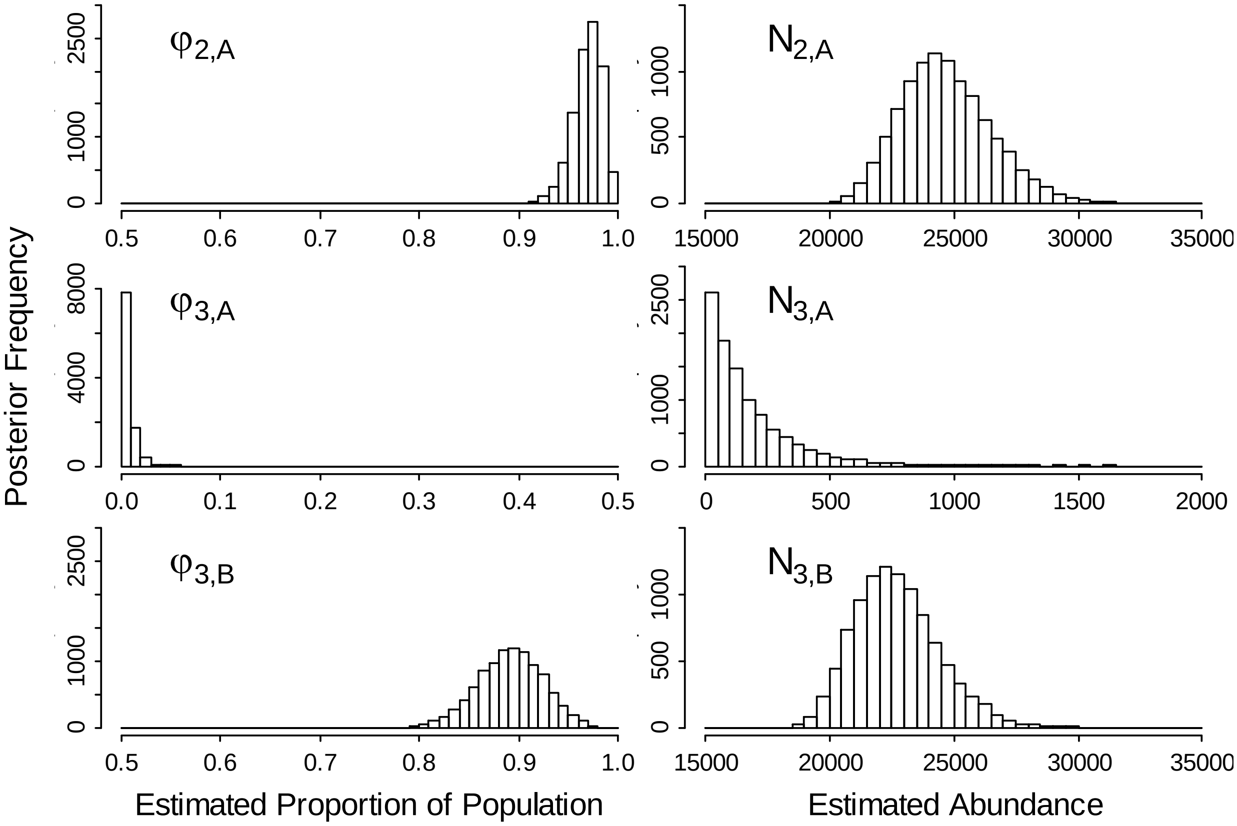

Figure 1.4.—Posterior distributions of derived parameters representing the estimated population proportions and abundances of Sea Lampreys at sites 2A (top panels); 3A (middle panels); and 3B (bottom panels) in the lower Cheboygan River (Figure 1.1).

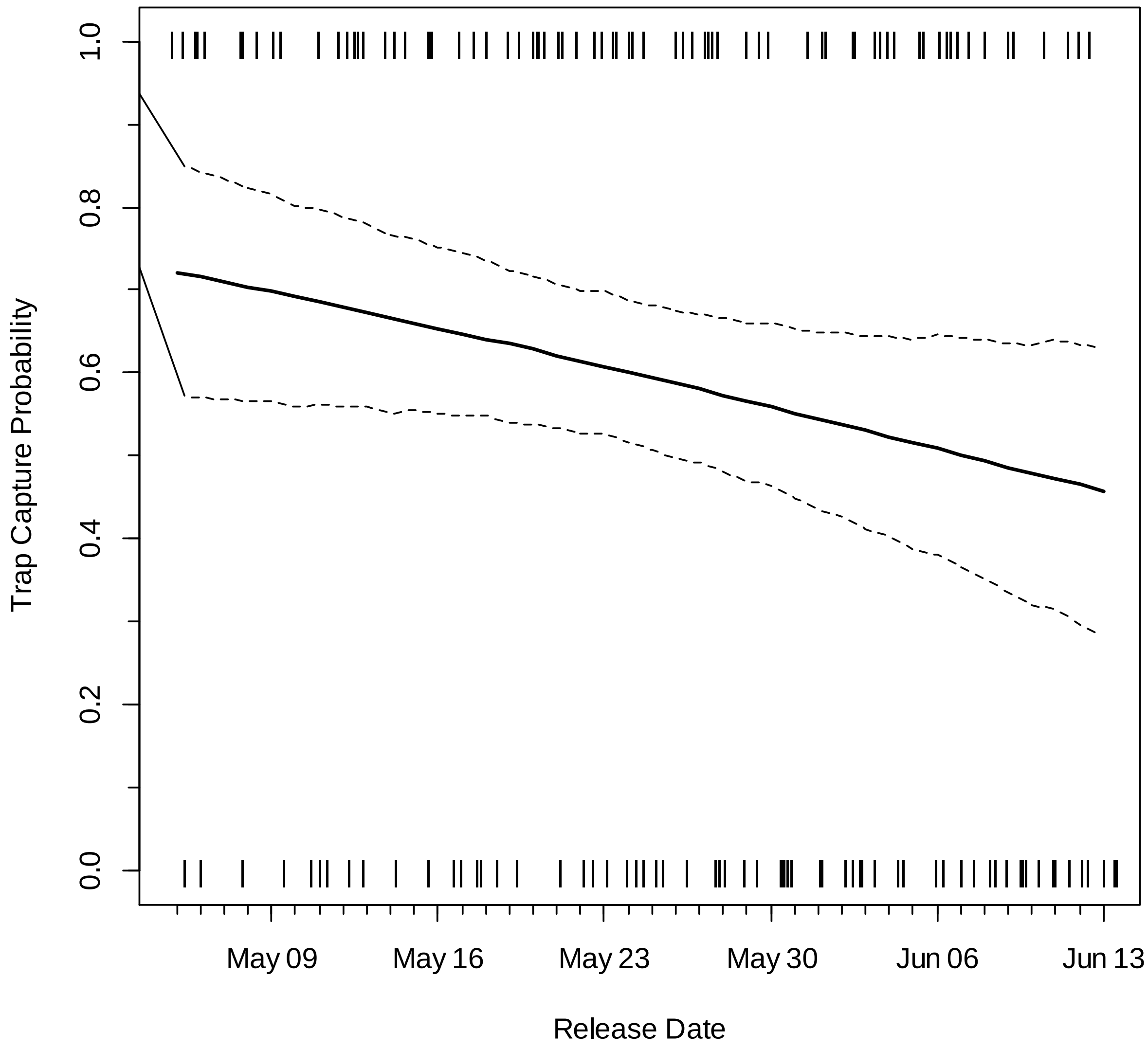

Figure 1.5.—Estimated trap capture probability as a function of release date for acoustic-tagged Sea Lamprey in the Cheboygan River, 2011. The solid line shows fitted values based on posterior median fitted values and broken lines represent 95% credible intervals. Ticks (with random horizontal jitter to prevent overlap; < 0.5 d) show the distribution of the data (0 = never caught in trap; 1 = caught in trap).

APPENDIX 1B

Convergence Diagnostics

Appendix 1B.—Methods used to determine burn-in, chain length, thinning interval, and confirm convergence for the Bayesian state-space model used to estimate movement, trap capture, dam passage, and detection probabilities of Sea Lampreys in the Cheboygan River, 2011.

I used the potential scale reduction factor (i.e., shrink factor; Gelman and Rubin 1992; Brooks and Gelman 1998) as criteria for the number of samples to discard at the start of each MCMC chain (i.e., burn-in). The minimum number of burn-in samples was estimated by examining Gelman-Rubin-Brooks plots, which showed the evolution of the shrink factor as the number of MCMC iterations increased. Plots were created using the gelman.plot function in the R package coda (Plummer et al. 2006) with all samples from three chains with overdispersed initial values, 5 000 samples per chain, and no thinning. Plots were used to identify the number of iterations at which the shrink factor remained close to 1.0 for all parameters, indicating that chains had converged to stationary distributions. Results (Figure 1.6), suggested that chains converged to stationary distribution after about 3,000 burn-in samples.

Total chain length and thinning interval were determined using the run length control diagnostics proposed by Raftery and Lewis (1992). I used the raftery.diag function in the R package coda with the last 10 000 samples from one chain of 20,000 samples and no thinning to (1) calculate the minimum number of posterior samples (N_{min}) required to estimate the posterior median of each parameter to within an accuracy of 1% with 95% probability; (2) determine the dependence factor (I; i.e., extent to which autocorrelation would inflate the total chain length); and (3) the total number of samples (N; i.e., chain length before burn-in and thinning) required to obtain N_{min} samples with no serial autocorrelation. Results (Table 1.4) suggested that 9,604 posterior samples (after burn-in and thinning) would be required to meet my desired accuracy and that, due to autocorrelation, only one sample out of every eight should be retained. To be conservative, I discarded the first 10,000 samples (i.e., burn-in) from a total chain of 110,000 samples and then retained every tenth sample (i.e., thinning). Therefore, all inferences were based on 10,000 samples that remained after burn-in and thinning. Autocorrelation plots (Figure 1.7) for each parameter were used to confirm that consecutive samples were not correlated within the final posterior sample. Trace plots (Figure 1.8) for each parameter were used to confirm that the posterior distribution was stationary.

Table 1.4.—Summary of Raftery and Lewis' (1992) run length control diagnostics for each parameter with estimated number of posterior samples (N_{min}; i.e., chain length after burn-in and thinning) required to achieve desired accuracy, dependence factor (I; i.e., extent to which autocorrelation inflates required total chain length), and the total chain length (N; i.e., chain length before burn-in and thinning) required to obtain N_{min} samples with no serial autocorrelation.

Parameter	N_{min}	I	N
β_1	9 604	5.94	57 075
β_2	9 604	7.52	72 184
deviance	9 604	3.79	36 426
$p_{2,A}$	9 604	2.41	23 188
$p_{3,B}$	9 604	4.12	39 528
$\varphi_{1,A,A}$	9 604	2.26	21 720
$\varphi_{1,A,C}$	9 604	2.27	21 758
$\varphi_{2,A,A}$	9 604	2.66	25 564
$\varphi_{2,A,B}$	9 604	4.99	47 898
$\varphi_{2,A,C}$	9 604	5.39	51 762
$\varphi_{3,B,B}$	9 604	2.25	21 646
$\varphi_{3,B,C}$	9 604	2.25	21 642

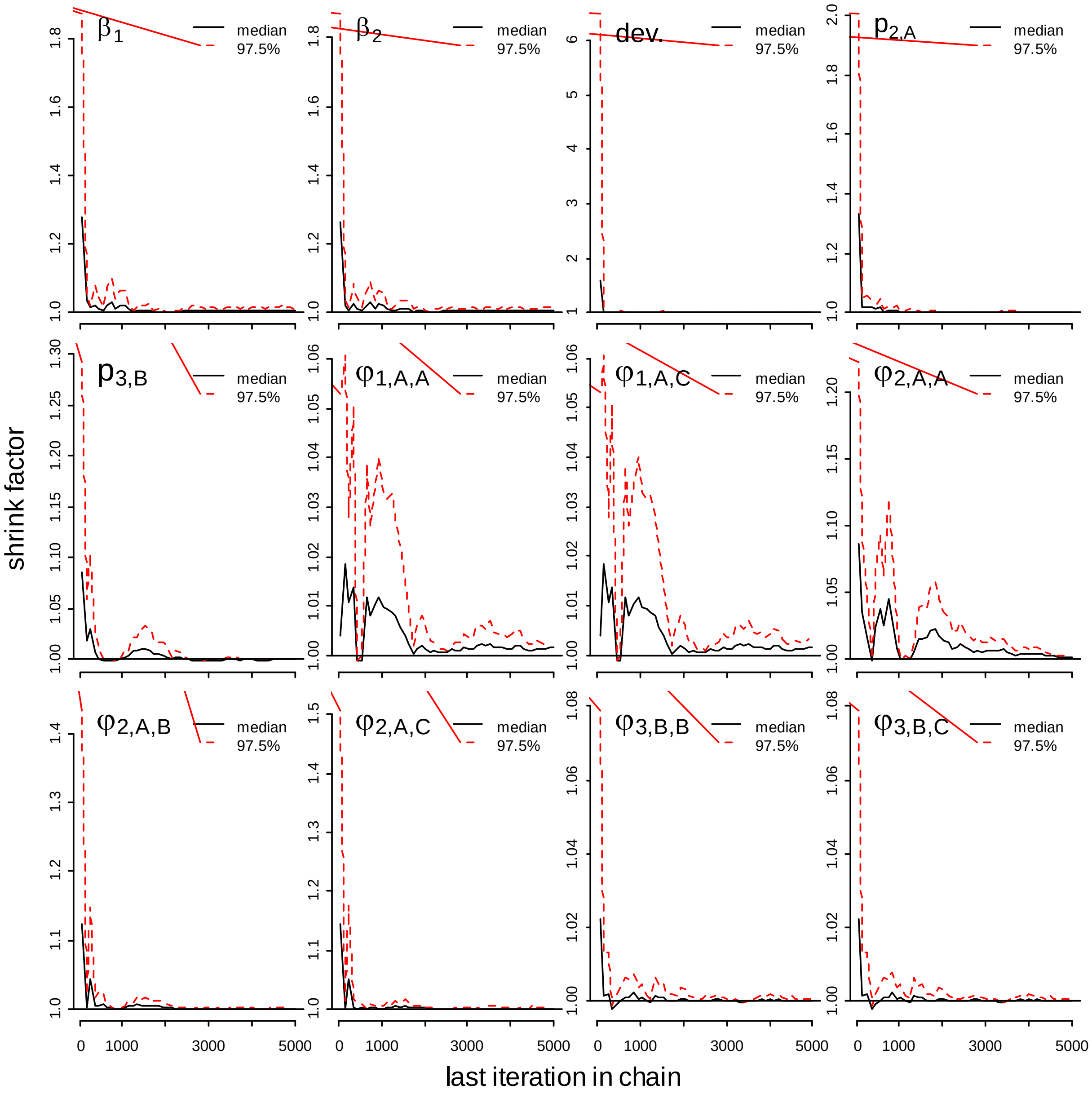

Figure 1.6.—Gelman-Rubin-Brooks plot showing evolution of Gelman and Rubin’s shrink factor for each parameter as the number of iterations increased in a chain of 5 000 samples (no thinning).

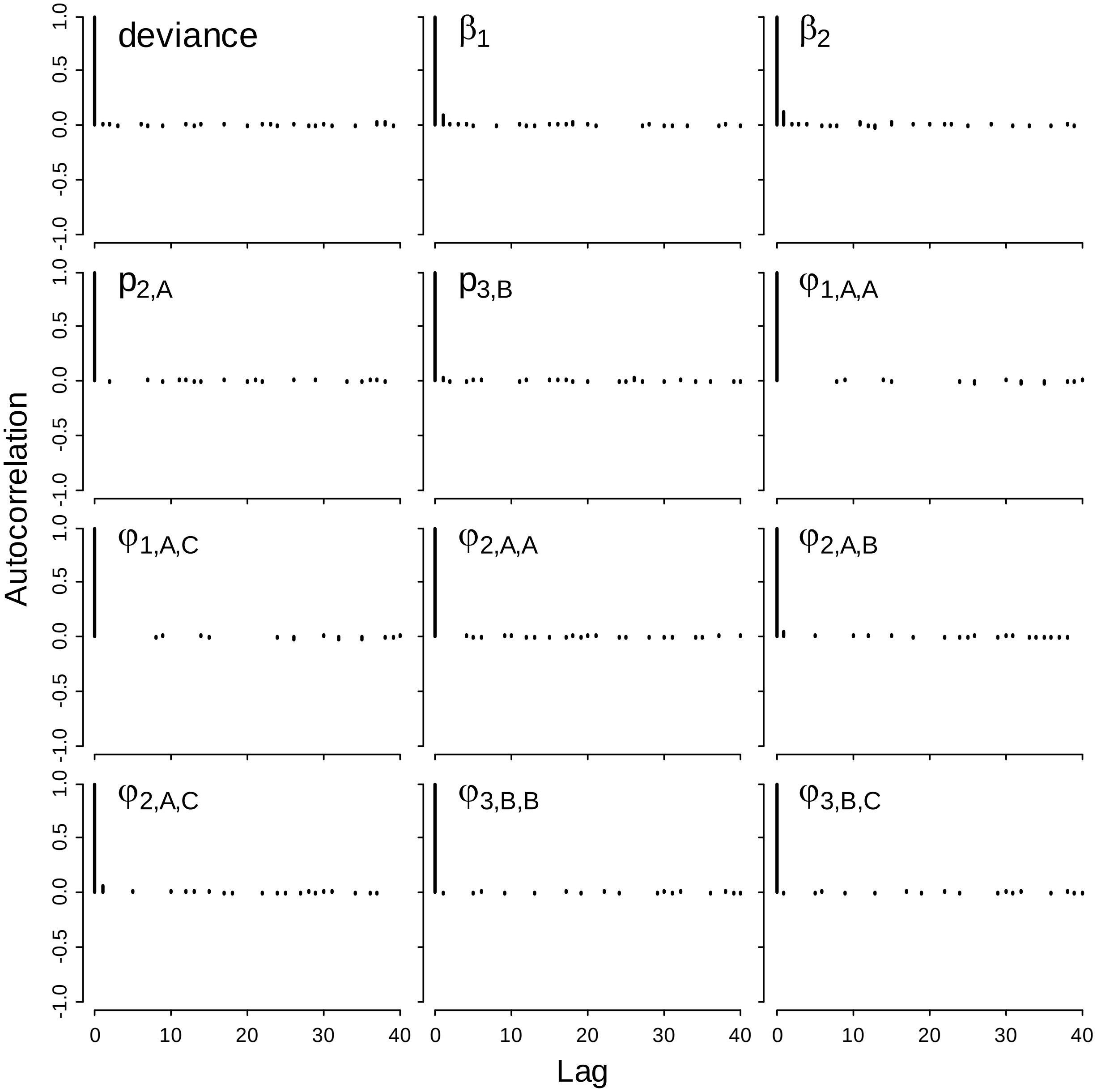

Figure 1.7.—Lagged autocorrelations of each parameter in a chain of 10,000 posterior samples (after burn-in and thinning) from the Bayesian state-space model.

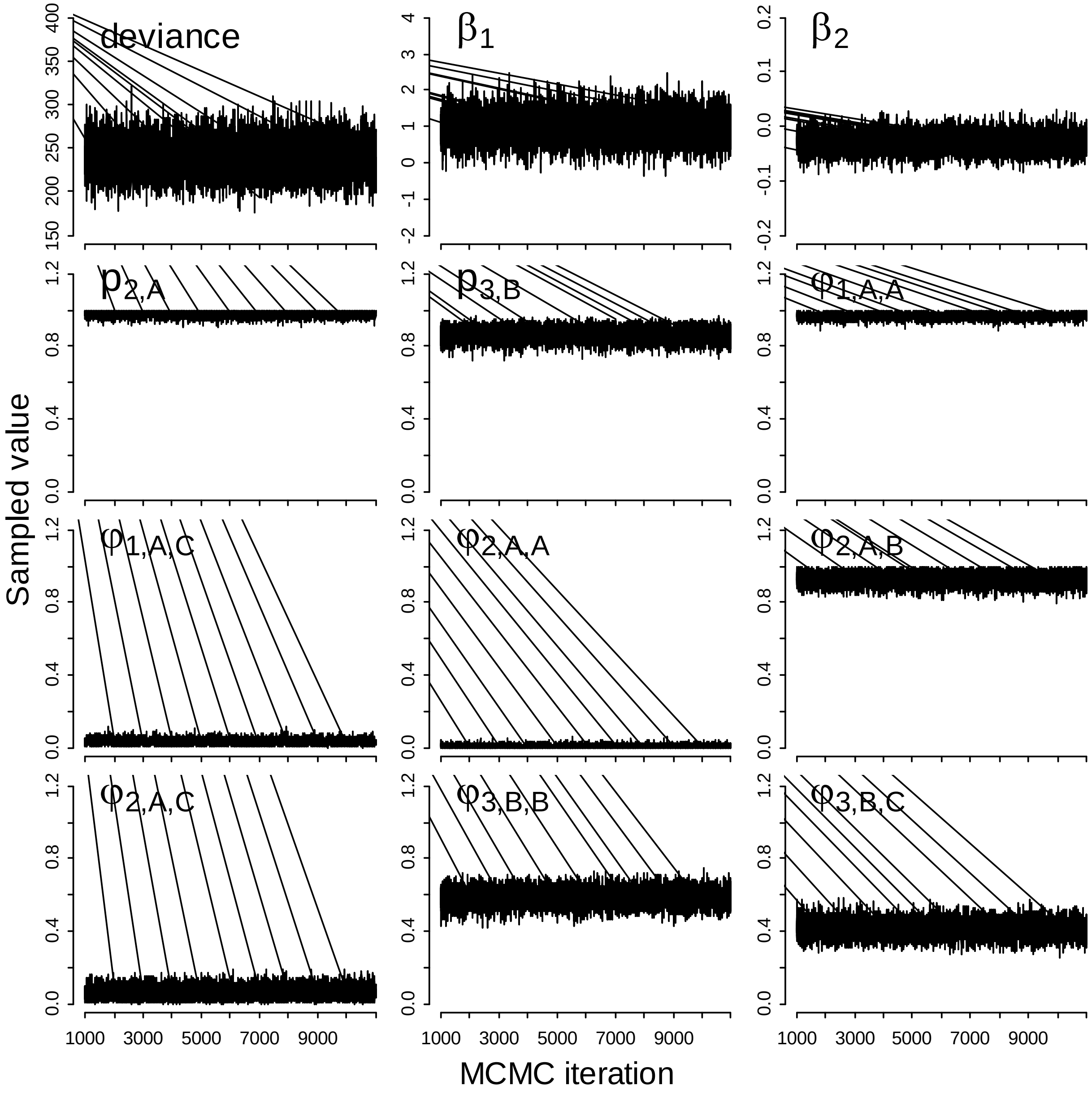

Figure 1.8.—Trace plots showing sampled value of each parameter for 10,000 posterior samples (after burn-in and thinning) of the Bayesian state-space model.

APPENDIX 1C

Prior Sensitivity

Appendix 1C.—Sensitivity of parameter estimates to prior probability distributions in a Bayesian state-space model used to estimate abundance, spatial distribution, movement, trap capture, dam passage, and detection probabilities of Sea Lampreys in the Cheboygan River during 2011.

Prior sensitivity should be evaluated in every Bayesian analysis because the choice of prior is subjective and posterior distributions can be influenced by the form of prior distribution. In the Bayesian state-space model used to estimate abundance, spatial distribution, movement, trap capture, dam passage, and detection probabilities of Sea Lampreys in the Cheboygan River during 2011, I used prior probability distributions for three purposes. First, priors were used to apply structural constraints (e.g., fixing probabilities to zero or one) when transition or detection was physically impossible or certain (e.g., $\varphi_{1,A,B} = 0$; Figure 1.1). My assumptions of perfect knowledge of those parameters should not require further justification. Second, "flat" priors (e.g., beta(1, 1)) were used when I had no prior information about the value of a parameter. In the absence of prior knowledge about a parameter, use of a flat prior is a natural choice, but it is not free of criticism because it implies that all values within the parameter space were equally plausible a priori. This was my choice, however, due to the lack of better information. When a flat prior is used, inferences are based on the data and the likelihood function because posterior probabilities are the product of the prior (with equal prior probability assigned to all values) and the likelihood function. Third, I used priors to specify assumptions needed to estimate parameters that were confounded with other parameters (i.e., the data did not contain information needed to separately identify each parameter). Specifically, I assumed that all tagged lampreys passing the dam would have been detected upstream (i.e., $p_{3,A} = 1$) and that all tagged lampreys caught in the trap were detected (i.e., $p_{4,B} = 1$). Those assumptions seemed reasonable based on ancillary observations, but I considered sensitivity of results to those assumptions because they were subjective.

Relaxing assumptions of perfect detectability upstream of the dam and in the trap

Detectability upstream of the dam.—Inferences from the model were potentially sensitive to assumptions about the probability of detecting a tagged lamprey upstream of the dam ($p_{3,A}$) because the detection probability upstream of the dam was confounded with the probability of passing upstream over the dam ($\varphi_{2,A,A}$). For example, 16 lampreys reached the dam but were not detected farther upstream (encounter history AA000). Using only the data, I could not determine how many of those lampreys passed upstream over the dam but were not detected be receivers upstream of the dam, or ceased migration below the dam. Therefore, an estimate of $p_{3,A}$ was needed to estimate $\varphi_{2,A,A}$. In the absence of any data to inform estimation of those parameters, the model used only the information in the prior probability distributions. In this analysis, inferences were based on the assumption that all tagged lampreys would have been detected by receivers upstream of the dam (i.e., $p_{3,A} = 1$). Alternatively, I could have used a flat prior probability for both parameters to represent the assumption that both outcomes were equally probable a priori or conducted auxiliary field tests to estimate $p_{3,A}$ and then specified a prior distribution that represented my knowledge of that parameter.

To evaluate sensitivity of results to the assumption that all tagged lampreys would have been detected upstream of the dam, I compared my results, based on my assumption that $p_{3,A} = 1$, to inferences based on two alternative prior distributions: beta(69, 9) and beta(1, 1). Prior distribution beta(69, 9), with mean of 0.885 and credible interval ranging 0.813-0.950 (95% HPDI), was used to represent the assumption that detection probability upstream of the dam was equal to the lowest detection probability estimated during the study (site 3B; see $p_{3,B}$, Table 1.2).

Although I do not expect this “less informative” prior to accurately reflect the true detection probability at site 3A, it was chosen to be conservative. Use of this prior also demonstrates how a prior distribution might be selected from auxiliary data. For example, beta(69, 9) would have represented my knowledge about $p_{3,A}$ if I had released 78 tagged lampreys above the dam (to estimate detection probability in the absence of any upstream passage) and 69 of those were subsequently detected at upstream receivers. Although such a release was not conducted, this prior was used to show how that information would have changed my inferences and may motivate the inclusion of such auxiliary data in future studies.

Inferences would not have changed if I had assumed that the prior probability of detection upstream of the dam ($p_{3,A}$) was 0.81-0.95 (i.e., beta(69, 9)) (Figure 1.9). Posterior modes of all transition probabilities differed by less than 0.005 between the two priors. However, if I had assumed no prior knowledge of the upstream detection probability (i.e., beta(1, 1)), then I would have inferred that the detection probability was 0.056 (posterior mode) with 95% credible interval (HPDI) ranging 0.000-0.853. With no prior information available about the detection probability above the dam, the model converged toward a low detection probability because it became less probable that any of the 16 lampreys with history AA000 would have passed the dam undetected. This inference does not seem plausible given my observations that receivers upstream of the dam consistently detected sentinel tags throughout the study and performed better than acoustic receivers downstream of the dam, where estimated detection probabilities were 0.88 and 0.98 (posterior modes). Nonetheless, only the probability of dam passage ($\varphi_{2,A,A}$), the proportion of the population that escaped upstream ($\Phi_{3,A}$), and the number of individuals that escaped upstream ($N_{3,A}$) would have been affected by use of a flat prior for $p_{3,A}$ (Figure 1.9). The point estimate (posterior mode) of $\varphi_{2,A,A}$ would have only increased from 0.001

to 0.005, however, the upper limit of the credible interval would have increased from 0.020 to 0.077 (95% HPDI). As a result, the 95% HPDI for $\Phi_{3,A}$ would have increased from 0-1.9% of the population to 0-7.5% of the population escaping above the dam, and the upper limit of 95% HPDI for $N_{3,A}$ would have increased from 514 lampreys to 1 943 lampreys that escaped above the dam.

Detectability in the trap.—Inferences from the model were potentially sensitive to assumptions about the probability of detecting a tagged lamprey in the trap ($p_{4,B}$) because the detection probability in the trap was confounded with the probability of trap capture ($\varphi_{3,B,B}$). For example, 47 lampreys that reached the spill basin were not detected in the trap (encounter history AAB00). Using only the data, I could not determine how many of those lampreys were caught in the trap but were not detected by trap personnel or were never caught in the trap. Therefore, the probability of detecting a lamprey in the trap ($p_{4,B}$) was needed to estimate the probability of entering the trap ($\varphi_{3,B,B}$). In the absence of any data to inform estimation of those parameters, the model used only the information in the prior probability distributions. In this analysis, inferences were based on the assumption that all tagged lampreys were detected by trap personnel ($p_{4,B} = 1$). Alternatively, I could have used a flat prior probability for both parameters to represent the assumption that both outcomes were equally probable or conducted auxiliary field tests to estimate $p_{4,B}$ and then used a prior distribution that represented my knowledge of that parameter. To evaluate sensitivity of results to the assumption that all tagged lampreys were detected in the trap, I compared my results, based on the assumption of perfect prior knowledge ($p_{4,B} = 1$), to inferences based on two alternative prior distributions: beta(90, 10) and beta(1, 1). Prior distribution beta(90, 10), with mean of 0.900 and credible interval ranging 0.840-0.954 (95% HPDI), was used to represent a hypothetical condition where about one of every ten acoustic-tagged fish caught in the trap was not identified by trap personnel. I consider this "less informative" prior to be conservative (i.e., the true detection probability of tagged lampreys in the trap was probably higher) because tag detection equipment was tested daily and occasional "double-scanning" of daily catches has never revealed any tagged lampreys missed by coded-wire tag detectors. Use of this prior also demonstrates how a prior distribution might have been selected from auxiliary data. For example, beta(90, 10) would have represented my knowledge about $p_{4,B}$ if I had placed 100 tagged lampreys in the trap and 90 of those were subsequently identified as tagged by trap personnel. Although I did not place any tagged lampreys in the trap to estimate the detection probability, this prior was used to show how that information would have changed my inferences and may motivate the inclusion of such auxiliary data in future studies.

As expected, the probability of entering the trap from the spill basin ($\varphi_{3,B,B}$; i.e., local trap efficiency), was sensitive to my assumption of perfect detectability in the trap (Figure 1.10). If I had assumed that the true detection probability was in the range 0.84-0.95 (i.e., $p_{4,B}$ ~ beta(90, 10)), then the point estimate of $\varphi_{3,B,B}$ would have increased from 0.602 to 0.673 and the credible interval for that parameter would have changed from 0.516-0.685 to 0.563-0.775. Posterior modes of all other transition probabilities differed by less than 0.004 between the two priors. Increased trap efficiency would not have changed the estimate of the proportion of the population vulnerable to the trap ($\Phi_{3,B}$) but the estimate of proportion of the population caught in the trap ($\Phi_{4,B}$; i.e., exploitation rate) would have increased from 0.542 to 0.585 (posterior mode) and the credible interval for that parameter would have changed from 0.457-0.613 to 0.503-0.696. A larger estimate of $\varphi_{3,B,B}$ would have also resulted in smaller estimates of spawner abundance (Figure 1.10). Credible intervals (95% HPDI) for the number of spawners that entered the river ($N_{1,A}$) would have changed from 21 828 – 29 299 to 19 426 – 26 878 and the upper limit of the credible interval for the number of lampreys that escaped above the dam ($N_{3,A}$) would have decreased from 514 to 449. If I had assumed no prior knowledge of $\mathrm{p}_{4,\mathrm{B}}$ (i.e., $p_{4,B} \sim$ beta(1, 1)), then I would have inferred that trap efficiency ($\varphi_{3,B,B}$) was 0.679 (posterior mode) with credible interval (95% HPDI) ranging 0.594-1.00. This increase in both the point estimate and uncertainty of $\varphi_{3,B,B}$ would have resulted in a further increase of the point estimate and uncertainty of the exploitation rate ($\Phi_{4,B}$) and decreased estimates of abundance, but would not have changed the estimate of the proportion of the population vulnerable to the trap ($\Phi_{3,B}$; Figure 1.10).

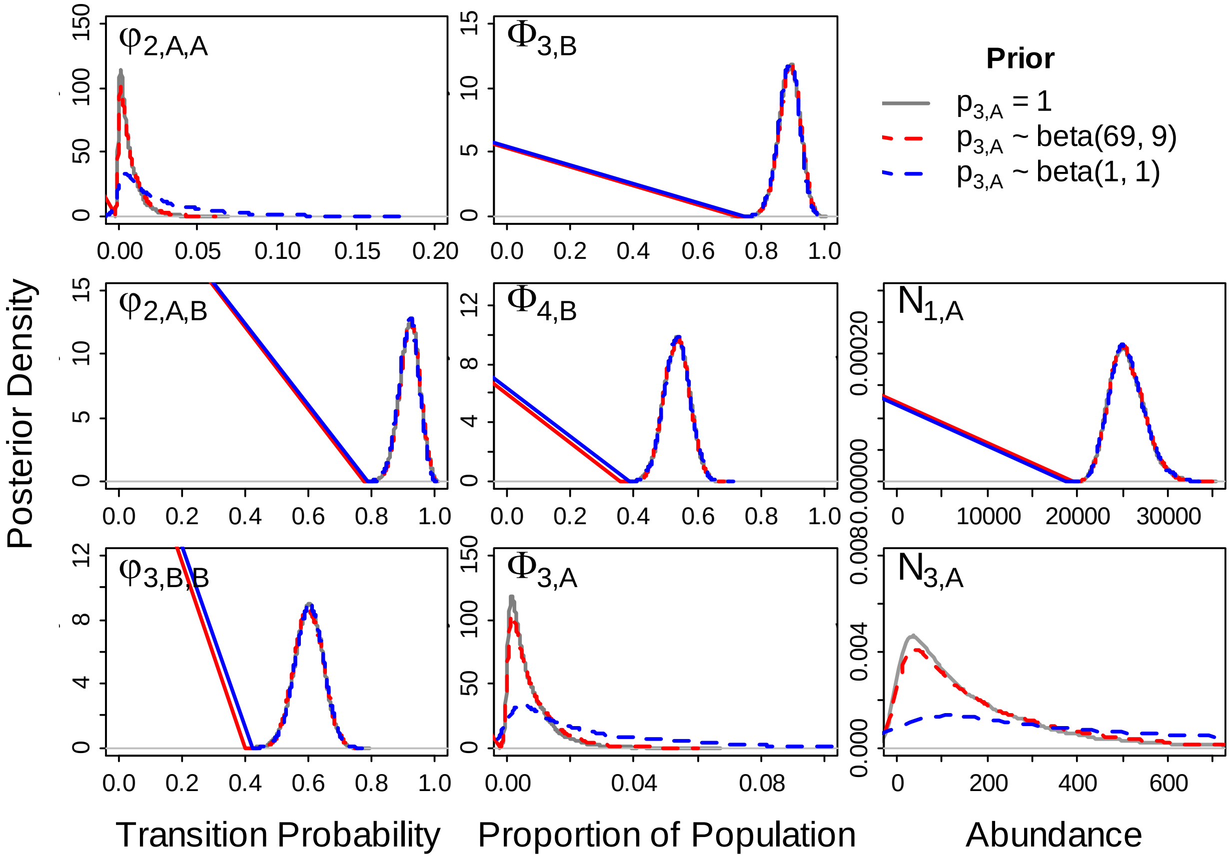

Figure 1.9.—Posterior distributions for fish movement probabilities (left column; $\varphi_{2,A,A}$, $\varphi_{2,A,B}$, $\varphi_{3,B,B}$), proportion of the population present at two locations (middle column; $\Phi_{3,B}$, $\Phi_{4,B}$, $\Phi_{3,A}$), and number of untagged lampreys at three locations (right column; $N_{1,A}$, $N_{3,A}$) under three prior distributions for $p_{3,A}$—the probability that a tagged Sea Lamprey was detected passing receivers upstream of the Cheboygan River Dam.

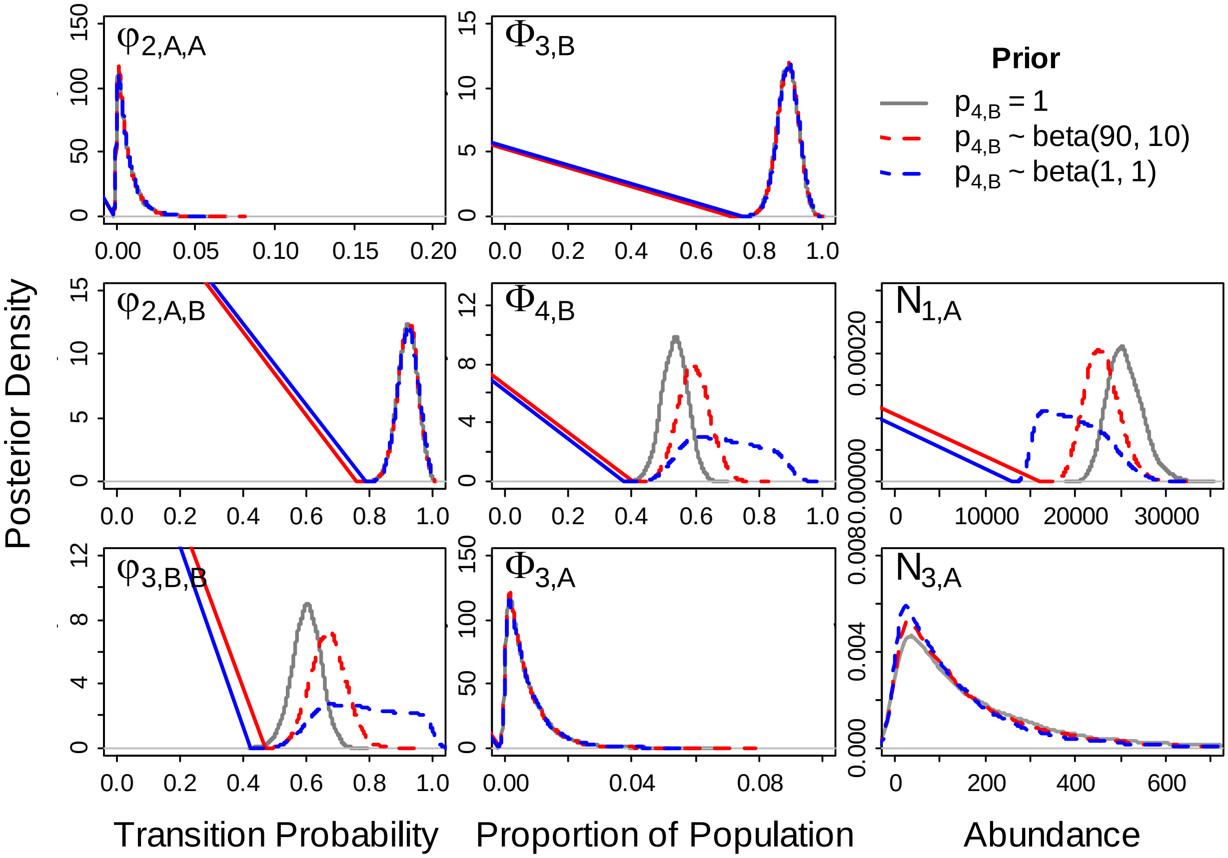

Figure 1.10.—Posterior distributions for fish movement probabilities (left column; $\varphi_{2,A,A}$, $\varphi_{2,A,B}$, $\varphi_{3,B,B}$), proportion of the population present at two locations (middle column; $\Phi_{3,B}$, $\Phi_{4,B}$, $\Phi_{3,A}$), and number of untagged lampreys at three locations (right column; $N_{1,A}$, $N_{3,A}$) under three prior distributions for $p_{4,B}$—the probability that a tagged Sea Lamprey was identified in the Cheboygan River trap.

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CHAPTER 2

USING ACOUSTIC TELEMETRY TO EVALUATE PERFORMANCE OF SEA LAMPREY TRAPS IN THE GREAT LAKES

Abstract

Acoustic telemetry was used to determine the current and possible future role of traps to control and assess invasive Sea Lamprey, *Petromyzon marinus*, in the St. Marys River, the connecting channel between Lake Superior and Lake Huron. Exploitation rates (i.e., fractions of the adult Sea Lamprey population removed by traps) at two upstream locations were compared among three years and two points of entry to the system. Telemetry receivers throughout the drainage allowed trap performance (exploitation rate) to be partitioned into two components: proportion of migrating Sea Lampreys that visited traps (availability) and proportion of available Sea Lampreys that were caught by traps (local trap efficiency). Despite analytical challenges and uncertainty due to behavioral effects of acoustic tag implantation on tagged Sea Lampreys, estimated exploitation rates (2.5–22.5% for upper St. Marys River; 0–11.1% for Echo River) for adult Sea Lampreys in the St. Marys River system were well below those needed to provide population control in the absence of lampricides. Local trap efficiency and availability estimates suggested that substantial increases in catch would require major changes to Sea Lamprey trapping systems, including improvements to existing traps, installation of new traps, or biological (e.g., pheromones) or physical (e.g., flow) modifications to attract more Sea Lampreys toward and into traps. Lower-than-expected local trap efficiency estimates suggested that traditional assessment methods underestimate abundance of spawning-phase Sea Lampreys in the St. Marys River and highlighted the need to evaluate the equal catchability assumption of mark-recapture models when a single trap is used for capture and recapture, and in general, the need to evaluate even the most basic of telemetry assumptions. These results demonstrated how bias associated with telemetry tags can be estimated and incorporated in models to improve inferences about parameters that are directly relevant to fishery management.

Introduction

The goal of an invasive species control program is to suppress target populations consistent with societal values. Pesticide application and physical removal are two strategies commonly applied soon after invasion—sometimes with only limited knowledge of the species ecology or life history. Fine-tuning those strategies or developing more cost-effective or socially-acceptable alternatives may require understanding how the spatial distribution of a population affects overall population dynamics, so that spatial bottlenecks or life history vulnerabilities can be identified (Simberloff 2003). However, the spatial distribution of a population can be difficult to predict or measure, especially for migratory or highly mobile fishes (Lucas and Baras 2000). Recent advances in fish tracking technology (Hockersmith and Beeman 2012; Cooke et al. 2013) allow fish population distributions to be characterized over large spatial and temporal scales. Here, I describe use of acoustic telemetry to determine the current and potential role of traps for control and assessment of invasive Sea Lamprey, *Petromyzon marinus*, in the St. Marys River—the waterway that connects Lake Superior and Lake Huron and one of the largest producers of parasitic Sea Lampreys in the Laurentian Great Lakes basin.

The Great Lakes have been drastically altered by establishment of non-indigenous fishes during the last century (Christie 1974) and future invasions are expected (Mills et al. 1993; Kolar and Lodge 2002; Rixon et al. 2005; Herborg et al. 2007). The arrival of Sea Lamprey through shipping canals in the early 1900s contributed to extirpation of several species, including the top predator, lake trout, *Salvelinus namaycush*, from three of the five lakes (Smith and Tibbles 1980; Hansen 1999). Since the 1950s, Sea Lamprey populations have been suppressed by application of pesticides that selectively target larval Sea Lampreys in streams. Barriers (low-head dams and electric weirs) have been used to block adult Sea Lampreys from obligatory stream spawning habitat, and, where trapping was feasible, adult Sea Lampreys were removed prior to spawning. Between 1997 and 2011, thousands of sterilized male Sea Lampreys were also released into the upper St. Marys River to suppress Sea Lamprey reproduction by competing with fertile males (Twohey et al. 2003; Bergstedt and Twohey 2007), but the sterile male release program was discontinued in 2011. A recent goal of the Sea Lamprey control program has been to increase the effectiveness of traps and barriers (McLaughlin et al. 2007), ideally to the point that they could contribute to the control strategy or replace chemical treatments.

The effectiveness of any population control strategy that targets adult Sea Lampreys depends on the proportion of individuals removed and the relation between the stock size (i.e., number of adults not removed) and recruitment (i.e., number of offspring that they produce; Haeseker et al. 2003; Jones et al. 2003; Haeseker et al. 2007). Stock-recruitment relationships are an important consideration of management decisions involving strategies that target adult life stages (Dawson and Jones 2009), and are required to reliably design and evaluate such strategies. Like many other fish species, estimated Sea Lamprey stock-recruitment relationships have been highly variable due to a large amount of density independent recruitment variation (Jones et al. 2003; Dawson and Jones 2009). Nonetheless, the ability to precisely and accurately estimate stock size and the proportion of a population removed by a control tactic, such as trapping, are critical to determine whether that tactic is likely to have a desired effect on future recruitment. Therefore, unbiased estimates of Sea Lamprey exploitation (i.e., the proportion of a population removed) and abundance are needed as a first step toward cost-effective control strategies that target adults, including strategies that use traps.

Contemporary estimates of the theoretical reduction in Sea Lamprey recruitment attributable to traps have been based on adult abundance estimates obtained using a time-stratified mark-recapture method similar to the one described by Schaefer (1951) but modified (hereafter, "modified Schaefer") for use at a single trapping location at an upstream-barrier used for both initial capture and recapture of marked individuals (Mullett et al. 2003). The use of the same type of traps and at one location for initial capture and recapture introduces potential for biased local trap efficiency and abundance estimates due to possible violation of the assumption that the probability of capture does not differ between marked and unmarked individuals (Pollock et al. 1990). Adult Sea Lamprey abundance estimates are not only used to indicate control program success, but have also been used to guide control strategies that depend on stock size. For example, annual theoretical reductions in reproduction associated with the sterile male release program in the St. Marys River were calculated based on the number of sterilized Sea Lampreys that were released during each year, the ratio of male to female Sea Lampreys in the unmarked population, and the number of Sea Lampreys in the unmarked population (Twohey et al. 2003; Sullivan and Adair 2012). Therefore, accurate adult Sea Lamprey abundance estimates were needed to plan and evaluate the sterile male release program, and would be needed for other strategies that target the adult life stage, including removals via traps. Recent studies have suggested that violation of the "equal catchability" assumption may vary among rivers and traps (Bravener and McLaughlin 2013; Holbrook et al. 2014). Despite the potential implications of biased stream-specific abundance and local trap efficiency estimates, the equal catchability assumption has not been rigorously or broadly evaluated.

The ultimate measure of trap performance is the proportion of the stream-wide population removed or exploitation rate. This depends on the proportion of adult Sea Lampreys in a stream that visit trap locations and on traps effectively capturing and retaining Sea Lampreys that pass near the trapping location (Bravener and McLaughlin 2013; Holbrook et al. 2014). Trap efficiencies derived from the modified Schaefer method provide an intuitive basis for evaluating trap performance, but the interpretation of trap efficiency estimates (and therefore abundance) has differed among traps due to variation among release sites used for marked Sea Lampreys. In some cases, modified Schaefer trap efficiency estimates have represented drainage-wide exploitation rates because marked Sea Lampreys were released at the river mouth. Those circumstances provided measures of trap performance at the drainage scale, but provided no information about “local” trap efficiency or abundance near traps. In other cases, modified Schaefer trap efficiency estimates have only represented a proportion of a stream-wide population because marked Sea Lampreys have been released near traps, in locations that would not have been reached by Sea Lampreys that spawned farther downstream or in downstream tributaries. Under those circumstances, the modified Schaefer method provided local estimates of trap efficiency and abundance but provided no basis for evaluating the location of the trap within the drainage or predicting the efficacy of alternative control strategies at the drainage scale. Spatial limitations of modified Schaefer estimates have been due, in part, to the need to physically capture and mark individuals at one location and then recover them at one or more upstream locations, but in most streams traps have only been effective when operated at upstream barriers to migration. More recently, telemetry has provided the ability to “observe” tagged individuals passively using automated receivers that listen for tagged fish at several locations concurrently. For example, Holbrook et al. (2014) used acoustic telemetry to evaluate performance of traps in the Cheboygan River by releasing tagged Sea Lampreys downstream of all spawning habitat and placing telemetry receivers near traps. In that study, telemetry and trap catch data were used to estimate the proportion of the stream-wide population that was caught (exploitation rate), the proportion available to traps given the spatial distribution of the adult Sea

Lamprey population and the location of traps in the drainage, and the local trap efficiency (i.e., the proportion of those available that were actually caught). Availability estimates for each trap represented the maximum proportion of the entire river population that could be removed if traps were 100% efficient (Holbrook et al. 2014). When evaluated at the drainage scale, estimates of exploitation, availability to traps and local trap efficiency provide an intuitive basis for evaluating performance of existing traps, prioritizing improvements among existing traps, and identifying locations for new traps.

I applied the conceptual framework proposed by Bravener and McLaughlin (2013) and extended by Holbrook et al. (2014) to evaluate Sea Lamprey traps in the St. Marys River system, which included traps in the upper St. Marys River and one tributary, the Echo River. My specific objectives were to (1) test assumptions required to estimate local trap efficiency, availability to traps, and exploitation from telemetry data; (2) estimate the proportion of the adult Sea Lamprey population in the St. Marys River that were caught in traps (i.e., exploitation rate); (3) estimate the proportion of the population present at each trap location (i.e., availability); (4) estimate the local efficiency of each trap (i.e., number of Sea Lampreys caught as a proportion of those available); and (5) estimate the number of adult Sea Lampreys present (i.e., abundance) near each trap and for the entire system. These objectives address questions that are critical for understanding the importance of traps to Sea Lamprey control and assessment and for predicting the benefits of alternative strategies.

Methods

Study site

The St. Marys River flows from Lake Superior into Lake Huron through a complex of braided channels (Figure 2.1). Adult Sea Lampreys may enter the St. Marys River from the main body of Lake Huron or from the North Channel. The upper St. Marys River and three tributaries to the northern channel, the Root, Echo, and Garden rivers, have been regularly treated with lampricides. Semi-permanent and portable Sea Lamprey traps, all attached to barriers, have been operated each year in the upper St. Marys River near Sault Ste. Marie (hereafter, “upper St. Marys River”) and at a low-head dam in the Echo River (Figure 2.1). Typical discharge ranges 1,100–3,100 m^3s^{-1} in the St. Marys River and 1–3 m^3s^{-1} in the Echo River.

Fish tagging and release

Adult Sea Lampreys were collected from traps in tributaries to northern Lake Huron (Cheboygan River) and Lake Michigan (Manistique River, Peshtigo River), and implanted with an acoustic tag, coded wire tag, or both. All Sea Lampreys implanted with an acoustic tag will be referred to as “acoustic-tagged”, even if they were also implanted with a coded-wire tag, and Sea Lampreys fitted only with a coded wire tag will be referred to as “coded-wire-tagged.” Sea Lampreys were collected outside the St. Marys River so that results would not be affected by previous experience at St. Marys River traps. Collection from barrier-integrated traps in other rivers was necessary because no other capture methods could provide adequate sample sizes. Tagged Sea Lampreys were released at one of two locations in the lower St. Marys River (Figure 2.1): (1) at a narrow point in Munuscong Lake about 45–60 river kilometers (rkm) downstream of the traps in the upper St. Marys River (depending on route) and about 60 rkm downstream of the Echo River trap; and (2) in the North Channel north of St. Josephs Island about 35–48 rkm (depending on migratory route used) downstream of traps in the upper St. Marys River and about 42 rkm downstream of the Echo River trap.

Acoustic-tagged Sea Lampreys ranged 410–610 mm in length (mean 504 mm) and 131–498 g (mean 270 g) in weight. Acoustic tags (model V9-2H and V9P-2H; Vemco, Halifax, Nova Scotia, Canada) transmitted uniquely coded signals every 40–80 seconds at a frequency of 69 kHz and power level of 151 dB (re 1 μPa at 1 m). V9-2H tags were 9 mm in diameter, 29 mm long, weighed 4.7 g in air (2.9 g in water), and had an expected minimum tag life of 80 days. V9P-2H tags were 9 mm in diameter, 47 mm long, weighed 6.4 g in air (3.5 g in water), and had an expected minimum tag life of 101 days. Size and battery life differences between tag models were due to integrated pressure transducers in V9P-2H tags that provided depth at time of detection. Depth data were not used in analyses described in this manuscript. Tag mass was 1.1–3.6% (median: 1.8%) of body mass for Sea Lampreys implanted with V9-2H and 1.3–4.5% (median: 2.4%) of body mass for Sea Lampreys implanted with V9P-2H tags.

Before surgery, each Sea Lamprey was anesthetized by immersion in 0.2 $ml\cdot L^{-1}$ clove-oil solution. Acoustic tags were implanted through a 2-cm ventral incision near the midpoint between the posterior gill pore and the anterior dorsal fin when sex was also determined by visual examination of the gonads. Each incision was closed with two interrupted surgeon's knots using a size 3-0 polydioxanone monofilament suture (PDSII, Ethicon). Glue (Vetbond, 3M) was applied to stabilize each knot. During 2011 and 2012, a minimally invasive (diameter 0.25 mm; length: 1.1 mm), uniquely numbered, coded wire tag (Northwest Marine Technology, Inc.; Shaw Island, WA) was injected into the dorsal musculature of some acoustic-tagged Sea Lampreys (348 in 2011; 142 in 2012; Table 2.1) to allow evaluation of acoustic tag retention (see *Assumptions*). Sea Lampreys were allowed to recover in an aerated tank for at least 48 h prior to release. Acoustic-tagged Sea Lampreys were released in groups of 49–68 Sea Lampreys with roughly equal sex ratios at each location on three dates during late spring 2010, 2011, and 2012 (Table 2.1).

To compare recovery rates of acoustic and coded-wire-tagged Sea Lampreys in traps, each group of acoustic-tagged Sea Lampreys released in 2011 and 2012 was paired with a release of 50 Sea Lampreys (equal sex ratio; Table 2.1) that were injected only with coded wire tags, as described above. Coded-wire-tagged Sea Lampreys were taken from the same source and were stored, handled, and transported the same as acoustic-tagged Sea Lampreys, but were not anesthetized or implanted with an acoustic tag. To minimize handling of Sea Lampreys that were not anesthetized, length was not measured and sex was determined based on external morphological assessment. Mass of coded-wire-tagged Sea Lampreys ranged 136–425 g in (mean: 257 g).

Tracking Sea Lamprey movements

Autonomous acoustic telemetry receivers (VR2W, Vemco, Halifax, Nova Scotia) were placed downstream of traps and adjacent to barriers in the St. Marys and Echo rivers to document arrival near traps (Figure 2.1). Each receiver recorded the unique identification number of each acoustic tag with date and time of detection for tagged fish in the vicinity. Two receivers, separated by about 350 m, were located in the Echo River about 12 rkm downstream of the Echo River trap. In the upper St. Marys River, 22–26 receivers, spaced 30–330 m, covered an area within 2.1 rkm downstream of traps.

Capture of Sea Lampreys in traps

Sea Lampreys were caught in barrier-integrated traps associated with shipping locks and hydroelectric generating stations in the St. Marys River. Traps were operated daily by the U.S.

Fish and Wildlife Service (USFWS) and Department of Fisheries and Oceans, Canada (DFO Canada). Each Sea Lamprey collected was checked for presence of an acoustic or coded wire tag using a metal detector (R-8000 tunnel detector; Northwest Marine Technology Inc., Shaw Island, Washington, USA) designed for detecting coded wire tags and visually inspected for evidence of tagging (i.e., incision or sutures). When present, acoustic tags were removed for identification and to confirm that they were still transmitting. When coded wire tags were suspected, Sea Lampreys were frozen (after removal of acoustic tag, if present) for future tag removal and identification. Each day, 10% of Sea Lampreys caught were marked with a week-specific combination of fin punches and released 1.5–3.5 rkm downstream of traps in the upper St. Marys River and about 10 rkm downstream of the trap in the Echo River; all other Sea Lampreys were removed from the system. Fin-punched Sea Lampreys were used to estimate abundance and local trap efficiency relative to the release site using the modified Schaefer method.

Data analysis

Parameter estimation.—A probabilistic model of Sea Lamprey movement was fit to individual movement data, collected with acoustic telemetry, to estimate the proportion of the population that was available to each trap (Figure 2.2). Local trap efficiencies were estimated from captures of tagged Sea Lampreys that were earlier detected near traps (i.e., available to traps). Availability and local trap efficiency estimates were combined to estimate the exploitation rate due to trapping, and this was further adjusted, based on comparison of recovery rates between acoustic and coded-wire-tagged Sea Lampreys, to account for biased recovery rates associated with acoustic tags.

Two independent likelihoods were used to estimate the proportion of Sea Lampreys that approached each trap site from each release site and the local efficiency of each trap. A third likelihood was used to estimate the effect of acoustic tagging on recovery in traps. The model was fit in a Bayesian framework, so inferences were based on posterior distributions, which were influenced by the observed data and prior knowledge about each parameter. No substantial prior knowledge was available for the parameters, so “flat” priors were used to reflect a-priori uncertainty about model parameter values. Samples from the posterior distribution of each parameter were obtained using Markov chain Monte Carlo (MCMC) simulation with the software program OpenBUGS (Lunn et al. 2009; Giminez et al. 2009; Ntzoufras 2009) and the R package R2OpenBUGS (Sturtz et al. 2005; R Core Team 2013). Inferences were based on 100,000 posterior samples of each parameter. The first 10,000 samples were discarded (i.e., burn-in) from an initial single chain of 310,000 samples, and then every third sample was retained (i.e., thinning). Burn-in was determined from three un-thinned chains, each with 10,000 samples, using Gelman and Rubin’s (1992) potential scale reduction factor (i.e., shrink factor). Among all parameters, the potential scale reduction factor was less than 1.02 after 10,000 samples. Total chain length and thinning interval were estimated using methods described by Raftery and Lewis (1992) to determine the number of iterations and thinning interval required to estimate the median of all parameters with less than 1% error. From a single un-thinned chain of 10,000 samples, after discarding the first 10,000 samples, autocorrelation ranged 1.0–2.41 among parameters and results suggested that a minimum chain length of only 9,604 samples (after burn-in and thinning) would be suitable. Convergence was confirmed by examining autocorrelation, trace, and posterior density plots for each parameter, including the deviance. The median of the posterior distribution of each parameter was used as a measure of central tendency because some posterior distributions were not symmetric. Uncertainty was quantified using 95% highest posterior density (HPD) intervals (Gelman et al. 2003; King et al. 2010).

Availability to traps.—The number of acoustic-tagged Sea Lampreys that moved from each release site to each trap site and were, therefore, available for capture (determined by detection on telemetry receivers) was used to estimate $\varphi_{i,h,k}$, the probability that a Sea Lamprey moved from release site h (h=1 for Munuscong Lake; h=2 for North Channel) to trap site k (k=1 for the upper St. Marys River; k=2 for Echo River) during the i^{th} year of the study (i=1 for 2010; i=2 for 2011; i=3 for 2012). A third value for k (k=3) represented Sea Lamprey that did not move to either trap site due to death or spawning elsewhere. Specifically, the number of acoustic tagged Sea Lampreys detected on telemetry receivers at each trap site was considered the outcome of a multinomial process, such that $\mathbf{D}_{i,h,}$~multinomial($\varphi_{i,h}$, $\mathbf{M}_{i,h}$), where for each year (i) and release site (h), $\mathbf{D}_{i,h}$ was a three-element vector with the number of tagged Sea Lampreys with each possible outcome (k), and $\mathbf{M}_{i,h}$ was the number of tagged Sea Lamprey released at site h. Flat Dirichlet distributions with concentration parameters [1, 1, 1] were used to represent the prior probabilities of $\varphi_{i,h}$. Release groups were stratified by year, release site, sex, and release date. It was assumed that $\varphi_{i,h}$ did not differ between sexes or among release dates and those assumptions were supported by auxiliary analyses (see Appendix). During previous telemetry studies, 26–44% of tagged Sea Lampreys ceased upstream migration after release (Kelso and Gardner 2000; Holbrook et al. in review). I assumed that such Sea Lampreys are not representative of untagged Sea Lampreys, so $\mathbf{M}_{i,h}$ only included those Sea Lampreys detected on telemetry receivers in the lower river after release. In this study, only 6.3% (69/1092) of all acoustic tagged Sea Lampreys were not detected on receivers in the lower river (Table 2.1).

Local trap efficiencies.—The number of acoustic-tagged Sea Lampreys that were detected on telemetry receivers near each trap site and subsequently captured (determined by detection in coded-wire-tag scanners) were used to estimate $p_{i,k}$, the probability that a Sea

Lamprey was caught at trap site k during the ith year, given that it was present at that site (i.e., detected on acoustic receivers). Specifically, the number of acoustic-tagged Sea Lampreys caught in trap k was considered the outcome of a binomial process, such that $\mathbf{R}_{i,k}$~binomial($p_{i,k}$, $\mathbf{D}_{i,k}$), where for each year (i) and trap site (k), $\mathbf{R}_{i,k}$ was the number of tagged Sea Lampreys caught, and $\mathbf{D}_{i,k}$ was the number of tagged Sea Lampreys detected on telemetry receivers. A flat uniform distribution over the interval [0, 1] was used to represent the prior probabilities of $p_{i,k}$. Release groups were stratified by year, trap, sex, and release date. For each release site during each year, $p_{i,k}$ was assumed to not differ between sexes, release sites, or among release dates and those assumptions were supported by auxiliary analyses (see Appendix 2B).

Assumptions.— In addition to the distributional assumptions explicitly listed above, it was assumed that: (1) behavior, including movement and capture, of tagged Sea Lampreys was representative of the unmarked population; (2) no acoustic-tagged Sea Lampreys passed telemetry receivers undetected; (3) no coded-wire-tagged Sea Lampreys passed through scanners undetected; (4) no coded-wire or acoustic tags were expelled prior to spawning or capture; and (5) no acoustic tags failed (due to battery discharge or mechanical failure) prior to spawning or capture. Those assumptions are typical of telemetry studies, but rarely evaluated due to logistical difficulty or large costs.

To determine if Assumption 1 was violated by anesthesia, surgery, or the presence of an acoustic tag in the body, I compared the proportions of acoustic and coded-wire-tagged Sea Lampreys recovered in traps in the upper St. Marys River. Specifically, I estimated $\theta_{i,h,t}$, the probability of recovering an acoustic-tagged Sea Lamprey (t = 2) as a proportion of the probability of recovering a coded-wire-tagged Sea Lamprey (t = 1). The number of coded-wire and acoustic-tagged Sea Lampreys caught from each release group was considered the outcome of a binomial process, such that $\mathbf{R}_{i,h,t}$~binomial($\theta_{i,h,t}$, $\mathbf{M}_{i,h,t}$), where $\mathbf{M}_{i,h,t}$ was the number of Sea Lampreys released and $\mathbf{R}_{i,h,t}$ was the number of Sea Lampreys caught from each release group. To estimate the proportional reduction in recovery associated with acoustic tags (hereafter, 'acoustic tag effect'), the probability of recovering an acoustic-tagged Sea Lamprey ($\theta_{i,h,2}$) was defined as the product of the probability of recovering a coded-wire-tagged Sea Lamprey ($\theta_{i,h,1}$) and the acoustic tag effect (ω), such that $\theta_{i,h,2} = \theta_{i,h,1} \times \omega$. Uniform distributions over the interval [0, 1] were used to represent prior probabilities of $\theta_{i,h,1}$ and ω. Release groups were stratified by year, release site, release date, and sex. $\theta_{i,h,1}$ was assumed to not differ between sexes or among release dates and ω did not differ between years, release sites, sexes, or among release dates. Those assumptions were supported by auxiliary analyses (see Appendix 2B). Coded-wire-tagged Sea Lampreys were not released in 2010, so acoustic tag bias in 2010 was assumed to not differ from 2011 or 2012. Recoveries from the Echo River trap were not used to estimate ω because few tagged Sea Lampreys were caught in that trap (Table 2.1). The reciprocal of the acoustic tag effect, 1/ω, defined as the odds of recovering a coded-wire versus acoustic-tagged Sea Lamprey, was also reported.

To determine if Assumption 1 was violated due to variables not associated with acoustic tags (e.g. sexual maturity of tagged vs untagged Sea Lampreys), the timing of recoveries was compared among acoustic-tagged, coded-wire-tagged, and unmarked Sea Lampreys. Comparisons were based on the assumption that all Sea Lampreys ascended the river prior to trap capture and remained in the river for some time (i.e., staging) before entering traps. Empirical cumulative distributions (ECDs) of daily captures were compared visually among groups within each year. To determine if differences between acoustic or coded-wire tagged and unmarked ECDs could have arisen from chance due to small sample sizes for tagged Sea

Lampreys, acoustic and coded-wire tagged ECDs were compared to 95% confidence regions for unmarked ECDs. Confidence regions for unmarked ECDs were constructed from 10,000 simulated ECDs, each comprised of a random draw of $n_{i,k}$ unmarked Sea Lampreys, with replacement, where $n_{i,k}$ was the number of acoustic-tagged Sea Lampreys captured at trap site k during year i.

To determine if Assumption 2 was violated, detection probabilities on telemetry receivers were estimated simply as the proportion of Sea Lampreys detected on telemetry receivers they were known to have passed (i.e., due to detection or capture farther upstream). Assumption 3 was not tested directly, but as a follow-up to this study all available Sea Lampreys (more than 2,400) from St. Marys River traps in 2013 were scanned a second time by an independent crew using an independent scanner of the same model. No coded-wire-tagged Sea Lampreys were detected during the second scan, suggesting that scanners in the St. Marys River were highly efficient. To determine if Assumption 4 was violated, all double-tagged Sea Lampreys (acoustic and coded wire) caught in traps were checked for intact tags. Similarly, each acoustic tag was checked for operation after capture to test Assumption 5.

Exploitation.—The proportion of Sea Lampreys from each release location that were caught (exploitation rate) by each trap during each year, $\lambda_{i,h,k}$, was estimated from acoustic-tagged Sea Lampreys as the product of availability and local trap efficiency for each combination of release (h) and trap sites (k) during each year (i), and adjusted for acoustic tag bias (ω), such that $\lambda_{i,h,k} = \frac{\varphi_{i,h,k} p_{i,k}}{\omega}$. Adjustment for acoustic tag bias was applied to $\lambda_{i,h,k}$, rather than to $\varphi_{i,h,k}$ and $p_{i,k}$ separately because the degree to which acoustic tag bias affected movement ($\varphi_{i,h,k}$), recovery ($p_{i,k}$), or both could not be estimated. To show sensitivity of inferences about availability and local trap efficiency to assumptions about the relative effect of acoustic tag bias on those parameters, I estimated bias-adjusted availability and local trap efficiency, such that $\varphi'_{i,h,k,\pi} = \frac{\varphi_{i,h,k}}{\omega^{(1-\pi)}}$ and $p'_{i,k,\pi} = \frac{p_{i,k}}{\omega^{\pi}}$, where ω was the estimated acoustic tag effect, and π was a scaling factor representing the proportion of acoustic tag bias applied to local trap efficiency. When $\pi = 0$ (i.e., $\omega^0 = 1$), local trap efficiency was not adjusted for acoustic tag bias, representing the case when only availability was affected by acoustic tag bias. Conversely, when $\pi = 1$ (i.e., $\omega^1 = \omega$), all acoustic tag bias was applied to local trap efficiency and none to availability. Finally, when $\pi = 0.5$, acoustic tag bias had proportionally equal effect on local trap efficiency and availability. Bias-adjusted $\varphi'_{i,h,k,\pi}$ and $p'_{i,k,\pi}$ were estimated for π ranging from 0 to 1 at increments of 0.05. Preliminary results from laboratory studies suggested that the magnitude of acoustic tag effect increased with time since tagging (C. Holbrook, unpublished data). Therefore, I speculated that the time elapsed between release and arrival at trap sites (i.e., detection on receivers), and between arrival at trap sites and capture, provided indirect evidence of the relative effect of acoustic tag bias on estimates of availability (i.e., release-arrival) and local trap efficiency (i.e., arrival-capture).

Abundance near traps.—The number of adult Sea Lampreys present at each trap location during each year, $\mathbf{N}_{i,k}$ (Figure 2.2), was estimated using a Peterson-type estimator (Seber 1982), such that $\mathbf{N}_{i,k,\pi} = \frac{\mathbf{C}_{i,k}}{p'_{i,k,\pi}}$, where $\mathbf{C}_{i,k}$ were the number of unmarked Sea Lampreys caught, and $p_{i,k,\pi}$ were bias-adjusted estimates of trap efficiencies for trap k during year i, as described above. To explore the sensitivity of abundance estimates to assumptions about the acoustic tag effect, $\mathbf{N}_{i,k,\pi}$ was estimated for ω^{π} ranging from π=0 to π=1 at increments of 0.05.

Telemetry-derived abundance estimates were compared to estimates obtained using a time-stratified Schaefer model, where a subset of Sea Lampreys caught in traps each day were marked with a week-specific combination of dorsal fin punches, and released downstream. The maximum likelihood estimate and coefficient of variation of abundance were estimated using the method described by Schaefer (1951), except that barrier-integrated traps were used for capture and recapture, as described by Mullett et al. (2003). To facilitate comparison of modified Schaefer estimates to telemetry-based estimates, Wald-type 95% confidence intervals for abundance were estimated by assuming that errors were log-normally distributed for modified Schaefer estimates. Frequentist (maximum likelihood) methods were used for the modified Schaefer model because those methods are used in the Sea Lamprey control program.

Abundance at release sites.—Reliable estimates of the number of unmarked Sea Lampreys that passed each release site in the lower St. Marys River were not possible because unmarked Sea Lampreys caught in traps represented an unknown mixture of Sea Lampreys that used each migration pathway through the lower river (Figure 2.2). The total number of unmarked Sea Lampreys that passed through the lower river (both release sites combined) during each year was estimated by expanding the number of unmarked Sea Lampreys caught in the upper St. Marys River by weighted bias-adjusted estimates of exploitation from each release site, such that

$\mathbf{N}^{*}_{i,\psi} = \mathbf{N}^{*}_{i,1} + \mathbf{N}^{*}_{i,2} = \frac{\mathbf{C}_{i,1}}{(\lambda_{i,1,1}\psi) + (\lambda_{i,2,1}(1-\psi))}$, where $\mathbf{C}_{i,1}$ was the number of unmarked Sea Lampreys caught in the upper St. Marys River, $\lambda_{i,1,1}$ and $\lambda_{i,2,1}$ were estimated proportions of Sea Lampreys that were released in Munuscong Lake and North Channel, respectively, and later caught in the upper St. Marys River, and ψ was the proportion of $\mathbf{N}^{*}_{i}$ that passed through Munuscong Lake (i.e., 1- ψ was the proportion of $\mathbf{N}^{*}_{i}$ that passed through North Channel). If all unmarked Sea Lampreys in the St. Marys River had passed through Munuscong Lake, then the best estimate of $\mathbf{N}^{*}_{i}$ would be obtained when $\psi = 1$ and the converse would be true if all unmarked Sea Lampreys passed through the North Channel. To explore the sensitivity of abundance estimates to assumptions about the proportion of Sea Lampreys passing through Munuscong Lake, $\mathbf{N}^{*}_{i,\psi}$ was estimated for ψ ranging from 0 to 1 at increments of 0.05.

Results

Testing assumptions

Effects of acoustic tags on probability of recovery in traps (Assumption 1).—The 95% HPD interval for the acoustic tag effect (ω) was [0.365; 0.792] (posterior median: 0.558), so coded-wire-tagged Sea Lampreys were 1.26–2.74 times more likely (95% HPD interval for 1/ ω; posterior median: 1.79 times more likely) to be recovered in traps than acoustic-tagged Sea Lampreys. Less time elapsed between release and arrival near traps sites than between arrival and capture (Figure 2.3), suggesting that acoustic tag bias affected estimates of local trap efficiency more than estimates of availability. Most (59 of 62) Sea Lampreys arrived near traps within 8.1 days after release (median ranged 3.3–5.6 days among traps and years), and were captured, on average, 24.7–32.8 days later (range of median duration among years) in the upper St. Marys River and 10.8 days after arrival in the Echo River (2011 only). Most tagged Sea Lampreys recovered in the Echo River spent more time at large than those recovered in the upper St. Marys River, thus the acoustic tag effect in the Echo River may have been overestimated from recoveries in the upper St. Marys River.

Effects of variables other than acoustic tags on timing of capture (Assumption 1).—The general pattern of the timing of trap catches was similar among unmarked, coded-wire-tagged, and acoustic-tagged Sea Lampreys (Figure 2.4). However, catches of acoustic- and coded-wire-tagged Sea Lampreys occurred earlier in the St. Marys River and later in the Echo River than would have been expected based on the number of acoustic-tagged Sea Lampreys caught and the cumulative catch distributions for unmarked Sea Lampreys. Respective median capture dates for acoustic-tagged Sea Lampreys during 2010, 2011, and 2012 were 11.4, 5.2, and 2.8 days earlier than for unmarked Sea Lampreys in the St. Marys River. During 2011 and 2012 (years when coded-wire-tagged Sea Lampreys were released), median capture dates for coded-wire-tagged Sea Lampreys were 4.3 and 0.1 days earlier than for unmarked Sea Lampreys. In all years, the earliest peaks of unmarked Sea Lampreys (i.e., steep segments of cumulative catch curves) were associated with larger catches of marked Sea Lampreys than would have been expected based on unmarked catches alone, especially in 2010. In the Echo River, catches of acoustic-tagged Sea Lampreys during 2010 and 2012 were insufficient for comparison to unmarked Sea Lampreys, but during 2011, median capture date of acoustic-tagged Sea Lampreys was 8.5 days later than for unmarked Sea Lampreys and 0.25 days earlier than for coded-wire-tagged Sea Lampreys. During 2011, 45% of unmarked Sea Lampreys were caught before any acoustic or coded-wire-tagged Sea Lampreys were caught, owing, in part, to release of tagged Sea Lampreys after the Echo River trap had begun catching unmarked Sea Lampreys.

Perfect detectability on acoustic receivers (Assumption 2).—No evidence existed that estimates were biased by imperfect detectability on telemetry receivers. All 628 acoustic-tagged Sea Lampreys detected on telemetry receivers near traps (565 in the upper St. Marys River; 63 in Echo River) were also detected on telemetry receivers in the lower river, suggesting that no Sea Lampreys with a functional acoustic tag passed receivers undetected in the lower river. Among acoustic-tagged Sea Lampreys caught in the upper St. Marys River traps, 98% (53/54) were detected by telemetry receivers in the upper river. The only tag that was recovered but not detected in the upper river was never detected on any telemetry receivers during the study and was not transmitting when recovered. Presumably, that acoustic tag failed shortly after tag implantation and before that Sea Lamprey passed through the lower river. All nine Sea Lampreys recovered with acoustic tags in the Echo River trap were detected on receivers at that site.

Tag expulsion and premature failure (Assumptions 4 and 5).—All acoustic and coded-wire tags were retained among 32 Sea Lampreys that were double-tagged and subsequently recovered in traps. Among 63 acoustic tags checked for acoustic tag operation after recovery in traps, 61 (97%) were functioning correctly and two were not functioning. One of the dead tags was detected on all telemetry receivers leading up to the trap, but was inadvertently frozen after the Sea Lamprey was caught, which may have caused the tag to cease operation prior to inspection. Assuming that tag operated properly until it was frozen, the rate of premature tag failure was low (1/63 = 1.6%). Moreover, the one clear case of premature failure (described above) would not have affected any parameter estimates because it was not detected on any telemetry receiver and, therefore, was omitted from the "effective" release sample size considered representative of the unmarked population.

Availability to traps

During all years of the study and from both release sites, more Sea Lampreys were available to traps in St. Marys River than traps in the Echo River, regardless of the bias proportion applied to availability (Figures 2.5, 2. 6). As greater proportion of tagging bias was applied to availability, point estimates of availability (posterior medians) increased and uncertainty increased. When availability was not adjusted for tagging bias (i.e., π=1), posterior medians of the proportion of Sea Lampreys available to traps in the St. Marys River ranged 0.629-0.686 for Sea Lampreys released in Munuscong Lake ($\varphi_{i,1,1,\pi}$) and 0.371–0.630 for Sea Lampreys released in the North Channel ($\varphi_{i,2,1,\pi}$). Under the same scenario, point estimates of availability to the Echo River trap ranged, among years, 0.012–0.029 for Sea Lampreys released in Munuscong Lake ($\varphi_{i,1,2,\pi}$) and 0.019–0.207 for Sea Lampreys released in the North Channel ($\varphi_{i,2,2,\pi}$). When all tagging bias was applied to availability (i.e., π=0), point estimates (posterior medians) of the proportion of Sea Lampreys available to traps in the St. Marys River ranged 1.123–1.226 for Sea Lampreys released in Munuscong Lake ($\varphi_{i,1,1,\pi}$) and 0.663–1.125 for Sea Lampreys released in the North Channel ($\varphi_{i,2,1,\pi}$). Availability cannot exceed 1.0, so estimates of $\varphi_{i,1,1,\pi} > 1.0$ at small π (π represented the proportion of tagging bias applied to local trap efficiency; Figure 5) suggested that large values of π were more plausible than small values of π. Under the same scenario, point estimates of availability to the Echo River trap ranged, among years, 0.021–0.051 for Sea Lampreys released in Munuscong Lake ($\varphi_{i,1,2,\pi}$) and 0.034–0.370 for Sea Lampreys released in the North Channel ($\varphi_{i,2,2,\pi}$).

The proportions of Sea Lampreys available to traps in the upper St. Marys River were highly sensitive to the proportion of acoustic tag bias that was applied to local trap efficiency (vs. availability). It seems most plausible, based on the assumption that the magnitude of the acoustic tag effect increased with time after release, that acoustic tag bias had only a small effect on Sea Lamprey movement from release to trap sites because most Sea Lampreys arrived at traps sites within one week after release, but two to seven more weeks elapsed before Sea Lampreys were caught in traps. Therefore, values on the right sides of Figures 2.5 and 2.6 (i.e., lowest availability and highest local trap efficiency across the range of π) seem more plausible than those on the left sides of those plots.

Local trap efficiencies

Local trap efficiency estimates were more precise in the upper St. Marys River than in the Echo River (Figures 2.6, 2.7) because few acoustic tagged Sea Lampreys entered the Echo River.

Point estimates and uncertainty increased as a greater proportion of tagging bias was applied to local trap efficiency. When local trap efficiency was not adjusted for tagging bias (i.e., $\pi=0$), point estimates (posterior medians) of local trap efficiency ranged 0.081–0.111 for traps in the upper St. Marys River ($p_{i,1,\pi}$) and 0.00–0.214 for traps in the Echo River ($p_{i,2,\pi}$). When all tagging bias was applied to local trap efficiency (i.e., $\pi=1$), point estimates (posterior medians) of local trap efficiency ranged 0.132–0.186 in the upper St. Marys River ($p_{i,1,\pi}$) and 0.00–0.373 in the Echo River ($p_{i,2,\pi}$).

In the upper St. Marys River, no overlap occurred between 95% confidence intervals of local trap efficiency derived from the modified Schaefer method and 95% HPD intervals of local trap efficiency derived from releases of acoustic-tagged Sea Lampreys in the lower river (Figure 2.5). Estimates of local trap efficiency derived from acoustic telemetry were lower than corresponding mark-recapture estimates, regardless of bias-adjustment method. In the Echo River, substantial overlap occurred in all years, owing to small sample size and large uncertainty in telemetry-derived estimates of local trap efficiency in the Echo River.

Exploitation

After adjusting estimates for bias due to acoustic tagging, 4.0–22.5% (95% HPD intervals) of Sea Lampreys that migrated through Munuscong Lake were later caught in the upper St. Marys River ($\lambda_{i,1,1}$) and 0.0–2.2% were later caught in the Echo River ($\lambda_{i,1,2}$; Figure 2.7). Similarly, 2.5–20.7% (95% HPD interval) of Sea Lampreys that migrated through the North Channel were later caught in the upper St. Marys River ($\lambda_{i,2,1}$) and 0.0–11.1% were later caught in the Echo River ($\lambda_{i,1,2}$). For each trap location, estimates of exploitation could not be combined to form a single drainage-level exploitation rate for each trap because unknown were the proportions of the drainage-wide adult Sea Lamprey population that passed each release location.

Abundance near traps

Upper St. Marys River.—When local trap efficiency estimates were not adjusted for acoustic tag bias (i.e., π=0), the range in estimates of adult Sea Lamprey abundance near traps in the upper St. Marys River was 51,894–151,607 Sea Lampreys during 2010 ($N_{1,1,\pi}$; 95% HPD interval), 32,674–88,711 Sea Lampreys during 2011 ($N_{2,1, ,\pi}$), and 56,380–113,574 Sea Lampreys during 2012 ($N_{3,1, \pi}$). Point estimates of abundance decreased as the proportion of bias applied to local trap efficiency increased (Figure 8). When all acoustic tag bias was applied to local trap efficiency (i.e., π=1), the estimated number of adult Sea Lampreys ranged 23,132-91,865 Sea Lampreys during 2010 ($N_{1,1,\pi}$; 95% HPD interval), 14,646–54,613 Sea Lampreys during 2011 ($N_{2,1,\pi}$), and 25,421–73,022 during 2012 ($N_{3,1,\pi}$). Modified Schaefer abundance estimates in the upper St. Marys River, from releases of fin-punched Sea Lampreys were lower than estimates based on acoustic tags and were 21,596–29,306 Sea Lampreys during 2010 (95% confidence interval), 12,666–17,719 Sea Lampreys during 2011, and 19,136–23,828 during 2012.

Based on modified Schaefer abundance efficiency estimates, the number of sterile males released in the upper St. Marys River (19,392 in 2010 and 22,909 in 2011), proportion of males in unmarked trap catches (63% males in 2010 and 64% in 2011), and the number of males removed by traps (4,815 in 2010 and 3,043 in 2011), the estimated ratio of sterile to fertile males ranged 1.4–2.2 (95% CI) in 2010 and 2.8–4.5 in 2011. Using telemetry-derived estimates of abundance during 2010, estimated ratio of sterile to fertile males ranged 0.2–0.7 when π=0 and 0.4–2.0 when π=1. Using telemetry-derived estimates of abundance during 2011, estimated ratio of sterile to fertile males range 0.4–1.3 when π=0 and 0.7–3.6 when π=1.

Echo River.— When local trap efficiency estimates were not adjusted for acoustic tag bias (i.e., π=0), estimates of adult Sea Lamprey abundance in the Echo River ranged 629–8,918

Sea Lampreys during 2010 ($N_{1,2,\pi}$; 95% HPD interval), 8,188–29,044 Sea Lampreys during 2011 ($N_{2,2,\pi}$), and 1,465–142,392 Sea Lampreys during 2012 ($N_{3,2,\pi}$). Point estimates of abundance decreased as the proportion of bias applied to local trap efficiency increased (Figure 2.8). When all acoustic tag bias was applied to local trap efficiency, the estimated number of adult Sea Lampreys ranged 277–5,154 Sea Lampreys during 2010 ($N_{1,2,\pi}$; 95% HPD interval), 3,905–17,641 Sea Lampreys during 2011 ($N_{2,2,\pi}$), and 658–80,604 Sea Lampreys during 2012 ($N_{3,2,\pi}$). Modified Schaefer abundance estimates in the Echo River, from releases of fin-punched Sea Lampreys, ranged 1,707–11,206 Sea Lampreys during 2010 (95% confidence interval), 6,317–11,162 Sea Lampreys during 2011, and 2,860–12,026 Sea Lampreys during 2012.

Abundance at release sites

The estimated total number of adult Sea Lampreys in the lower St. Marys River ($N^{*}_{\mathrm{i},\psi}$) was somewhat sensitive to the proportion of unmarked Sea Lampreys assumed to have entered the lower St. Marys River through Munuscong Lake (ψ) during 2010 and 2011, but not during 2012 (Figure 9). Differences in estimates of N^{*}_{i} over the range of ψ were driven by differences in exploitation by traps in the upper St. Marys River ($\lambda_{i,h,1}$) between release sites (Figure 7). Across the range of ψ, 95% HPD intervals for abundance in the lower river ranged 37,599–224,554 Sea Lampreys during 2010 ($N^{*}_{1,}$), 22,930–151,141 during 2011 ($N^{*}_{2,}$), and 36,238–117,383 during 2012 ($N^{*}_{3,}$).

Discussion

Even after accounting for estimated tagging biases, exploitation rates of St. Marys River traps, estimated from acoustic telemetry, were substantially lower than previous estimates. Previous analyses aimed at assessing the potential management benefits (reduced production of parasitic Sea Lampreys in the St. Marys River: Haeseker et al. 2007) assumed that both trap exploitation rates, and (consequently) sterile male release ratios were substantially higher than these findings suggest. Lower exploitation rates estimated in this study imply less effective control of adult Sea Lamprey reproductive success. Local trap efficiency and availability estimates for both trapping locations indicate that substantial increases in catch would require changes to existing Sea Lamprey trapping systems so that more Sea Lampreys would be attracted toward and into traps, or require installation of new traps in new locations, or both. Lower trap efficiency estimates for acoustic-tagged lampreys, versus modified Schaefer estimates for fin-punched lampreys, even after accounting for acoustic tag effects, also suggest that the equal catchability assumption of modified Schaefer estimates deserves more attention, particularly because this method is used to enumerate adult Sea Lampreys on numerous other Great Lakes rivers and is used in calculation of total number of spawning-phase Sea Lampreys in each lake (Mullett et al. 2003).

Implications for trap-based population control

Availability estimates suggested that traps in the upper St. Marys River have greater potential to provide population control, at the drainage scale, than the trap in the Echo River (Figures 2.5, 2.6). While more than half of the Sea Lampreys in the St. Marys River system were available to traps in the upper St. Marys River, low availability to the Echo River trap suggested that even if all adult Sea Lampreys in the Echo River had been caught during 2010 and 2012, less than 5% of adult Sea Lampreys in the St. Marys River drainage would have been removed. Availability to individual traps also varied substantially among years, so several years of study would be needed to adequately evaluate existing trap locations or to identify suitable locations for new traps. For example, Sea Lampreys that entered the study area through the North Channel were more likely to be captured in the Echo River during 2011 than 2010 or 2012 (Figure 2.7), and this variation was attributed to higher availability to the Echo River trap in 2011 than in other years (Figure 2.6). Similarly, greater exploitation at the upper St. Marys River during 2012 than 2010 or 2011 was driven, in part, by the relatively greater number of Sea Lampreys that moved to the upper St. Marys River from the North Channel in that year (Figure 2.5).

Although the causes of differences in availability among traps and years are not known, such variability among years offers some hope that if underlying causes can be understood, environmental modifications (e.g., pheromones, alarm substances, flows) might be used to improve availability to traps that are not in the primary migration route, attract Sea Lampreys toward efficient traps, or deter Sea Lampreys from entering tributaries without traps. Synthesized pheromones offer potential to draw more Sea Lampreys toward and into traps (Twohey et al. 2003; Wagner et al. 2006; Li et al. 2007), but more research is needed to fully realize their potential (Johnson et al. 2013). Chemical alarm cues offer potential to deter Sea Lampreys from tributaries with no traps or poor traps (Imre et al. 2010; Wagner et al. 2011). Finally, changes in flow and temperature can stimulate migratory behavior (Binder et al. 2010), so modification of those variables might offer potential to alter migration pathways or attract Sea Lampreys toward traps in rivers with dams.

The most obvious way to ensure high availability of adult Sea Lampreys to new traps is to place traps at the river mouth where the traps will be encountered by all adults entering the stream. Unfortunately, the current dependence on migration barriers (dams) for trapping means that existing traps are located near the end, rather than at the start of riverine spawning migration. In systems where barriers are close to stream mouths, barrier-integrated traps may have access to most or all of the spawning population. For example, in the Cheboygan River where a barrier-integrated trap is located only 2.5 km from the lake (versus 45–60 km upstream of release sites in the current study) 83–96% of adult Sea Lampreys were estimated available to the trap (Holbrook et al. 2014). Ironically, rivers with barrier-integrated traps close to the river mouth offer the best opportunities for trap-based control, but are also in most cases the least expensive rivers to treat with lampricides. Further, most existing methods for trapping Sea Lampreys in the absence of barriers (e.g., fyke nets) have only been used in small rivers due to logistical constraints and have not been formally used or evaluated for Sea Lamprey control due to low efficiencies compared to barrier-integrated traps. Understanding the tradeoff between availability and local trap efficiency for lower-river versus upper-river trapping locations is a first step toward developing effective open-channel traps.

Unless traps are located at river mouths, or downstream of all spawning habitat in a tributary, some fraction of the spawning population can spawn and will never encounter a trap in a system. Therefore, local trap efficiencies may need to be near perfect if traps are ever to replace lampricides for stream-specific control. For example, if 70% of adult Sea Lampreys in the St. Marys River drainage were available to traps, then all Sea Lampreys available to those traps would need to have been captured in order to remove 70% of the adult Sea Lamprey population in that drainage. Although results from this study represented only one drainage, local trap efficiency estimates (modified Schaefer method) among 33 traps that each caught more than 200 Sea Lampreys ranged 4–76% (median: 33%) in 2012 (summarized from Sullivan and Adair 2012). While low local trap efficiency suggests that great potential exists to improve traps, trap efficiencies in the upper St. Marys River have not increased during the last few decades, despite substantial effort to improve those traps, including the construction and operation of two new semi-permanent traps in 2006 and 2009, portable traps in 2010, and large-scale flow modifications in 2011 and 2012. Using passive integrated transponder telemetry and video monitoring in the upper St. Marys River, Bravener and McLaughlin (2013) found that only 12–13% of tagged Sea Lampreys encountered trap entrances, and of those only 18–31% entered the trap. They concluded that improved trapping success may require moving traps to locations with higher encounter rates, deploying more traps to improve overall encounter rates, using attractants or repellents to improve encounter rates, and redesigning trap openings to encourage entrance. Until highly-efficient trapping technologies can be developed, low-head barriers and chemical control methods will remain the backbone of the Sea Lamprey control program, at least for the foreseeable future.

Together, local trap efficiency and availability estimates suggest that trap-based control will require substantial advances in trapping technology, especially in systems as large and complex as the St. Marys River. Most trap designs have been motivated by the need for a barrier and attractant water flow to promote trap discovery and entrance. However, variation in efficiency among traps suggests that room for improvement exists. Better understanding of the variables that influence behavior of adult Sea Lampreys between river entry and spawning are needed to more reliably design and operate highly effective Sea Lamprey traps over a broad range of conditions. Efforts to develop mechanistic movement models have proven useful for designing behavioral guidance systems for other fishes (Goodwin et al. 2006).

Not surprisingly, lampricides offer much greater capacity for Sea Lamprey control compared to existing traps, but the points discussed above raise the question: Are the costs of trap installation, operation, and maintenance justified by the number of Sea Lampreys they remove? This question has been addressed to some degree (Haeseker et al. 2007; Dawson and Jones 2009) but the stock-recruit relation remains a critical uncertainty for such analyses.

Nonetheless, removal of individuals from the population is only one function of barrier-integrated traps. Traps also provide Sea Lampreys for population assessment and research (including development of alternative controls) and population assessment.

Implications for trap-based assessment and sterile-male releases

Differences between local trap efficiencies derived from acoustic-tagged and fin-punched Sea Lampreys in the upper St. Marys River suggest that adult abundance has been under-estimated in some locations with the modified Schaefer method. These differences have implications for stream-specific abundance estimates, lake-wide estimates, and theoretical estimates of suppression due to trapping and sterile male releases. One explanation for potential violation of the equal catchability assumption, offered by Bravener and McLaughlin (2013), is that the barrier integrated traps may capture a subset of the population that is predisposed to capture, owing to behavioral, physiological, or personality differences among individuals. Although my results in the upper St. Marys River were consistent with those of Bravener and McLaughlin (2013), a recent study found no difference between telemetry-based and modified Schaefer estimates of local trap efficiency in the Cheboygan River (telemetry: 60%; modified Schaefer: 62%; Holbrook et al. 2014). Evidently, violation of the equal catchability assumption can vary among traps likely due geographical differences among river systems and traps, but has not been broadly evaluated among traps. A need remains to empirically evaluate the causes and consequences of capture heterogeneity.

Adult abundance estimates in the upper St. Marys River, derived using acoustic telemetry, suggest that the ratio of sterile males to fertile males, a key metric used to predict the efficacy of the sterile male release program, was smaller than previously assumed. During 1997–2011, 16,743–43,184 sterile male Sea Lampreys (mean: 25,611 Sea Lampreys, among years) were released each year. Based on local trap efficiency estimates (modified Schaefer method) that ranged 25–59% (mean: 39%) and adult abundance estimates that ranged 8,162–38,829 Sea Lampreys (mean: 20,706 Sea Lampreys) among years, the estimated ratio of sterile to fertile males ranged 1.7–6.4 (mean: 3.6). The range of plausible abundance estimates obtained during this study (Figure 2.8) suggest that the actual target ratios of sterile to fertile males (telemetry-derived: 0.2–2.0 during 2010 and 0.4–3.6 in 2011) would have been lower than estimates based on the modified Schaefer model (1.4–2.2 in 2010 and 2.8–4.5 in 2011). While there is ample evidence, including *in situ* egg viability surveys conducted before and after 2011 (Bergstedt et al. 2003; Adair and Sullivan 2013) that releases of sterile males reduced the number of viable eggs in the upper St. Marys River, ratios based on acoustic telemetry suggest that the magnitude of the effect, and therefore the cost effectiveness, of sterile male releases was lower than previously expected. Ultimately, however, the effects of sterile male releases on recruitment to the parasitic life stage cannot be quantified because the magnitude of density-dependence during the larval life stage is unknown. In the St. Marys River, lampricide treatments (granular bayluscide) have contributed another source of uncertainty in the population-level effect of sterile male releases on recruitment to the parasitic life stage. Rigorous evaluations of control strategies that influence reproductive success (spawning and hatching), including sterile male releases and removal of individuals via traps, not only require accurate estimates of adult Sea Lamprey abundance (stock size), but also require understanding variables that influence survival between hatching and metamorphosis.

Future directions

The apparent negative effects of acoustic tags on behavior of Sea Lampreys (including movement and trap capture) added some complexity to analyses and uncertainty to estimates of exploitation, availability, local trap efficiency, and abundance. Although I was able to adjust estimates using paired releases of acoustic- and coded-wire-tagged Sea Lampreys, future studies will benefit from improved tagging methods. I am not aware of any specific guidelines for Sea Lamprey tagging, but information from Pacific lamprey, *Entosphenus tridentatus*, telemetry studies have suggested that the diameter of the tag is an important variable (Moser et al. 2007). Preliminary laboratory studies suggested that the acoustic tag effect was not related to anesthesia, incision, or presence of an object in the body cavity per se, but a combination of tag diameter and time since tagging that caused internal impingement due to longitudinal tag movement within the body cavity (C. Holbrook, unpublished data). Research is needed to identify the specific mechanism underlying the acoustic tag effect and develop methods that mitigate this problem so that the behavior of tagged adult Sea Lampreys will not be affected after release.

Release of Sea Lampreys that were captured in other systems and the timing of releases relative to upstream migration of the unmarked population also created sources of potential error and uncertainty during this study. Use of Sea Lampreys from other rivers is not expected to affect the ability of Sea Lampreys to orient toward spawning habitat in the St. Marys River, because Sea Lampreys do not home to natal streams (Bergstedt and Seelye 1995). However, the tendency for Sea Lampreys tagged with coded-wire and acoustic tags to be captured earlier than unmarked Sea Lampreys, although slight in some years (Figure 2.4), raises concern that Sea Lampreys captured in "early-run" streams might spawn earlier than unmarked conspecifics after release into "late-run" streams. Compared to unmarked Sea Lampreys in the St. Marys River, the Sea Lampreys released during this study may have been physiologically advanced in maturity due to prior experience in warmer water than the St. Marys River. Similarly, telemetry-based trap evaluations may be sensitive to timing of release of tagged fish relative to migration and capture of unmarked fish in the population of interest. Inadvertent releases of tagged Sea Lampreys after catches of unmarked Sea Lampreys had begun in the Echo River (Figure 2.4) did not likely affect estimates of availability to traps because no obvious differences occurred among release dates. However, this concern could be avoided in future studies by sampling directly from the river of interest. Unfortunately, existing capture methods for Sea Lampreys in large open channels are not likely to be efficient enough to provide sample sizes needed. To avoid those concerns, a priority for future studies should be to develop more effective methods for capturing migrating Sea Lampreys from the target river system.

In spite of the uncertainties and challenges described above, this study provided insights into the spatial dynamics of Sea Lamprey trapping in the most geographically complex interconnecting waterway in the Great Lakes. Few telemetry studies have also had the ability to empirically evaluate assumptions about the behavioral effects of telemetry transmitters in the field at scales relevant to management. Results from this study highlight the importance of testing even the most basic assumptions of mark-recapture and telemetry methods, and demonstrates how bias can be estimated and incorporated in models to improve inferences about parameters directly relevant to fisheries management. The framework used this study should also be readily applicable to others systems in which invasive species control is limited by knowledge of spatial population dynamics.

APPENDICES

APPENDIX 2A

Main Tables and Figures

Table 2.1.— Number of adult male and female Sea Lampreys implanted with acoustic tags, coded wire tags, or both, and released (M; number that were detected on telemetry receivers in the lower St. Marys River in parentheses) in Munuscong Lake (Site = 1) and the North Channel (Site = 2), with number detected near traps in the upper St. Marys River (D_{USM}) and Echo River (D_{ECH}), and number captured in the upper St. Marys River (R_{USM}) and Echo River (R_{ECH}) during 2010, 2011, and 2012.

Release			Male					Female				
Date	Site	Tag Type	M	D_{USM}	D_{ECH}	R_{USM}	R_{ECH}	M	D_{USM}	D_{ECH}	R_{USM}	R_{ECH}
2010-04-26	1	acoustic	25 (20)	13	0	2	0	25 (24)	17	0	2	0
2010-04-26	1	cwt	0			0	0	0			0	0
2010-04-26	2	acoustic	24 (24)	12	0	1	0	26 (24)	8	1	0	0
2010-04-26	2	cwt	0			0	0	0			0	0
2010-05-10	1	acoustic	25 (23)	18	1	2	0	25 (24)	12	0	1	0
2010-05-10	1	cwt	0			0	0	0			0	0
2010-05-10	2	acoustic	25 (25)	10	0	1	0	25 (24)	9	2	1	1
2010-05-10	2	cwt	0			0	0	0			0	0
2010-05-27	1	acoustic	25 (24)	16	0	2	0	25 (22)	11	0	0	0
2010-05-27	1	cwt	0			0	0	0			0	0
2010-05-27	2	acoustic	25 (24)	10	1	0	0	25 (25)	13	0	0	0
2010-05-27	2	cwt	0			0	0	0			0	0
2011-05-19	1	cwt	0			0	0	0			0	0
2011-05-19	2	both	25 (24)	4	9	1	2	25 (25)	11	4	1	1
2011-05-19	2	cwt	0			0	0	0			0	0
2011-05-20	1	both	25 (19)	13	0	1	0	24 (19)	14	0	1	0
2011-05-20	1	cwt	25			3	0	25			2	0
2011-05-20	2	acoustic	25 (25)	15	1	3	0	25 (24)	8	4	0	0
2011-05-20	2	cwt	25			1	2	25			1	4
2011-05-25	1	both	25 (19)	11	1	2	0	25 (21)	10	1	1	0
2011-05-25	1	cwt	25			3	0	25			2	1
2011-05-25	2	both	25 (24)	8	6	1	3	25 (24)	9	5	1	1
2011-05-25	2	cwt	25			0	0	25			1	1
2011-06-02	1	both	25 (25)	16	1	1	0	25 (23)	16	0	0	0
2011-06-02	1	cwt	25			2	1	25			1	0
2011-06-02	2	both	48 (47)	18	9	0	0	51 (49)	17	12	1	1

Table 2.1 (cont'd)

Release			Male					Female				
Date	Site	Tag Type	M	D_{USM}	D_{ECH}	R_{USM}	R_{ECH}	M	D_{USM}	D_{ECH}	R_{USM}	R_{ECH}
2011-06-02	2	cwt	25			1	2	25			0	2
2012-05-09	1	both	32 (28)	22	0	3	0	34 (29)	24	0	5	0
2012-05-09	1	cwt	25			5	1	25			5	0
2012-05-09	2	both	33 (33)	24	1	1	0	28 (27)	20	0	3	0
2012-05-09	2	cwt	25			8	0	25			2	0
2012-05-18	1	acoustic	33 (30)	22	1	2	0	34 (32)	21	0	3	0
2012-05-18	1	cwt	25			2	0	25			2	0
2012-05-18	2	acoustic	34 (34)	23	1	2	0	28 (27)	18	0	2	0
2012-05-18	2	both	1 (1)	0	0	0	0	5 (5)	3	0	1	0
2012-05-18	2	cwt	25			3	0	25			4	0
2012-05-24	1	acoustic	33 (32)	20	0	2	0	33 (30)	16	1	2	0
2012-05-24	1	cwt	25			1	0	25			3	0
2012-05-24	2	acoustic	24 (22)	14	1	2	0	33 (33)	14	0	0	0
2012-05-24	2	both	9 (9)	5	0	0	0	0 (0)	0	0	0	0
2012-05-24	2	cwt	25			2	0	25			2	0

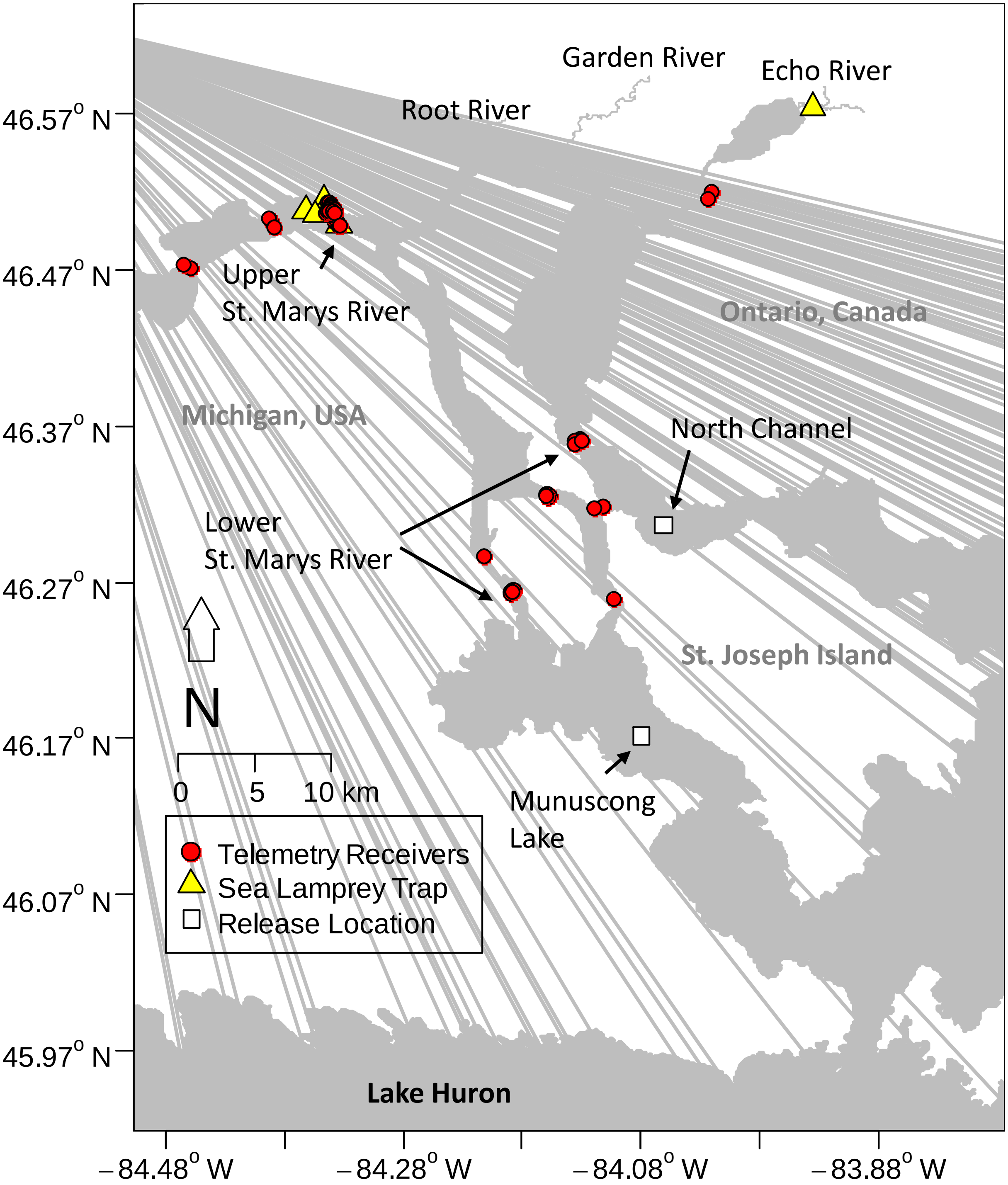

Figure 2.1.—Map of the study area showing locations of acoustic telemetry receivers and adult Sea Lamprey traps in the St. Marys River.

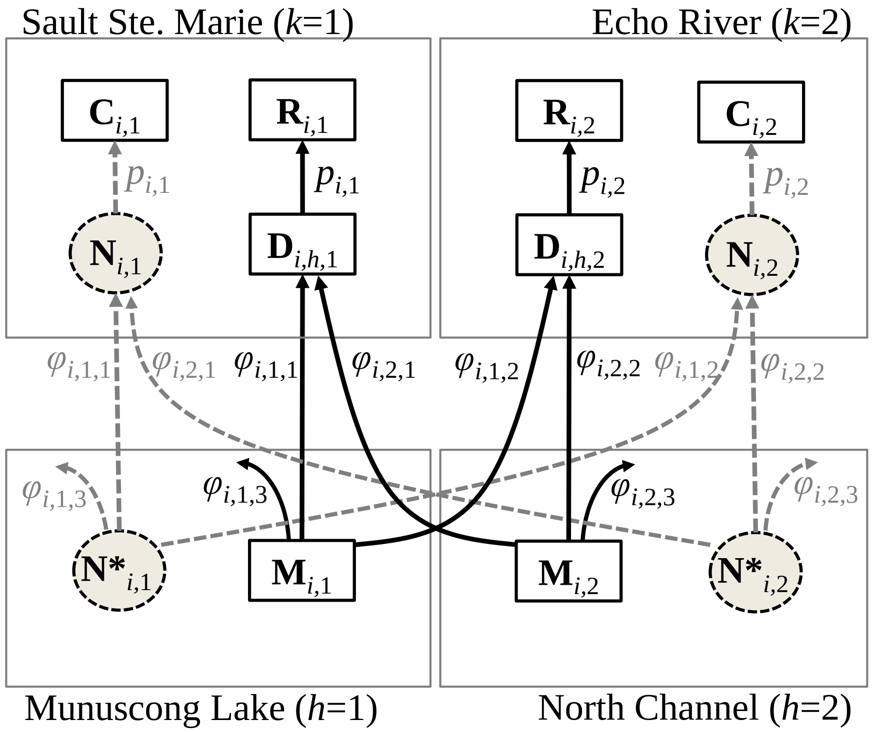

Figure 2.2.—Graph of model used to estimate year-specific (i) availability ($\varphi_{i,h,k}$) of adult Sea Lampreys from release locations to traps based on number of tagged Sea Lampreys released ($\mathbf{M}_{i,h}$) and later detected ($\mathbf{D}_{i,h,k}$) on telemetry receivers near traps; local trap efficiency ($p_{i,k}$) based on $\mathbf{D}_{i,h,k}$ and number caught ($\mathbf{R}_{i,k}$); number of unmarked adults present at each release ($\mathbf{N*}_{i,h}$) and trap site ($\mathbf{N}_{i,k}$) based on telemetry-derived availability and local trap efficiency estimates (solid arrows) and the number of unmarked Sea Lampreys caught in each trap ($\mathbf{C}_{i,k}$). Observed quantities are enclosed in empty boxes. Estimated quantities are enclosed in grey circles. Note: $N*_{i,1}$ and $N*_{i,2}$ were not directly estimable, but $N*_I = N*_{i,1} + N*_{i,2}$ was estimated.

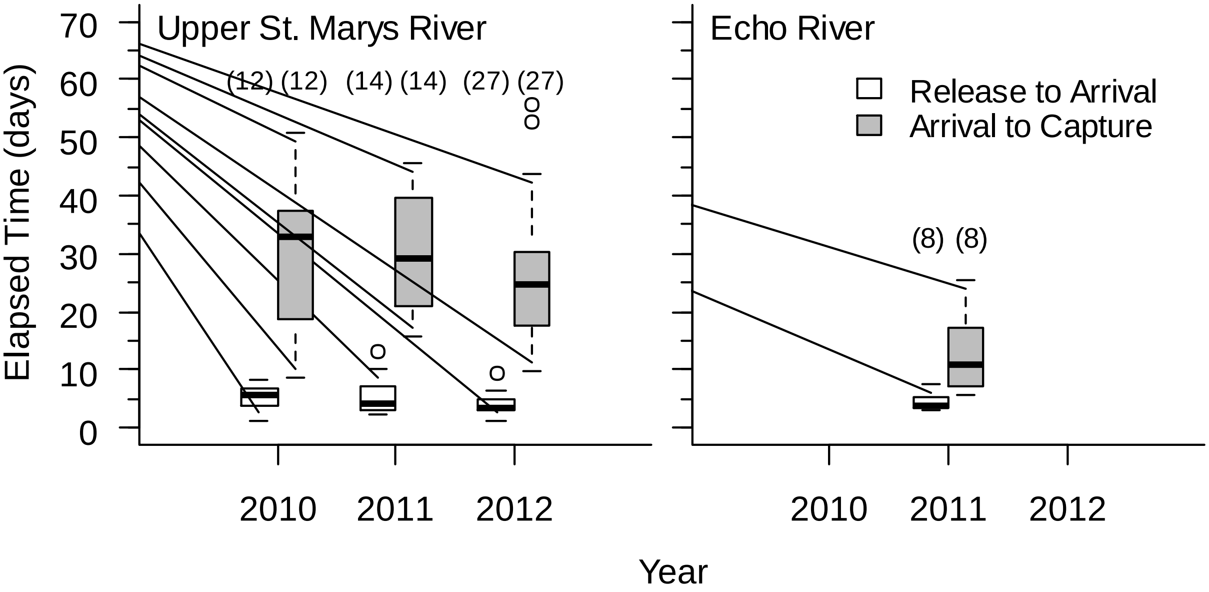

Figure 2.3.—Distribution of elapsed time, among acoustic-tagged adult Sea Lampreys, between release into the lower St. Marys River and arrival near trap sites (white boxes; determined by first detection on acoustic receivers in the upper St. Marys River and Echo River) and between arrival near trap sites and capture in traps (grey boxes). Sample sizes (number of Sea Lampreys) are shown in parentheses above each box. Box limits show first and third quartiles, whiskers show observations within 1.5 times the interquartile range of the median, and symbols show observations beyond whiskers.

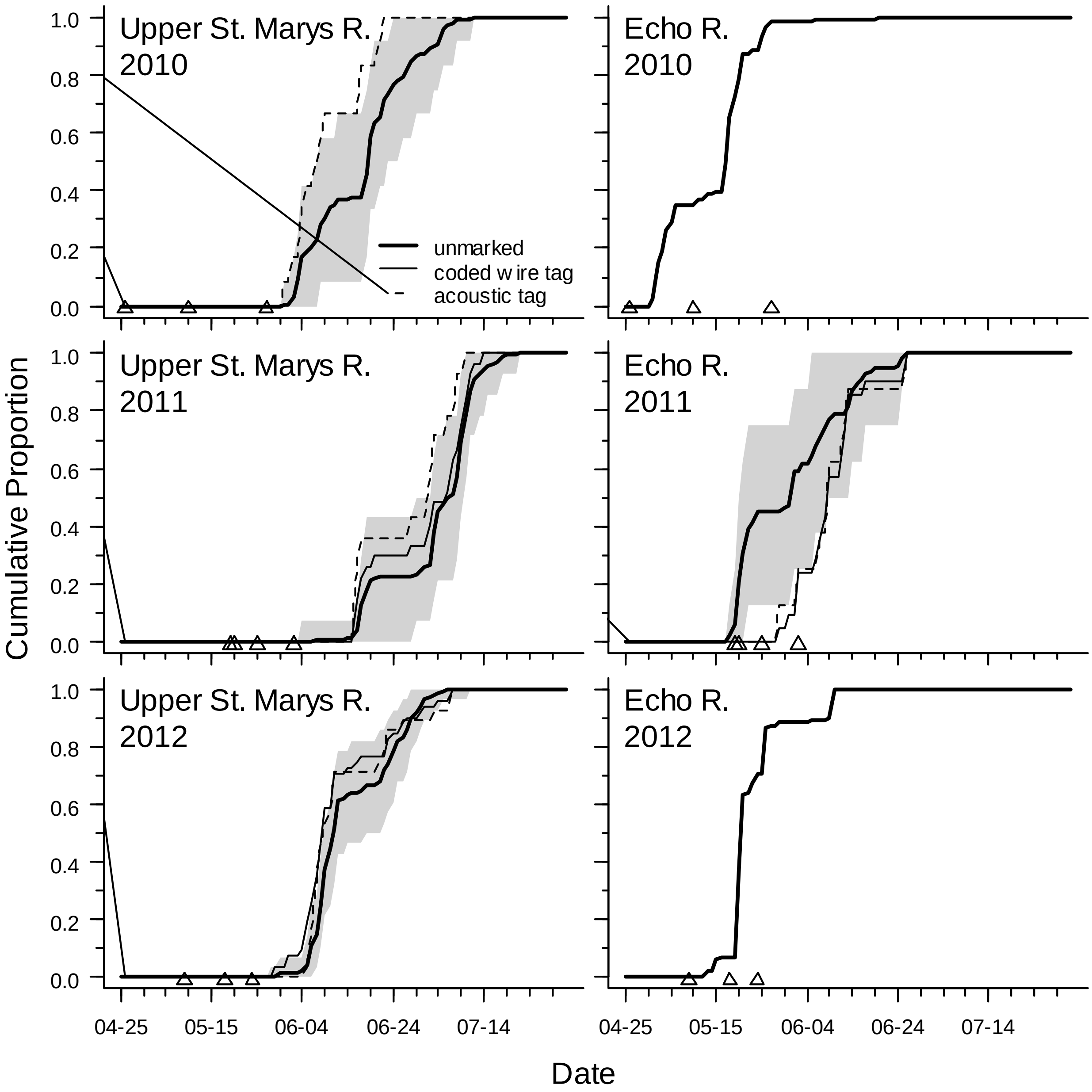

Figure 2.4.—Daily cumulative proportions of unmarked (heavy solid lines), acoustic tagged (light solid lines), and coded wire tagged (broken lines) Sea Lampreys caught in traps in the upper St. Marys River and Echo River during 2010–2012. Open triangles show dates when acoustic and coded wire tagged Sea Lampreys were released in the lower St. Marys River. Shaded regions show bootstrap 95% confidence regions for cumulative proportions of unmarked Sea Lampreys.

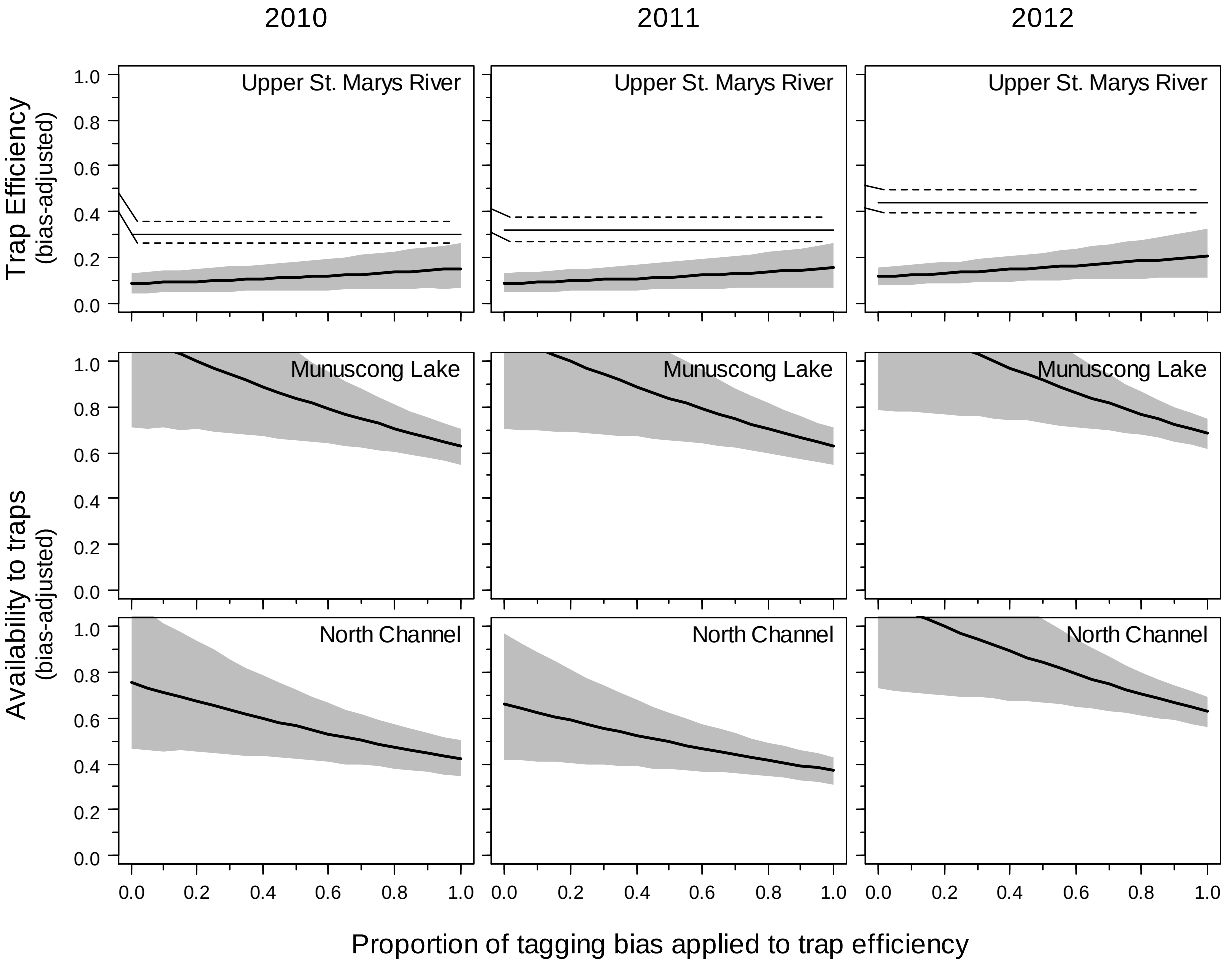

Figure 2.5.—Estimated local efficiency of traps in the upper St. Marys River (top row; heavy solid lines are posterior medians; shaded regions are 95% HPD intervals) and estimated proportion of Sea Lampreys that were available to traps in the upper St. Marys River from each release site in the lower St. Marys River, as a function of the proportion of acoustic tag bias applied to local trap efficiency during 2010–2012. In top panels, broken lines show 95% confidence limits around local trap efficiency estimates (light solid line) from the modified Schaefer method.

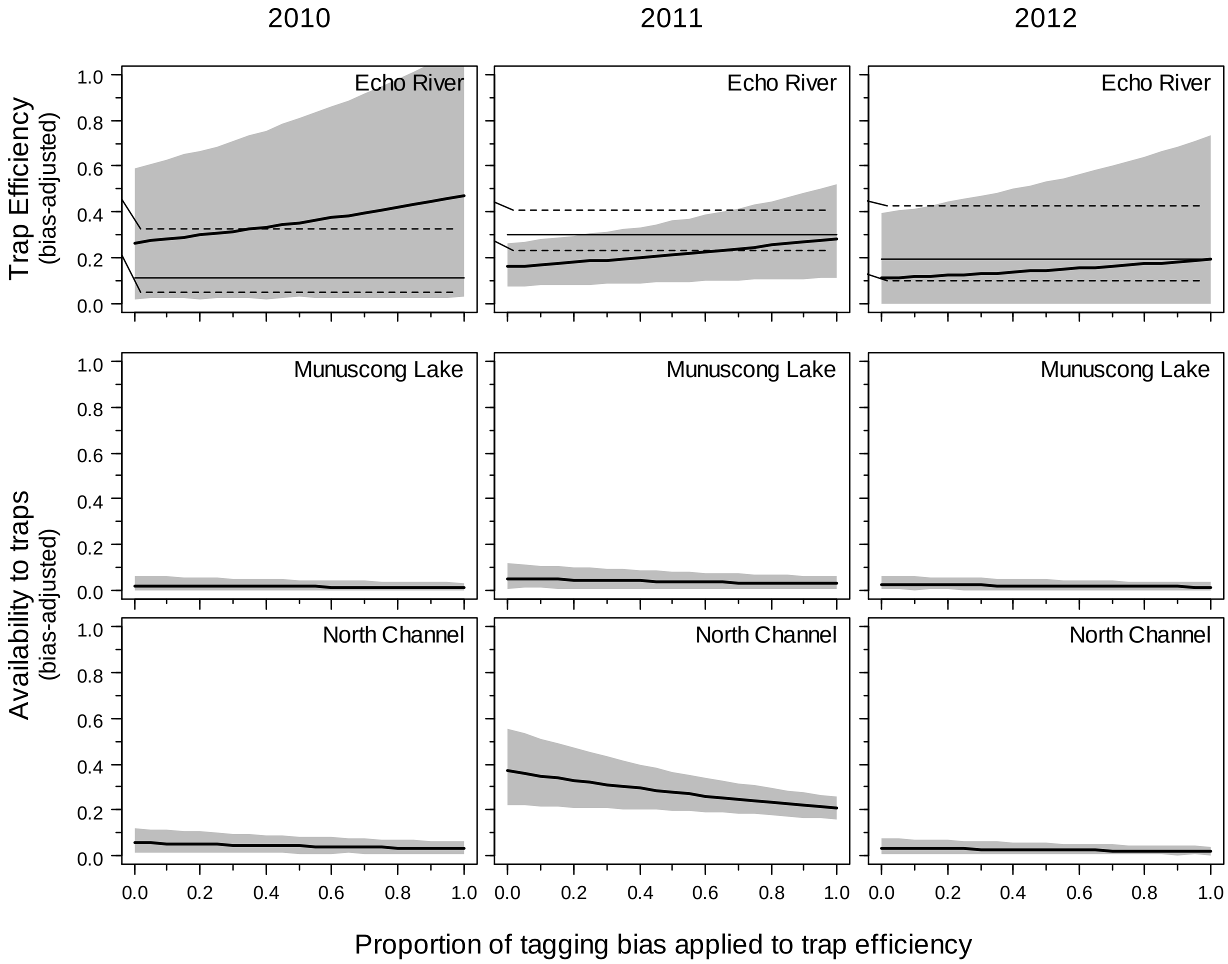

Figure 2.6.—Estimated local efficiency of the adult Sea Lamprey trap in the Echo River (top row; heavy solid lines are posterior medians; shaded regions are 95% HPD intervals) and estimated proportion of Sea Lampreys that were available to the trap in the Echo River from each release site in the lower St. Marys River, as a function of the proportion of acoustic tag bias that was applied to local trap efficiency during 2010–2012. In top panels, broken lines show 95% confidence limits around local trap efficiency estimates (light solid lines within 95% CI) from the modified Schaefer method.

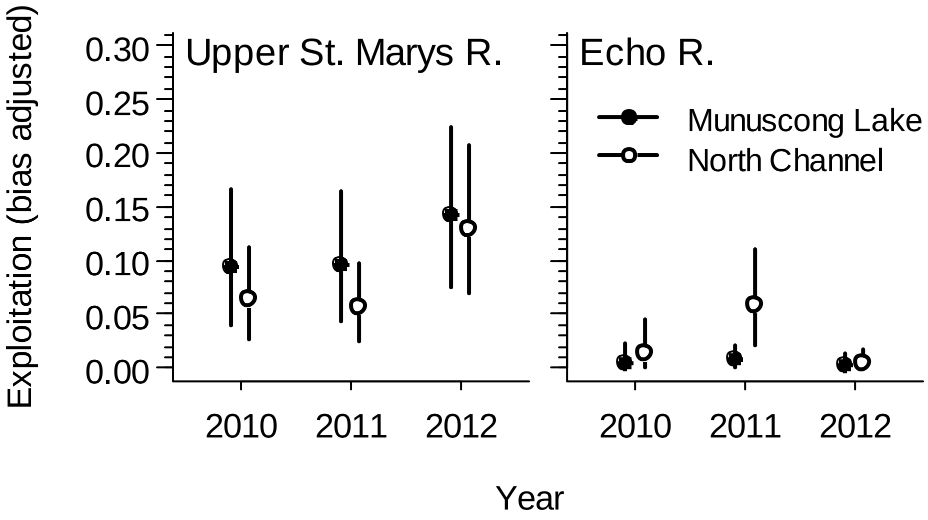

Figure 2.7.—Estimated proportion of adult Sea Lampreys that migrated through Munuscong Lake and the North Channel and were later caught (exploitation, adjusted for acoustic tag bias) in traps in the upper St. Marys River and Echo River during 2010, 2011, and 2012. Solid lines show 95% HPD intervals.

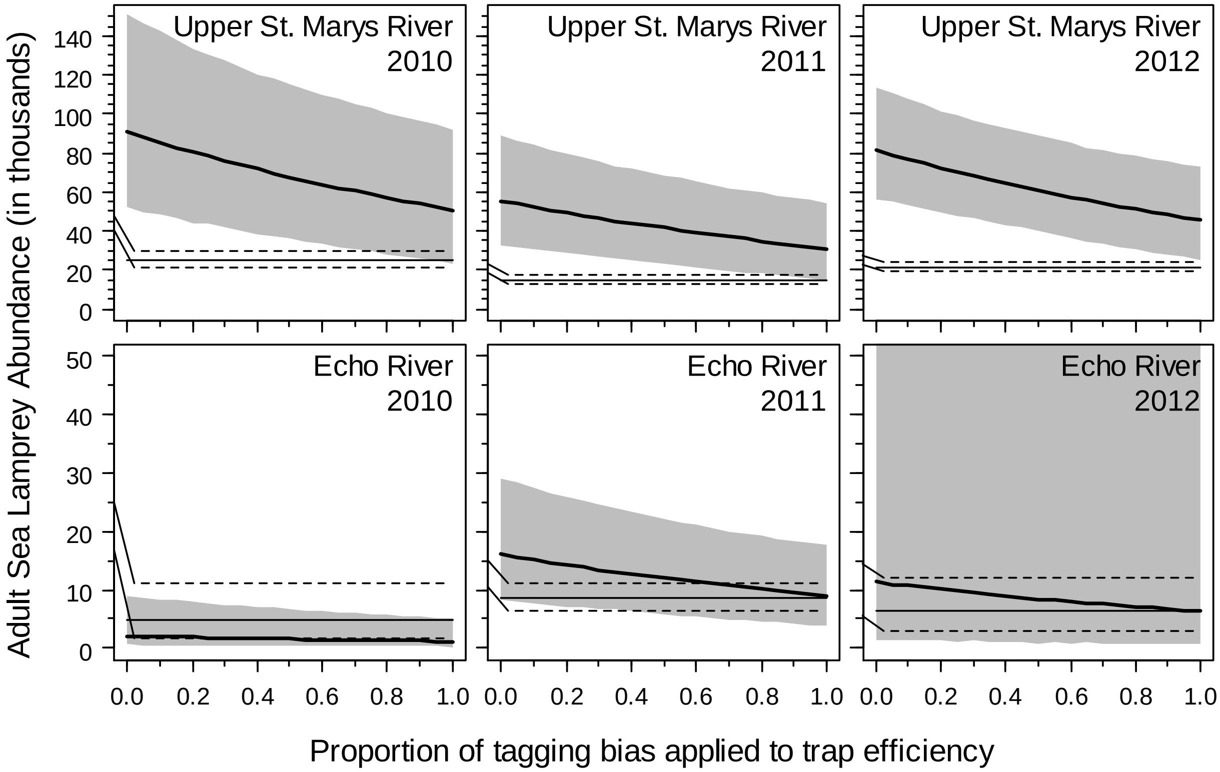

Figure 2.8.—Estimated number of adult Sea Lampreys (heavy solid line show posterior medians; shaded regions show 95% HPD intervals) near traps in the upper St. Marys and Echo Rivers, as a function of the proportion of acoustic tag bias applied to local trap efficiency during 2010–2012. Broken lines show 95% confidence intervals around abundance estimates (light solid lines) from the modified Schaefer method.

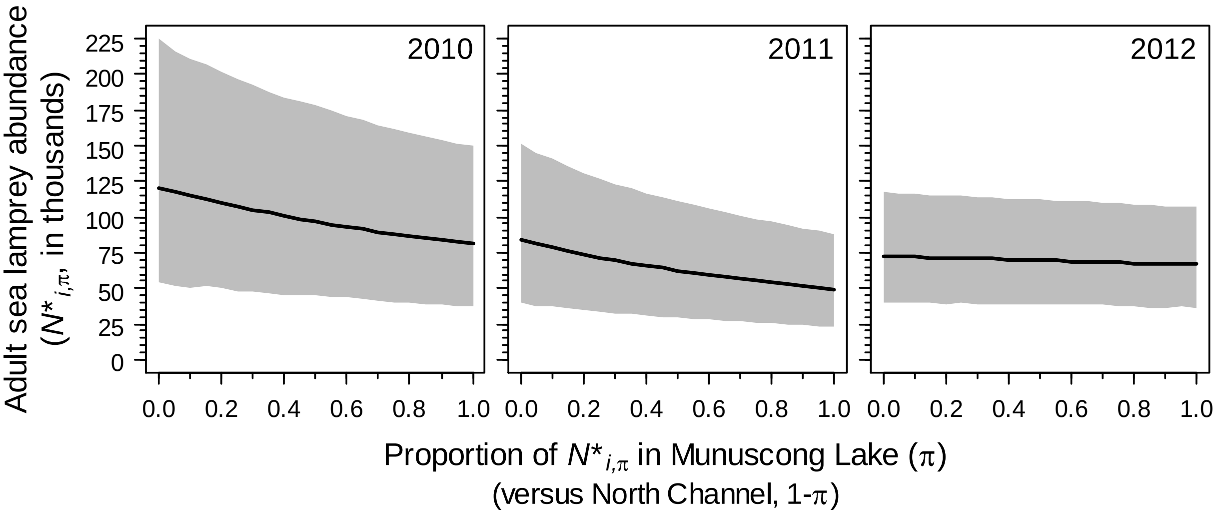

Figure 2.9.—Estimated number of adult Sea Lampreys in the lower St. Marys River as a function of the proportion of spawning-phase Sea Lampreys that entered the lower river through Munuscong Lake (versus the North Channel) during 2010–2012. Solid lines show posterior medians and shaded regions show 95% HPD intervals.

APPENDIX 2B

Model Checking

Appendix 2B.—Model checking and tests of model-specific assumptions about variables that influenced availability to traps, local trap efficiency, and the effect of acoustic tags on recovery of tagged Sea Lampreys in traps in the St. Marys River during 2010–2012.

Availability to traps

I assumed that the proportion of Sea Lampreys available to each trap ($\varphi_{i,h,k}$), from each release location during each year, did not differ between sexes or among replicate release groups (i.e., release date) during each year. To determine if those assumptions were supported by the data, I fit a set of candidate models in which the proportion of Sea Lampreys available, $\varphi_{i,h,k,m,j}$, to each trap (k = 1, 2) from each release site (h = 1, 2), during each year (i = 1, 2, 3) was estimated separately for each sex (m = 1, 2) within each replicate release group (j = 1, 2, 3). Four candidate models were fit to the data using Markov chain Monte Carlo (MCMC) simulation with OpenBUGS. The Deviance Information Criterion (DIC) was calculated, such that $DIC = \bar{D} + 2 \times pD$, where $\bar{D}$ was the mean of the posterior deviance, $pD = \bar{D} - D\left(\hat{\theta}\right)$ was an estimate of the effective number of parameters, and $D\left(\hat{\theta}\right)$ was the deviance at the posterior median of each parameter (Spiegelhalter et al. 2002). The posterior median was used as the plug-in deviance ($D\left(\hat{\theta}\right)$) because some posterior distributions were not symmetrical. Posterior distributions represented 100,000 samples derived from a single chain of 310,000 samples, from which the first 10,000 samples were discarded, and then every third sample was retained. The model with the smallest DIC was considered the best model and the difference in DIC (ΔDIC) between models was used as weight of evidence supporting each model over the best model. Since DIC is expected to behave similar to AIC, I also calculated DIC weights following Burnham and Anderson (2002).

While DIC can be useful for identifying the model, or subset of models, that offers optimal tradeoff between bias and precision to predict future observations, it does not indicate how well a model fits the data. Posterior predictive checks were used to evaluate goodness-of-fit for the assumed model. Specifically, I compared the observed number of tagged Sea Lampreys that moved to each trap site ($\mathbf{D}_{i,h,k,m,j}$) from each release site to the distribution of $\mathbf{D}_{\boldsymbol{rep}(i,h,k,m,j)}$, where $\mathbf{D}_{\boldsymbol{rep}(i,h,k,m,j)}$ were expected outcomes under the model. For each posterior sample of $\varphi_{i,h,k}$, $\mathbf{D}_{\boldsymbol{rep}(i,h,k,m,j)}$ was drawn from a multinomial distribution, such that $\mathbf{D}_{\boldsymbol{rep}(i,h,k,m,j)} \sim$ multinomial($\varphi_{i,h,k}$, $\mathbf{M}_{i,h,m,j}$). Any $\mathbf{D}_{i,h,k,m,j}$ that were not contained within the 95% HPD intervals for $\mathbf{D}_{\boldsymbol{rep}(i,h,k,m,j)}$ were considered more extreme than expected under the model.

Model selection results, based on DIC, supported the assumption that availability to traps did not differ between sexes or among replicate release groups within traps (Table 2.2). Posterior predictive checks suggested that the model fit the data reasonably well. Among 38 release groups (differentiated by sex, release site, and release date), only two observations were more extreme than expected under the model. In the first case, 15 tagged male Sea Lampreys, released in the Munuscong Lake on the first release date during 2011, moved to the upper St. Marys River, whereas 9-14 Sea Lampreys (95% HPD interval) were expected, under the model. In the second case, 14 tagged female Sea Lampreys, released in the North Channel on the third release date in 2012, moved to the upper St. Marys River, whereas 15–26 Sea Lampreys (95% HPD interval) were expected, under the model. Thus, in the most extreme departures from model predictions, observed outcomes only differed by one Sea Lamprey in each case.

Local trap efficiency

I assumed that local efficiency ($p_{i,k}$) of each trap during each year did not differ between sexes or among replicate releases within each year. To determine if those assumptions were supported by the data, I fit a set of candidate models in which $p_{i,k,m,j}$ at each trap (k = 1, 2) during each year (i = 1, 2, 3) was estimated separately for each sex (m = 1, 2) within each replicate release group (j = 1, 2, 3). Four candidate models were fit to the data and DIC was calculated and summarized for each model, as described for availability. To evaluate model fit, I compared the observed number of tagged Sea Lampreys caught in each trap ($\mathbf{R}_{i,k,m,j}$) to the distribution of $\mathbf{R}_{\boldsymbol{rep}(i,k,m,j)}$, where $\mathbf{R}_{\boldsymbol{rep}(i,k,m,j)}$ were expected outcomes under the model. For each posterior sample of $p_{i,k}$, $\mathbf{R}_{\boldsymbol{rep}(i,k,m,j)}$ was drawn from a binomial distribution, such that $\mathbf{R}_{\boldsymbol{rep}(i,k,m,j)}$ ~ binomial($p_{i,k}$, $\mathbf{R}_{i,m,j}$). Any $\mathbf{R}_{i,k,m,j}$ that were not contained within the 95% HPD intervals for $\mathbf{R}_{\boldsymbol{rep}(i,k,m,j)}$ were considered more extreme than expected under the model.

Model selection results, based on DIC, supported the assumption that trap efficiencies did not differ between sexes or among replicate release groups within traps (Table 2.3). Posterior predictive checks suggested that the model fit the data reasonably well. Among 19 groups at each trap (differentiated by sex and release date), no observations were more extreme than expected under the model.

Effects of acoustic tags on recovery in traps

I assumed that the probability of recovering a coded-wire-tagged Sea Lamprey ($\theta_{i,h}$) in the upper St. Marys River from each release site during each year did not differ between sexes or among replicate releases within each year, and that the acoustic tag effect (ω) did not differ among years, between release groups, between sexes, or among replicate release groups. A step-wise model selection approach was used to determine if those assumptions were supported by the data. First, I fit a set of candidate models in which $\theta_{i,h,m,j}$ for each release site (h = 1, 2) during each year (i = 1, 2) was estimated separately for each sex (m = 1, 2) within each replicate release group (j = 1, 2, 3). Four candidate models were fit to the data and DIC was calculated and summarized for each model, as described for availability to traps. Second, using the assumed model for $\theta_{i,h,m,j}$, I fit a set of candidate models in which $\omega_{i,h,j,m}$ was estimated separately for each sex (m = 1, 2), within each replicate release group (j = 1, 2, 3), at each release site (h = 1, 2) during each year (i = 1, 2). Sixteen candidate models were fit to the data and DIC was calculated and summarized for each model, as described for availability to traps.

Model fit was evaluated by comparing the number of number of coded-wire-tagged and acoustic-tagged Sea Lampreys recovered from each release group to the expected numbers under the model. To compare the observed number of tagged Sea Lampreys caught in each trap ($\mathbf{R}_{i,h,m,j,t}$; where t=1 for coded-wire-tagged Sea Lampreys and t=2 for acoustic-tagged Sea Lampreys) to the distribution of $\mathbf{R}_{\boldsymbol{rep}(i,h,m,j,t)}$, where $\mathbf{R}_{\boldsymbol{rep}(i,h,m,j,t)}$ were expected outcomes under the model. For each posterior sample of $\theta_{i,h,m,j}$ and $\omega_{i,h,j,m}$, $\mathbf{R}_{\boldsymbol{rep}(i,h,m,j,t)}$ was drawn from a binomial distribution, such that $\mathbf{R}_{\boldsymbol{rep}(i,h,m,j,1)} \sim \text{binomial}(\theta_{i,h,m,j}, \mathbf{R}_{i,h,m,j,1})$ and $\mathbf{R}_{\boldsymbol{rep}(i,h,m,j,2)} \sim \text{binomial}(\theta_{i,h,m,j} \times \omega_{i,h,j,m}, \mathbf{R}_{i,h,m,j,2})$. Any $\mathbf{R}_{i,h,m,j,t}$ that were not contained within the 95% HPD intervals for $\mathbf{R}_{\boldsymbol{rep}(i,h,m,j,t)}$ were considered more extreme than expected under the model.

Model selection results, based on DIC supported the assumption that the probability of recovering a coded-wire-tagged Sea Lamprey did not differ between sexes or among replicate release groups (Table 2.4). The DIC-best model for the acoustic tag effect provided evidence the tag effect may have differed among release dates within years (Table 2.5), although the small DIC difference suggests that the evidence for such a difference was weak. Posterior predictive checks suggested that the model fit the data reasonably well. Among 48 releases (differentiated by release site, sex, and release date), only two observations were more extreme than expected under the model. In the first case, three tagged male Sea Lampreys, released in the North Channel on the first release date in 2011, were caught in the upper St. Marys River, whereas 0–2

Sea Lampreys (95% HPD interval) were expected, under the model. In the second case, eight male Sea Lampreys released in the Munuscong Lake on the first release date during 2012 were caught in the upper St. Marys River, whereas 0–6 Sea Lampreys (95% HPD interval) were expected, under the model. Thus, in the most extreme departures from model predictions, observed outcomes only differed by one and two Sea Lampreys.

Table 2.2.—Model selection results for a set of candidate models used to test the assumption that availability to traps did not differ between sexes (sex) or among replicate release dates (repl) at each release site (rsite) for acoustic-tagged Sea Lampreys released in the lower St. Marys River during 2010–2012.

Model	Independent Variables	PD	$\bar{D}$	DIC	ΔDIC	W_{DIC}
4	year, rsite	11.4	267.1	278.5	0.0	0.998
2	year, rsite, sex	21.6	269.1	290.7	12.3	0.002
3	year, rsite, repl	31.6	269.9	301.5	23.0	<0.001
1	year, rsite, sex, repl	58.7	285.8	344.5	66.1	<0.001

Table 2.3.—Model selection results for a set of candidate models used to test the assumption that local efficiency of traps in the upper St. Marys and Echo rivers did not differ between sexes (sex) or among replicate release dates (repl) for acoustic-tagged Sea Lampreys released in the lower St. Marys River during 2010–2012.

Model	Independent Variables	PD	$\bar{D}$	DIC	ΔDIC	W_{DIC}
4	year, trap	5.1	95.5	100.6	0.0	0.905
2	year, trap, sex	9.4	96.3	105.8	5.2	0.067
3	year, trap, repl	13.4	94.1	107.5	6.9	0.028
1	year, trap, sex, repl	23.0	98.0	121.0	20.4	<0.001

Table 2.4.—Model selection results for a set of candidate models used to test the assumption that the probability of recovering a coded-wire-tagged Sea Lamprey ($\theta_{i,h,m,j}$) in the upper St. Marys River did not differ between sexes (sex) or among replicate release dates (repl) at each release site (rsite) for acoustic-tagged Sea Lampreys released in the lower St. Marys River during 2010–2012.

	Independent Variables						
Model	Recovery (θ)	Tag Effect (ω)	PD	$\bar{D}$	DIC	ΔDIC	W_{DIC}
4	year, rsite	year, rsite, sex, repl	12.8	147.6	160.4	0.0	0.790
3	year, rsite, repl	year, rsite, sex, repl	19.7	144.4	164.0	3.6	0.130
2	year, rsite, sex	year, rsite, sex, repl	16.5	148.6	165.0	4.6	0.080
1	year, rsite, sex, repl	year, rsite, sex, repl	29.7	148.5	178.2	17.8	<0.001

Table 2.5.—Model selection results for a set of candidate models used to test the assumption that the effect of acoustic tags ($\omega_{i,h,m,j}$) on the probability of recovering a Sea Lamprey in the upper St. Marys River did not differ among years, between release sites (rsite), between sexes (sex), or among replicate release dates (repl) at each release site (rsite) for tagged Sea Lampreys released in the lower St. Marys River during 2010–2012.

	Independent Variables						
Model	Recovery (θ)	Tag Effect (ω)	pD	$\bar{D}$	DIC	ΔDIC	W_{DIC}
15	year, rsite	repl	6.3	148.0	154.3	0.0	0.304
16	year, rsite	(none)	4.9	151.5	156.4	2.1	0.106
9	year, rsite	year, repl	7.7	149.2	157.0	2.7	0.079
10	year, rsite	rsite, repl	7.9	149.2	157.1	2.8	0.075
11	year, rsite	sex, repl	8.0	149.1	157.1	2.8	0.074
6	year, rsite	year, rsite	6.5	150.9	157.4	3.2	0.063
12	year, rsite	year	5.5	152.0	157.5	3.3	0.059
14	year, rsite	rsite	5.7	152.0	157.7	3.4	0.055
7	year, rsite	year, sex	6.8	151.3	158.1	3.8	0.045
13	year, rsite	sex	5.8	152.4	158.2	3.9	0.044
4	year, rsite	year, sex, repl	10.3	148.8	159.2	4.9	0.026
2	year, rsite	year, rsite, sex	8.5	151.6	160.0	5.8	0.017
3	year, rsite	year, rsite, repl	10.1	150.0	160.1	5.8	0.017
8	year, rsite	rsite, sex	6.9	153.3	160.2	5.9	0.016
1	year, rsite	year, rsite, sex, repl	12.8	147.6	160.4	6.2	0.014
5	year, rsite	rsite, sex, repl	10.4	151.3	161.7	7.4	0.007

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CHAPTER 3

MOVEMENTS OF ADULT SEA LAMPREYS AMONG REACHES OF A LARGE RIVER DURING SPAWNING MIGRATIONS

Abstract

Acoustic telemetry was used to describe the spatial distribution of adult Sea Lampreys (*Petromyzon marinus*) among reaches and braided tributaries of the St. Marys River. My objective was to determine if migration behavior of adult Sea Lampreys was consistent with the current conceptual model of spawning migration. Data from a three-year study provided a longitudinal movement history for each of 1,092 Sea Lampreys, released at two locations in the lower river that represented possible points of entry to the study system. Behavior of Sea Lampreys was consistent with the expectation that most adult Sea Lampreys make directed upstream movements until they encounter a barrier or spawning habitat. Results suggested that most Sea Lampreys (posterior median range among years: 0.578–0.712 for Munuscong Lake release site and 0.268–0.542 for North Channel release site) spawned in the upper reaches of the St. Marys River near Sault St. Marie or in the three tributaries to the upper North Channel (posterior median range among years: 0.046–0.087 for Munuscong Lake release site and 0.246–0.458 for North Channel release site), and that Sea Lampreys released in the lower North Channel were more likely to spawn in one of the three tributaries to the North Channel than Sea Lampreys released in the lower shipping channel (Munuscong Lake). The proportion of spawners at each location differed between release sites and among years due to differences in route selection probabilities at downstream bifurcations of the channel. However, the proportion of Sea Lampreys that ceased migration in the upper St. Marys River on the west side of Sugar Island after arrival at Sault Ste. Marie was larger than expected because this was at least 3 km downstream of the known spawning area near a complex of locks and dams. Results were used to infer the potential benefits of manipulating migration pathways for control of Sea Lamprey populations.

Introduction

Selection of a spawning location has profound consequences to the fitness of a migratory fish, as evident from the strong tendency of most migratory fishes to home to natal streams (Northcote 1984; Quinn and Dittman 1990). For many migrating fishes, such as Pacific salmon (*Oncorhynchus spp.*) knowledge of the variables influencing migration success have aided management of variables that might threaten the sustainability or conservation of valued stocks. Most often, such management actions are intended to promote selection of the correct or best migration pathway (Jansen et al. 2007; Perry et al. 2010) or timely arrival at suitable spawning areas (Boggs et al. 2004). For non-homing fishes, environmental variables that influence migration behaviors have even greater consequences to individuals and populations because they can much more strongly influence *where* a fish spawns. Therefore, understanding the processes that influence migration behavior and spawning site selection can be especially useful for planning and prioritizing activities intended to increase (e.g., for conservation or restoration) or decrease (e.g., for invasive species) fitness, and hence recruitment.

The Laurentian Great Lakes were severely disrupted by the arrival of invasive Sea Lamprey, *Petromyzon marinus*, through the Welland Canal in the early 1900s (Smith and Tibbles 1980; Hansen 1999). Since the late 1950s, Sea Lamprey populations have been suppressed with selective pesticides (lampricides) that target larvae in streams, barriers that block access to spawning habitat, traps that remove adults prior to spawning, and from 1997 to 2011, releases of sterilized male Sea Lampreys to compete with fertile males (Christie and Goddard 2003; Twohey et al. 2003; Bergstedt and Twohey 2007). Much effort has been directed toward understanding and predicting the relative effectiveness and cost of treatment options within each drainage so that options can be prioritized (Schleen et al. 2003). Recent research has also focused on ways to encourage or discourage adult Sea Lampreys from entering streams by use of attractants (Sorensen and Vrieze 2002; Johnson et al. 2013; Twohey et al. 2013), repellants (Imre et al. 2010; Wagner et al. 2011), or electric guidance systems (Johnson et al. 2014). If developed, those strategies offer potential to optimize Sea Lamprey control at the drainage level; however, the effectiveness of those strategies at a given location will depend upon the proportion of adult Sea Lampreys that arrive at that location and their subsequent behavior. Therefore, understanding the spatial distribution of adult Sea Lampreys and more generally, variables influencing migration behavior are needed to inform application of behavioral guidance strategies that target adult Sea Lampreys.

Like other anadromous fishes, Sea Lamprey use environmental cues to navigate and orient toward spawning habitats. Sea Lampreys do not home to natal streams (Bergstedt and Seelye 1995). Rather, stream selection and upstream migration are determined by “migratory” pheromones released by larval conspecifics (Sorensen and Vrieze 2003; Wagner et al. 2009; Vrieze et al. 2011). Sea Lampreys are primarily nocturnal during migration, especially at low temperatures (Andrade et al. 2007; Binder and MacDonald 2008A), and seek refuge under rocks, woody debris, or other structures during daytime. In general, migration activity increases with temperature and, in some streams, discharge (Almeida et al. 2002; Binder et al. 2010). Sea Lampreys may remain in one place for several weeks prior to spawning (Almeida et al. 2002), but it is not well understood how lampreys select a location for pre-spawn “staging” or how barriers may affect the onset of this behavior. Spawning occurs in early summer and peak activity has been observed when stream water temperature is about 17 to 19 °C (Applegate 1950; Beamish 1980). Spawning site and mate selection are mediated by pheromones elicited by conspecific adults (Li et al. 2002; Johnson et al. 2009), water quality (e.g., water temperature, dissolved oxygen), water velocity, and substrate quality (e.g., size, type). Despite a wealth of information about the variables that influence migration behavior in Sea Lampreys, most of the current knowledge of Sea Lamprey ecology has come from those habitats where animals are easily observed—namely in small streams or at barriers within streams (Bergstedt and Swink 1995). Several critical uncertainties remain in the current conceptual model for the Sea Lamprey spawning migration, especially in large (non-wadable) rivers (McLaughlin et al. 2007). Fortunately, emerging technologies (e.g., telemetry, sonar imaging) are increasingly providing the ability to "observe" fish in environments where conventional methods cannot be used.

I used acoustic telemetry to determine if migration behavior of adult Sea Lampreys in the St. Marys River were consistent with the current conceptual model of Sea Lamprey behavior during spawning migration. The St. Marys River is a good example of a system in which multiple control strategies are implemented concurrently. Sea Lampreys spawn within the main channel of the St. Marys River and its tributaries. Tributaries have been treated regularly with the lampricide 3-trifluoromethyl-4-nitrophenol (TFM).The upper St. Marys River and North Channel have been treated with lampricide granular Bayluscide. Bayluscide is considered a cost-effective alternative to TFM in deep and large-volume environments because its granules sink to the bottom before dissolving, concentrating the lampricide within and near the substrate. However, TFM treatments in small streams generally kill a larger proportion of a target larval population than Bayluscide treatments in large rivers. I hypothesized that (1) most adult Sea Lampreys would show uninterrupted, nocturnal, upstream movement to areas inhabited by larvae; (2) the proportion of Sea Lampreys using each route upstream of channel bifurcations would be positively associated with discharge, water temperature, and larval abundance in each route; (3) most adult Sea Lampreys would remain near areas occupied by larvae until water temperatures reached about 10 °C; (4) adult Sea Lampreys would move short distances to spawning habitat when temperatures exceed about 10 °C; and (5) when Sea Lampreys encountered a migration barrier, most Sea Lampreys would cease migration near that barrier, as long as larvae were present at that location.

Acoustic telemetry data from a three-year study provided a longitudinal movement history for each of 1092 Sea Lampreys, released at two locations in the lower river that represented possible points of entry to the study system (see Chapter 2). To test hypotheses, I (1) described the final locations of adult Sea Lampreys (presumed spawning locations) among reaches and tributaries throughout the study area; (2) compared directionality of migration among locations; (3) quantified route selection probabilities at channel bifurcations (including tributaries, diverging and converging channels) and compared those probabilities among locations and years; and (4) compared propensity to cease migration after arrival between reaches with and without a barrier. Results provided a quantitative, descriptive foundation needed to understand variables that influence Sea Lamprey spawning locations in large rivers with multiple possible migration routes. This information furthers understanding how these variables influence (1) the probability that adult Sea Lampreys encounter and remain near barriers and structures commonly associated with barriers (e.g., traps, fishways); (2) propensity to spawn in locations where offspring would be most susceptible to lampricides (e.g., small tributaries); and (3) the potential benefits of manipulating migration pathways for control of Sea Lamprey populations the Great Lakes or restoration of native lampreys elsewhere (e.g., Sea Lampreys in the Atlantic or Pacific Lamprey).

Methods

Study site

The St. Marys River is the primary outflow from Lake Superior and is considered a major source of Sea Lamprey to Lake Huron. Median daily discharge at the city of Sault Ste. Marie, Michigan during May–July ranged 1,022–2,114 m^3/s in 2010, 982–2,138 m^3/s in 2011, and 1,109–2,212 m^3/s in 2012. Within each day in 2010, 2011, and 2012, maximum discharge was typically (median among days) 4.3, 2.7, and 2.4 times greater than minimum discharge, and greatest discharge was commonly observed during day due to hydro-electric operations. Downstream of Sault Ste. Marie, where several hydro-electric dams, navigation locks, and spill gates are believed to block upstream migrating Sea Lampreys, the river splits into two main flow routes. The more southern route flows between Sugar Island and the mainland of Michigan, USA (Figure 3.1) and is a dredged shipping channel with relatively uniform depth across its width. The dredged shipping channel is well-defined from Sault Ste. Marie to Munuscong Lake, including each side of Neebish Island. The more northern route that flows between Sugar Island and the mainland of Ontario, Canada, known as the North Channel (Figure 3.1), has not been uniformly dredged and has greater variability in substrate and depth than the shipping channel.

The upper St. Marys River was treated with granular Bayluscide during each year of this study. Three tributaries to the North Channel, Echo, Root, and Garden rivers, were treated with TFM during the study. Portions of the Root River known to produce larval Sea Lampreys (51.7 rkm in each year) were treated with TFM in 2009 and 2010. All portions of the Garden River known to produce larval Sea Lampreys (73.7 rkm) were treated with TFM in 2009, a small portion of which (10.3 rkm in two tributaries) were treated again in 2010, and the remainder (60.4 rkm in the main-stem) were treated again in 2011. Portions of the Echo River known to produce larval Sea Lampreys were treated, including 7.2 rkm in 2008, 2.6 rkm in 2010, 16.1 rkm in 2011, and 16.7 rkm in 2012. Among those streams, the Garden River is considered to have the greatest potential to produce larval Sea Lampreys and the Echo River is considered to have the smallest potential to produce larval Sea Lampreys (Mike Steeves, DFO, personal communication). Discharge in each tributary was assumed to be roughly an order of magnitude smaller than discharge in the North Channel. Discharge in the tributaries during summers of 2010–2014 ranged 1.2–5.7 (median 3.7) m^3/s in the Root River, 4.2–10.0 (median 8.3) m^3/s in the Garden River, and 0.1–0.9 (median 0.3) m^3/s in the Echo River. In contrast, discharge of the North Channel, measured on six dates in 2010, 2011 and 2012 near sites CKI and GRD (Figure 3.1) ranged 296–532 (median 473) m^3/s.

Fish collection, tagging, and release

Adult Sea Lampreys (N = 1092) were collected from adult Sea Lamprey traps in three tributaries to northern lakes Huron (Chebogan River) and Michigan (Peshtigo and Manistique rivers), implanted with acoustic transmitters (V9-4H and V9P-4H; VEMCO, Nova Scotia, Canada), and released at two locations in the lower St. Marys River (Figure 3.1) during 2010, 2011, and 2012, as described in Chapter 2.

Telemetry receivers

Acoustic telemetry receivers (model VR2W, VEMCO) were deployed at 20–25 sites in 2010, 2011, and 2012; 15 of those sites were included in these analyses (Figure 3.1). No receivers were placed in the Garden River (site GRD) in 2010, but all other sites were monitored in all years. All receivers were deployed prior to release of any Sea Lampreys in each year and removed after Sea Lamprey traps were removed from the upper St. Marys and Echo rivers, typically during first week of August. At some sites, multiple receivers were placed across the river channel to ensure that all Sea Lampreys would be detected during passage.

Water temperature and river discharge

Water temperature was recorded at various locations throughout the study area using temperature-sensing acoustic tags (model V7TP-6L and V13T-4L; VEMCO) that transmitted temperature to nearby telemetry receivers every 500–700 seconds, temperature loggers (Hobo Water Temp Pro-V2; Onset Computer Corporation, Bourne, MA) that recorded water temperature every 15–30 minutes, water quality sondes (model 6920V2-2; YSI Inc., Yellow Springs, OH) that recorded water temperature every 15–30 minutes, or by gauging stations operated by NOAA (data retrieved from <http://tidesandcurrents.noaa.gov/>). Discharge data for the St. Marys River at Sault Ste. Marie were obtained from USGS Michigan Water Science Center. At the time that discharge data were obtained (06 January 2015), they were considered provisional and subject to revision (Thomas Weaver, USGS, personal communication).

Data processing

False positive detections can be recorded on acoustic telemetry receivers when two or more tag signals arrive concurrently on a receiver (Pincock 2012; Beeman and Perry 2013). To remove false-positive detections, I omitted all detections from the dataset that were not within 30 minutes of another detection of the same ID code on each receiver. As a result, I removed 0.39 % (28,211 of 7,303,720) of tag detections; including 0.43% in 2010; 0.27% in 2011 and 0.47% in 2012. Data were also filtered to resolve some spatial ambiguity (simultaneous detections on distant receivers). Specifically, I omitted sequential detections among sites at SSM, CKI, or ISL (3.0–4.3 rkm apart) and between URC and LRC (2.8 rkm apart) when the interval between those detections was less than 15 minutes. As a result, I omitted 767 detections. I also omitted one fish (ID: 4974) that was never detected after release, but caught in a trap, indicating that its transmitter was not working properly (see Chapter 2). I defined arrival of each Sea Lamprey at each receiver site as the date and time of the first detection at that site after detection (or release) at a different site. Each pair of consecutive arrival events for each tagged Sea Lamprey defined a movement event among sites (hereafter, 'site-transition').

Estimating detection probabilities and imputing missing detections

All tagged Sea Lampreys were assumed to have been detected at each telemetry receiver site during passage. To check for violations of that assumption, I compared each site-transition for each tagged Sea Lamprey to the set of plausible first-order (i.e., direct) site-transitions. First-order site-transitions were identified based on the structure of the river system. For example, following release in Munuscong Lake, a tagged Sea Lamprey could not be detected on any receivers without passing sites RNS or LRC, so only two first-order site-transitions were plausible after release at MNS (Figure 3.1). When an observed site-transition was not in the set of plausible first-order site-transitions (i.e., the fish must have been missed by receivers at one or more sites) I then checked if the observed movement could have arisen as a result of a second-order movement (derived from the set of first-order transitions) between those sites. Among 5,474 total site-transitions, 18 (0.3 %; 3 in 2010; 11 in 2011; 4 in 2012) were not identified as first-order site-transitions, and 17 of those could be explained by a single second-order transition. Therefore, the location of the missed detection was inferred. One observed transition (MNB–

LRC) could be explained by two second-order transitions (i.e., fish could have passed by LRC or RNS), but fine-scale tracking data (CMH, unpublished data) indicated that the fish approached LRC from downstream, so it was determined that the fish was missed by receivers at RNS (Figure 3.1). Timestamps for all missed detections were chosen as the midpoint of timestamps at the other stations. Direction of movement (i.e., upstream or downstream) was assigned to each observed and imputed movement based on direction of river flow among sites.

Data analysis

Spatial distribution of spawners

I used a multinomial model to estimate the proportion of Sea Lampreys within each year that was last detected at each location. To eliminate bias due to possible behavioral effects associated with handling and release (see Kelso and Gardner 2000), I only included Sea Lampreys that were detected at least once after release (see Chapter 2). Specifically, I assumed that the number of Sea Lampreys that ceased migration after detection at each station in each year (y_{ijk}), was the outcome of a multinomial process, such that $y_{ijk} \sim multinomial(\theta_{ijk}, N_{ij})$; where θ_{ijk} was the probability that a Sea Lamprey released at the *j*th release site during the *i*th year ceased migration at the *k*th monitoring station, and N_{ij} was the number of tagged Sea Lampreys detected on at least one receiver after release at the *j*th release site during the *i*th year. The model was fit with Markov chain Monte Carlo Simulation (MCMC) using the software program OpenBUGS (Lunn et al. 2009; Giminez et al. 2009; Ntzoufras 2009). A flat Dirichlet prior distribution was used to represent lack of prior knowledge of each θ_{ijk} . Inferences were based on the distribution of 10,000 posterior samples for each parameter, derived from a single chain of 11,000 samples (i.e., 1,000 burn-in samples and no thinning). Trace and autocorrelation plots of each parameter were used to confirm that chains were well-mixed and free of autocorrelation. The median among posterior samples was used as a point estimate of each parameter and uncertainty was summarized by 95% highest posterior density (HPD) intervals (Gelman et al. 2003; King et al. 2010).

Directionality, route selection, and cessation of migration

A multinomial model was also used to estimate the proportion (φ_{ijkm}) of tagged Sea Lampreys that moved to each possible destination station after arrival at each telemetry receiver and was further conditioned on direction of movement (upstream or downstream) at time of arrival. Specifically, I assumed that $y_{ijkm} \sim \mathit{multinomial}(\varphi_{ijkm}, N_{ijm})$; where y_{ijkm} was the number of times that a tagged Sea Lamprey moved from (or were released at) the *j*th site to the *k*th possible destination site in the *i*th year, given that it was moving in the *m*th direction (*i* = 1 for upstream and 2 for downstream) when it arrived at site *j*, and N_{ijm} was the number of times that a tagged Sea Lamprey arrived at site *j* in the *m*th direction during year *i*. I assumed that φ_{ijkm} was equal among all Sea Lampreys for each site, year, and direction. The number of possible destination sites (*K*) varied among sites based on the number of possible first-order transitions at each location and ranged from one to five among sites. For example, after release at Munuscong Lake (site MNS), a Sea Lamprey could only be detected at sites LRC or RNS because only two observable destination states were possible from that site. After arrival at sites SSM and ECH, Sea Lampreys could also have been caught in traps, so additional states represented traps in the upper St. Marys (site SMT) and Echo (site ECT) rivers (Figure 3.1). Finally, one additional state, denoted by 'XXX', was used to indicate that a tagged Sea Lamprey was not later detected (or captured) at any other site. In some cases (e.g., sites BRS, ECH, GRD, and RTR when Sea Lampreys were moving upstream; sites DCK, RNS, and LRC when Sea Lampreys were moving downstream) transition to “XXX” represented emigration from the study area. At other locations (e.g., sites SSM, ISL, and CKI) transition to “XXX” represented cessation of migration, due to spawning or death, within a reach bounded by receivers. However, I was not able to differentiate spawning and death with these data. The model was fit using MCMC and summarized as described above. No telemetry receivers were installed in the Garden River in 2010, so $\varphi_{2010,GRM,GRD,1}$ was derived by assuming that the proportion of Sea Lampreys that ceased migration after detection at site GRM in 2010 ($\varphi_{2010,GRM,XXX,1}$) was not different than proportion that ceased migration in 2011 or 2012. Therefore, posterior samples of $\varphi_{2010,GRM,XXX,1}$ and $\varphi_{2010,GRM,GRD,1}$ were adjusted accordingly.

A binomial model was used to estimate the proportion (ψ_{ij}) of tagged Sea Lampreys that entered the secondary channel (i.e., route with smallest discharge) versus the primary channel at each of five bifurcations within the study area. Specifically, I assumed that the number of Sea Lampreys (y_{ij}) that used the secondary channel after arrival at each bifurcation in each year was the outcome of a binomial process, such that $y_{ij} \sim binomial(\psi_{ij}, N_{ij})$; where N_{ij} was the number of tagged Sea Lampreys that arrived at the *j*th bifurcation in the *i*th year. Only the first upstream arrival at each bifurcation was used for each tagged Sea Lamprey. During each year, route selection probabilities were estimated at six bifurcations, denoted by the closest site downstream of the bifurcation and the site located within the secondary channel. The model was fit using MCMC and summarized as described above, except that a flat uniform distribution was used to represent lack of prior knowledge about each ψ_{ij}.

Penalized spline regression (Crainiceanu et al. 2005) was used to determine if the probability (ψ_{ij}) of entering each of the three tributaries to the North Channel changed over time within each year and to explore potential relations between ψ_{ijt} and water temperature. Penalized spline regression is a semi-parametric approach in which a set of polynomial curves are fit through the range of data; each anchored to the next at a pre-specified location, or knot. In contrast to other approaches (e.g., logistic regression), the relation between the covariates and the response are determined by the data, not by the model. I used penalized spline regression in this case because to allow the relationship to change over time (Giminez et al. 2006). Following Crainiceanu et al. (2005), I assumed that selection of the secondary migration route (y_{ijt} = 1) versus the primary migration route (y_{ijt} = 0) for the *j*th bifurcation in year *i* was the outcome of a Bernoulli process in which the probability of success was dependent upon the time *t* when a Sea Lamprey arrived at the bifurcation, such that y_{ijt} ~ Bernoulli(ψ_{ijt}) and $log\,it(\psi_{ijt}) = \beta_0 + \beta_1 t + \sum_{k=1}^{K} b_k (t - k_k)^3$, where β_0 and β_1 are the slope and intercept of a linear function (fixed effect) and $\sum_{k=1}^{K} b_k (t - k_k)^3$ is an offset imposed by the random effect $b_k \sim normal(0, \sigma_b^2)$ and the distance between time *t* and *k*th knot. I used *K* = 10 knots and the position of the knots was determined so that the *k*th knot was the sample quantile of time corresponding to probability *k*/(*K* + 1). The continuous covariate, *t*, were centered and standardized. Vague normal prior distributions were used (e.g., $N(0, 1.0 \times 10^6)$) for β_0 and β_1 and vague gamma distributions for precision of b_k (i.e. $\sigma_b^{-2} \sim Gamma(0.01, 0.01)$). Posterior distributions of each ψ_{ijt} were derived for *t* equal to each day of the migration period and posterior medians and 95 % HPD regions were plotted against median daily water temperature in each tributary and in the main-stem North Channel (site GRM).

Penalized spline regression was also used to determine if the probability of ceasing migration at two sites in the upper St. Marys River ($\varphi_{i,SSM,XXX,t}$ and $\varphi_{i,ISL,XXX,t}$) changed over time within each year and to explore potential relations among $\varphi_{i,j,XXX}$, discharge, and water temperature at Sault St. Marie. Model structure was exactly the same as described for route selection. Posterior distributions of $\varphi_{i,SSM,XXX,t}$ and $\varphi_{i,ISL,XXX,t}$ were derived for *t* equal to each day of the migration period and posterior medians and 95 % HPD regions were plotted against median daily water temperature and median discharge at Sault Ste. Marie during 23:00–01:00 (UTC – 04:00) each night. Discharge at night was used because Sea Lampreys were assumed to be most active during that time period.

Results

Spatial distribution of spawners

Detection probability estimates were high (> 0.99) at all sites, such that after imputation, I assumed perfect information about movement of tagged Sea Lampreys among sites. The proportion of Sea Lampreys that were last detected at each station varied among sites, release locations, and years (Figure 3.2). A greater proportion of Sea Lampreys released in Munuscong Lake ceased migration in the upper reaches of the St. Marys River containing sites SSM and ISL (range of medians among combined posterior proportions: 0.578–0.712, among years) than all other sites combined. The point estimate (posterior median) of proportion of Sea Lampreys released in Munuscong Lake that were last detected at each site ranged 0.009–0.019 among years above the Soo Locks (sites OVP and BRS, combined); 0.046–0.087 in the Echo, Root, or Garden rivers (sites ECH, RTR, and GRD, combined); 0.034–0.057 in the upper North Channel (sites GRM, BLL, and CKI, combined); and 0.170–0.287 in the lower river (sites RNS, LRC, URC, MNB, and DCK, combined). Among Sea Lampreys released in the North Channel, the proportion that ceased migration in the upper-most reaches of the St. Marys River containing sites SSM and ISL was lower than for those released in Munuscong Lake, ranging 0.268–0.542 (posterior median) among years. The point estimate of proportion of Sea Lampreys released in the North Channel that ceased migration after arriving at other sites ranged 0.007–0.011 above the Soo Locks (sites OVP and BRS, combined); 0.246–0.458 in the Echo, Root, or Garden rivers (sites ECH, RTR, and GRD, combined); 0.064–0.102 in the upper North Channel (sites GRM, BLL, and CKI, combined); and 0.107–0.225 in the lower river (sites RNS, LRC, URC, MNB, and DCK, combined).

Directionality, route selection, and cessation of migration

When moving upstream (i.e., last detected on a receiver farther downstream) Sea Lampreys were more likely to continue moving upstream after arrival at each site (i.e., next detected at a site farther upstream) than to reverse direction, cease migration, or exit the study area; Figure 3.3). Sea Lampreys that entered the three tributaries (e.g., sites ECH, GRD, and RTR) were more likely to remain in those tributaries than to return to the North Channel. Sea Lampreys that approached Sault St. Marie (site SSM) were more likely to cease migration than to return to downstream sites. Only two tagged Sea Lampreys were ever observed upstream of SSM (e.g., at sites OVP or BRS).

After release downstream in Munuscong Lake (site MNS), the most common upstream migration pathway, used by 55–63 % (range of posterior medians among years) of Sea Lampreys released at MNS, was through the upbound shipping channel on the east side of Neebish Island (i.e., past site RNS), while fewer Sea Lampreys (28–32 %; range of posterior medians among years) migrated upstream through the downbound shipping channel on the west side of Neebish Island (i.e., past site LRC; Figure 3.3). After reaching RNS from downstream, most Sea Lampreys moved upstream to MNB, then to ISL and SSM, and few Sea Lampreys crossed over into the lower North Channel to site DCK via STR. After reaching LRC from their release point in Munuscong Lake, most Sea Lampreys continued migrating upstream to URC, then to ISL and SSM. The proportion (0.11–0.21; range of posterior medians among years) of Sea Lampreys that ceased migration after arriving at ISL from downstream was similar to the proportion that ceased migration at other sites in the lower river (e.g., MNS, URC, URC; Figure 3.1).

After release in the North Channel (site NCH), the most common upstream migration pathway, used by 75–89 % (range of posterior medians among years) of Sea Lampreys released at NCH, was through the North Channel on the east side of Sugar Island (i.e., past site DCK), while fewer Sea Lampreys (8–22 %; range of posterior medians among years) crossed over into the upbound shipping channel between Neebish and Sugar Islands (i.e., past site MNB; Figure 3.3). After reaching DCK from downstream, most Sea Lampreys moved upstream to GRM, then continued upstream to BLL, CKI, and SSM, while fewer Sea Lampreys entered the Echo, Garden, or Root rivers (sites ECH, GRD, RTR). Most Sea Lampreys that entered the Echo, Garden, and Root rivers remained in those tributaries, although the estimate for ECH was larger and more uncertain in 2010 and 2012 than during 2011. Some Sea Lampreys were also caught in the adult Sea Lamprey trap (site ECT) in the Echo River.

When first present at SSM in 2010 and 2011, tagged Sea Lamprey that arrived from either CKI or ISL were about equally likely to cease migration or move downstream 3 rkm to ISL (Figure 3.3). In 2012, however, tagged Sea Lamprey were about twice as likely to cease migration after arriving at SSM than to move downstream to ISL. Greater propensity to remain near SSM in 2012 than in 2010 or 2011 may have contributed to the greater proportion of spawners that ceased migration at SSM in 2012 versus 2010 or 2011 (Figure 3.2). Sea Lampreys that reached ISL by moving downstream (most from SSM and not CKI) were about equally likely to cease migration or return upstream to SSM, and to a lesser degree, continue moving downstream to MNB or URC (Figure 3.4).

When Sea Lampreys were moving downstream (i.e., previously detected at a site farther upstream), only a small tendency occurred at some sites to continue moving downstream (i.e., next detected on a site farther downstream (Figure 3.4). At many sites (e.g., LRC, RNS, GRM, BLL), tagged Sea Lampreys moving downstream were about equally or more likely to move back upstream or cease migration than to continue moving downstream.

The proportion of Sea Lampreys that entered the secondary channel (channel with smaller discharge) at each junction varied among sites and years (Figure 3.5). After release in the lower shipping channel (site MNS), the relative probability of entering the downbound channel (e.g., past site LRC) versus the upbound shipping channel (e.g., past site RNS) was similar among years. Route selection probabilities were more variable among years at the other two lower-river junctions, and an inverse pattern was observed between the two sites among years. For example, Sea Lampreys were most likely to enter the shipping channel (i.e., past site MNB) after release in the lower North Channel during 2010 and 2012, and least likely to pass MNB during 2011. In contrast, Sea Lampreys that reached that junction from the shipping channel (after detection at site RNS) were most likely to enter the lower North Channel (i.e., past site DCK) in 2011, and least likely to pass DCK in 2010 and 2012. However, some overlap occurred among HPD intervals at those sites.

The proportion of Sea Lampreys that entered each tributary to the North Channel also varied among years (Figure 3.5). The proportion of Sea Lampreys that entered the Echo and Garden rivers was higher in 2011 than in 2010 and 2012. The proportion of Sea Lampreys that entered the Root River was similar among years, but suggested a decreasing trend among years. While route selection probabilities in the lower river may be directly related to bulk flow dynamics such as relative discharge among channels, the proportion of Sea Lampreys that entered each tributary was probably at least an order of magnitude greater than the proportion of discharge that entered the North Channel from each of those streams. Results suggest that variation in route selection at each junction was not closely related to time since lampricide treatment, because all streams were treated immediately prior to or during the study. Weak evidence existed that the probability of entering a tributary increased (e.g., GRD in 2010) or fluctuated over time within a migration season (e.g., ECH in 2011; Figure 3.6). However, there was no evidence that the daily probability of entering a tributary was related to temperature of the main channel, temperature of the tributary, or difference in temperature between the main channel and the tributary (Figure 3.6).

The strong tendency for Sea Lampreys to cease migration in the Root, Garden, and Echo rivers (Figure 3.3) was associated, with the warmer water in those tributaries when compared to the upper North Channel (Figure 3.6). Results also showed that the Soo Locks (site SSM) are a barrier to the migration of most Sea Lampreys in the upper St. Marys River. Although many Sea Lampreys that reached the Soo Locks ceased migration in that region, many also dropped back downstream after arriving at SSM (Figure 3.3) and many presumably spawned around ISL or farther downstream. Some evidence existed that the probability of ceasing migration near SSM peaked for Sea Lampreys arriving at that location during the middle of the spawning migration period in 2010 and 2011, but was constant throughout the spawning migration period in 2012 (Figure 3.7). The peak in cessation of migration at SSM in 2010 and 2011 occurred when water temperature exceeded about 10 °C, which is generally considered by Sea Lamprey control personnel a good indicator of when Sea Lamprey traps begin catching Sea Lampreys. Differences in the probability of ceasing migration at SSM in 2012 versus 2011 or 2010 did not seem to be related to differences in water temperature or discharge during night, when it was assumed that Sea Lampreys were most active. In contrast to SSM, the probability of ceasing migration after arriving at ISL increased during the study period in all years (Figure 3.7).

Discussion

Observed behavior of Sea Lampreys reported here was consistent with the expectation that most adult Sea Lampreys make directed upstream movements until a barrier or spawning habitat is reached and supported the assumption that vessel passage locks, hydroelectric dams, and compensating gates at Sault Ste. Marie prevent upstream passage of Sea Lampreys. To my knowledge, the main channels of the St. Marys River and North Channel have not been surveyed for spawning habitat due to river depth in those locations. Patterns of movement suggested that most Sea Lampreys ceased migration in the upper shipping channel below Sault St. Marie or in the three main tributaries to the upper North Channel. Therefore, I assumed that most Sea Lampreys spawned in those locations. Sea Lampreys released in the lower North Channel were more likely to enter and remain in one of the three tributaries to the North Channel than Sea Lampreys released in the lower shipping channel (Munuscong Lake). Primary locations identified in this study as probable spawning sites were near Sault Ste. Marie and in the Echo, Garden, and Root rivers and consistent with past observations based on larval surveys and lampricide treatments (Robinson et al. 2013). The proportion of spawners at each location differed between release sites and among years due to differences in route selection probabilities at downstream junctions. However, the proportion of Sea Lampreys that ceased migration in or around the shipping channel on the west side of Sugar Island (site ISL) after arrival at Sault Ste. Marie was larger than expected based on my hypothesized conceptual model. This suggests that previously unidentified spawning habitat on the west side of Sugar Island may account for a substantial proportion of spawning habitat in the St. Marys River. Results suggested that propensity to drop downstream after arrival at SSM determined the proportion of spawners that ceased migration at ISL, but not at other sites. Low proportions of Sea Lampreys that ceased migration in lower reaches of the river are consistent with low densities of larval Sea Lampreys throughout the lower river, but could also resresent emigration from the system or death prior to spawning in the lower river (Kelso and Gardner 2000).

The proportions of Sea Lampreys that entered the Echo, Garden, and Root rivers from the North Channel each year were higher than expected given an hypothesis that discharge is positively associated with attractiveness for migrating fish; discharge in each of those tributaries was about an order of magnitude smaller than discharge in the North Channel itself. As well, these streams were treated with lampricides in the year prior to and again during this study and therefore likely had little attractant pheromones from larval Sea Lampreys (Sorensen and Vrieze 2003). These results show the ability of Sea Lampreys, facilitated by lack of homing and use of generalist migratory cues, perhaps from other native lamprey species in those drainages, to quickly colonize vacant habitats (Almeida et al. 2002; Lasne et al. 2014) and was consistent with the need to re-treat tributaries with lampricides within a few years after treatment. Given that streams were treated just prior to and during this study, even larger proportions of Sea Lampreys might be expected to enter those streams in the years after this study, suggesting that in a typical year more than half the adult Sea Lampreys that enter the study area from the North Channel could spawn in those tributaries.

In large rivers like the St. Marys River, the proportion of Sea Lampreys that spawn in small tributaries is useful for understanding what proportion of the drainage-wide adults spawn in locations regularly treated with lampricides. Given that the Echo, Garden, and Root rivers are treated on regular cycles and that TFM treatments in small rivers are generally more effective than Bayluscide treatments in large rivers, increasing the proportion of Sea Lampreys that enter those tributaries could improve Sea Lamprey control in the St. Marys River. Although, I was not able to identify variables that influenced route selection probabilities, variability among years, especially in the Echo River, provides some hope that mechanisms could be identified if relevant factors were studied at the appropriate scale. Given its small size compared to the shipping channel and relatively small distances between tributaries, the North Channel might also be a good location to test and deploy attractants (Sorensen and Vrieze 2002; Johnson et al. 2013; Twohey et al. 2013), repellants (Imre et al. 2010; Wagner et al. 2011), or electric guidance systems (Johnson et al. 2014) to encourage entrance into tributaries, discourage upstream migration in the North Channel, or both. However, any such strategies employed in the North Channel would primarily target the portion of the St. Marys River population that enters from the lower North Channel because only a small proportion of Sea Lampreys released in Munuscong Lake entered the North Channel (either through the lower river via DCK or in the upper river via CKI). Therefore, further benefit would be realized by increasing the probability that Sea Lampreys enter the North Channel from the upbound shipping channel in the lower river and preventing Sea Lampreys from the lower North Channel from entering the shipping channel.

Route selection probabilities in the lower river indicated that only a small proportion of Sea Lampreys that enter the study area from Munuscong Lake cross over into the North Channel and vice versa. At junctions like the one upstream of MNS, where both channels are dredged and presumably have similar physical properties (because they are converging after diverging farther upstream), the proportion of Sea Lampreys that use each route may simply be determined by river channel topography and water velocities near the substrate. However, the dynamics of the junction between the shipping channel and the North Channel are more complex because that junction is shallower than the primary channels on either side of it and because the North Channel is typically warmer (due to effect of Lake George) than the shipping channel. Given the size of the river at those locations and the two-to-one split around Neebish Island, manipulating migration routes in this part of the river seems much more challenging than in the upper North Channel. Alternatively, additional control may be attempted by promoting entry into another tributary to the shipping channel (e.g., Charlotte River) or by promoting retention near SSM (once reached).

Propensity to fall back downstream away from the barrier was not consistent with expectations, but has been observed by others (Applegate 1950; Kelso and Gardner 2000; Almeida et al. 2002). Propensity for downstream-migrating Sea Lampreys to reverse direction or cease migration suggests that downstream-migrating Sea Lampreys do not show strong directional migration, but may be searching for migratory cues. Greater tendency to move downstream from SSM to ISL in 2010 and 2011 than in 2012 suggested that habitat suitability or conspecific cues were not as attractive to Sea Lampreys in the earlier years as they were in 2012. Although inter- and intra-annual variability did not seem to be related to water temperature or discharge, I hypothesize that it may be related to larval densities between SSM and ISL. If such processes could be understood, the system may be managed or manipulated to increase the number of Sea Lampreys that cease migration near SSM, where they may be more susceptible to traps and more offspring of spawners may be limited to a smaller nursery area and vulnerable to treatment with Bayluscide.

Movement of Sea Lampreys away from Sault Ste. Marie may also explain why efficiencies of traps in the upper St. Marys River have not improved despite efforts to improve those traps in recent years. Among three years of this study, efficiency of traps in the upper St. Marys River was highest in 2012 (see Chapter 2), when the probability of ceasing migration near SSM was also highest among years. Similarly, Bravener and McLaughlin (2013) showed that the probability of encountering traps at SSM was a primary factor limiting trapping success and that Sea Lampreys rarely returned to traps after failed entry. In their study during 2009, Sea Lamprey were released after peak trap catch, and Sea Lampreys released earlier in the run were more likely to encounter traps than Sea Lamprey released later in the run. Those observations are consistent with expectations if the probability of ceasing migration near SSM in 2009 were similar to 2010 and 2011 and if releases of Sea Lampreys by Bravener and McLaughlin (2013) coincided with the descending region of the curve (i.e., June, Figure 3.7). Results suggest that low encounter rates may also be related to the probability that Sea Lampreys dropped down stream to ISL.

The ascending and descending regions of the curves representing probability of ceasing migration over time (Figure 3.7) may represent two different phases of Sea Lamprey spawning migration: the former being river ascent and searching for suitable rearing habitat (facilitated by migratory pheromones from larval conspecifics) and the latter being searching for specific spawning location, mates, or both. Propensity to remain in tributaries was also consistent with earlier trap catches in the Echo River than in the upper St. Marys River (see Chapter 2) and is likely mediated by higher temperatures in tributaries than in the main stem of the North Channel. However, these results were not consistent with Kelso and Gardner (2000) who observed that many Sea Lampreys emigrated from Lake Superior tributaries prior to spawning.

These results show that telemetry can provide a rigorous foundation for estimating fish movement rates at a range of spatial and temporal scales, and should motivate more multi-disciplinary research into the movement ecology of migratory fishes. Future research would benefit from careful evaluation of the influence of hydrodynamics, river topography, and water chemistry (including pheromones)on migration route selection..

APPENDIX

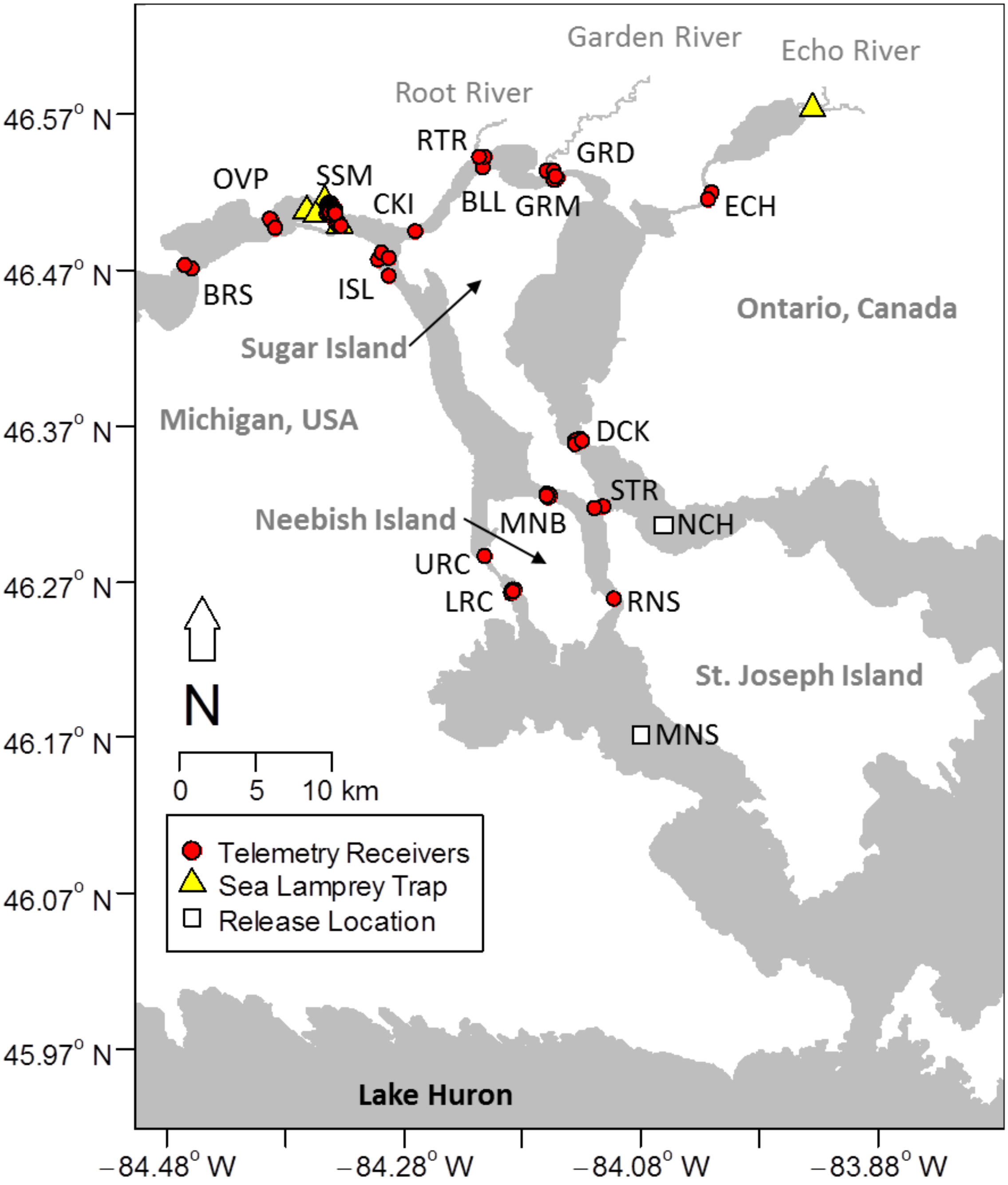

Figure 3.1.— Map of the St. Marys River with locations of acoustic telemetry receivers, Sea Lamprey release sites, and adult Sea Lamprey traps.

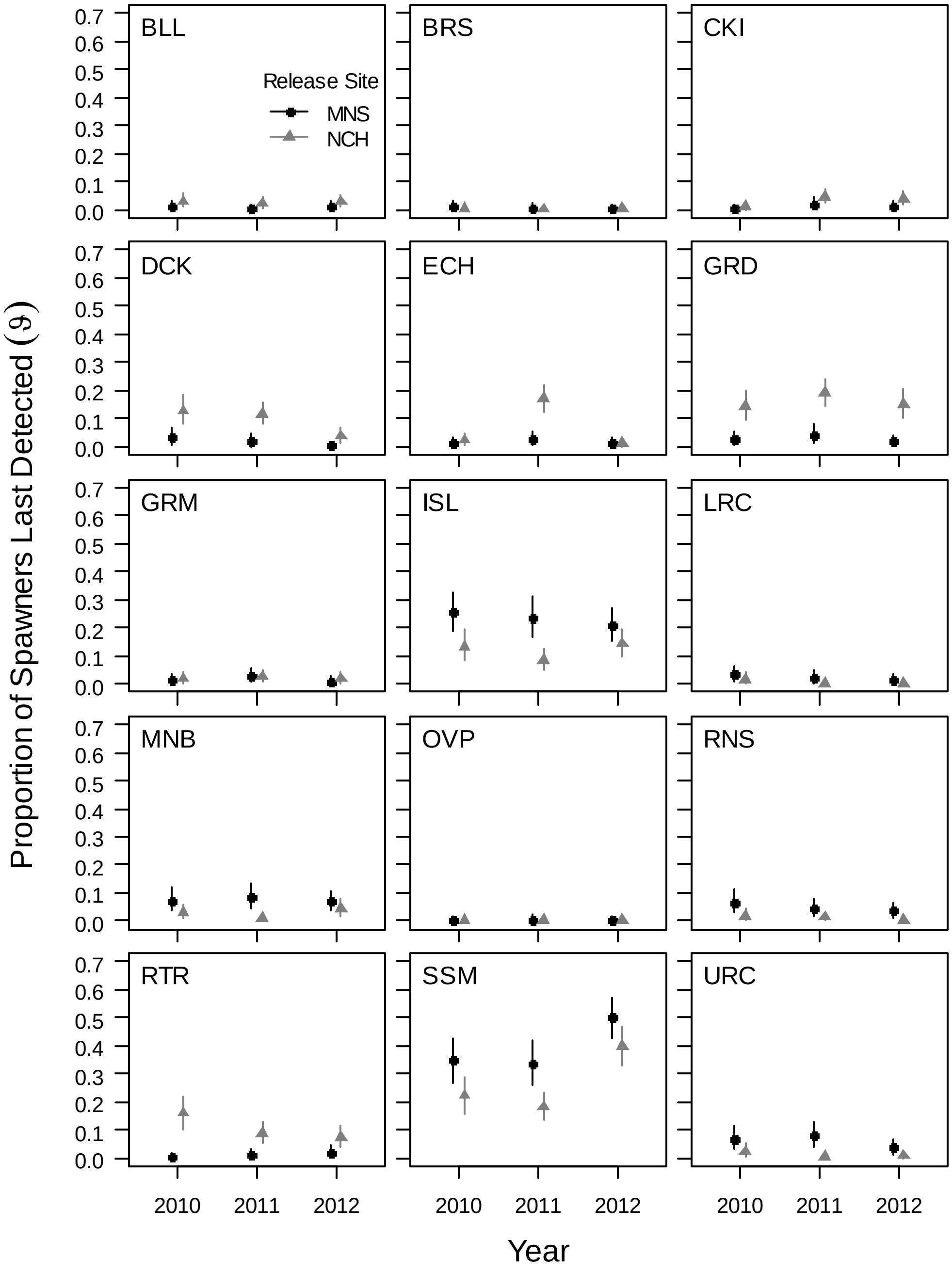

Figure 3.2.—Posterior median (closed symbols) and 95% HPD interval (solid lines) estimates of acoustic-tagged adult Sea Lampreys released into Munuscong Lake (black symbols and lines) and North Channel (grey symbols and lines) that were last detected at each telemetry receiver station (top-left corner of each panel) in the St. Marys River and tributaries during 2010, 2011, and 2012. See Figure 3.1 for receiver station locations.

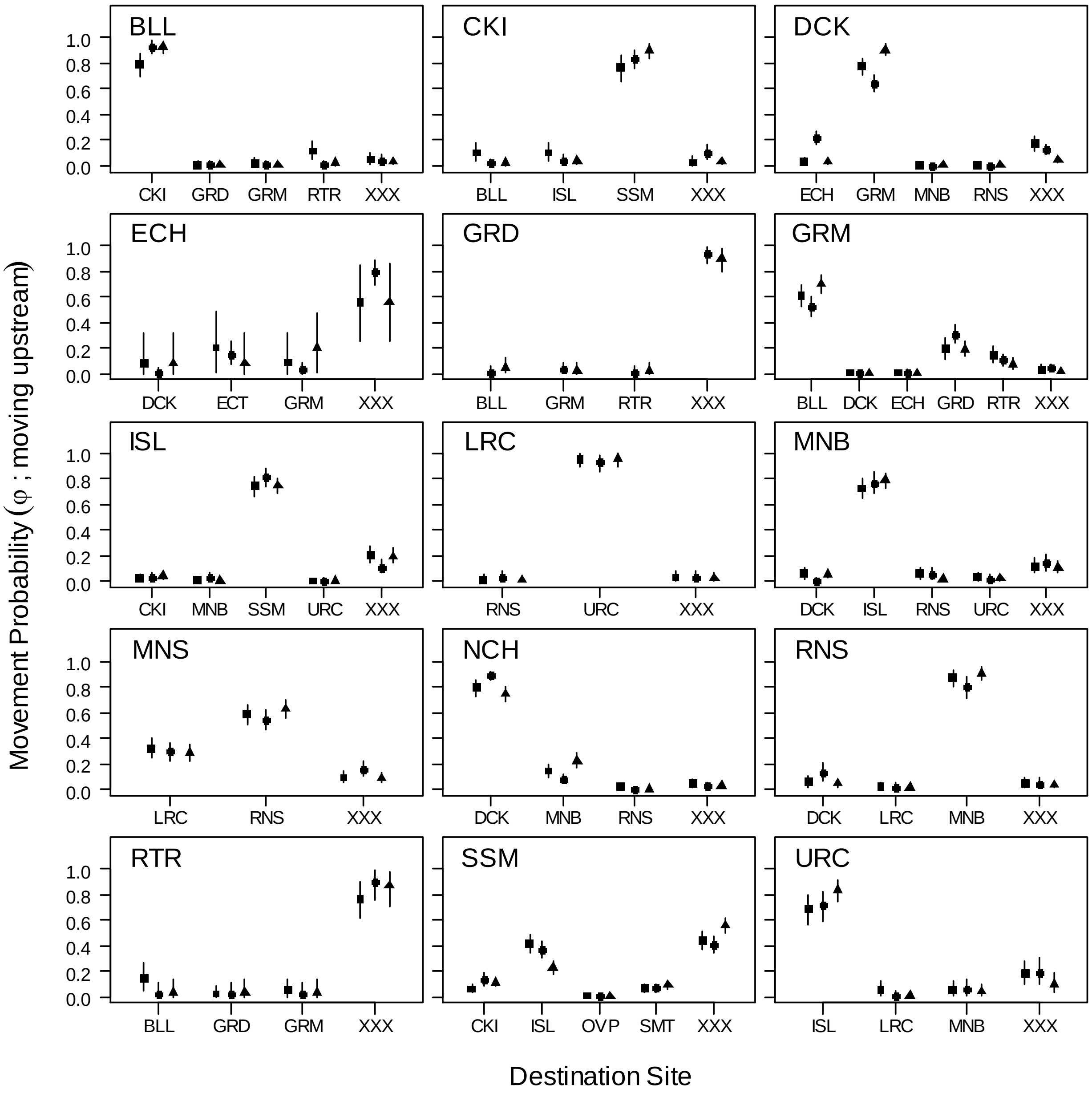

Figure 3.3.—Estimated probabilities of moving from each site (three-letter code in top left corner of each panel) to each possible destination site, given that the fish was moving upstream when it arrived in 2010 (squares), 2011 (circles), or 2012 (triangles). Site codes ECT and SMT represent adult Sea Lamprey traps in the Echo and upper St. Marys rivers, respectively. Site code XXX represents cessation of movement (never detected at any other site). All other site codes refer to sites shown in Figure 3.1.

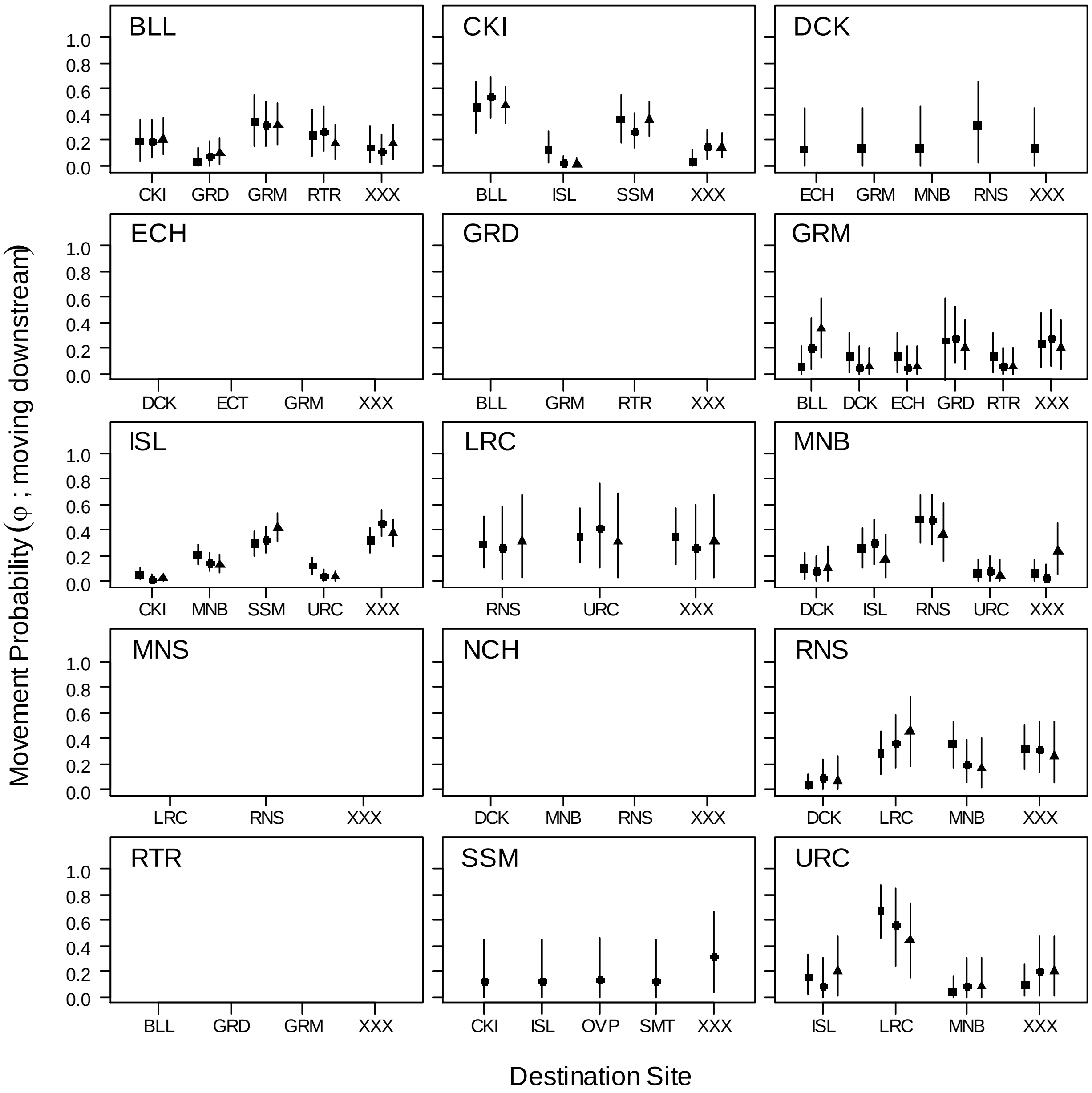

Figure 3.4.—Estimated probabilities of moving from each site (three-letter code in top left corner of each panel) to each destination site, given that the fish was moving downstream when it arrived in 2010 (squares), 2011 (circles), or 2012 (triangles). Site codes ECT and SMT represent adult Sea Lamprey traps in the Echo and upper St. Marys rivers, respectively. Site code XXX represents cessation of movement (never detected at any other site). All other site codes refer to sites shown in Figure 3.1.

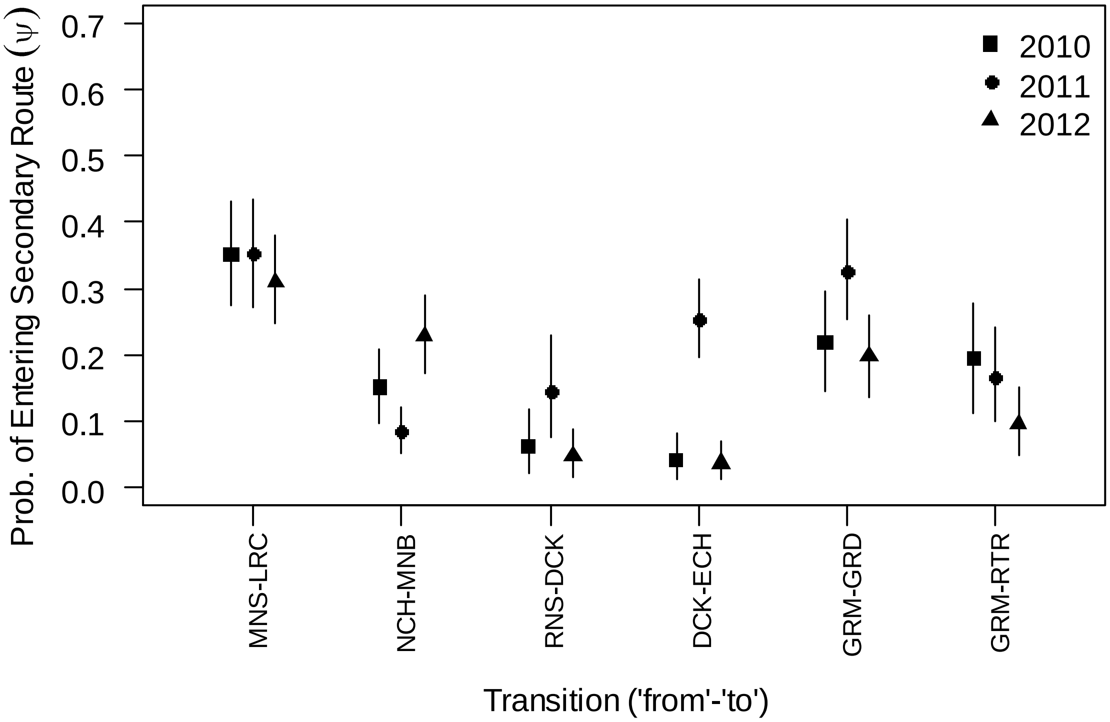

Figure 3.5.—Estimated probabilities of entering the secondary channel (i.e., channel with smallest discharge) after detection on telemetry receivers downstream of six confluences in the St. Marys River in 2010, 2011, and 2012. Symbols show posterior medians and lines show 95% HPD regions.

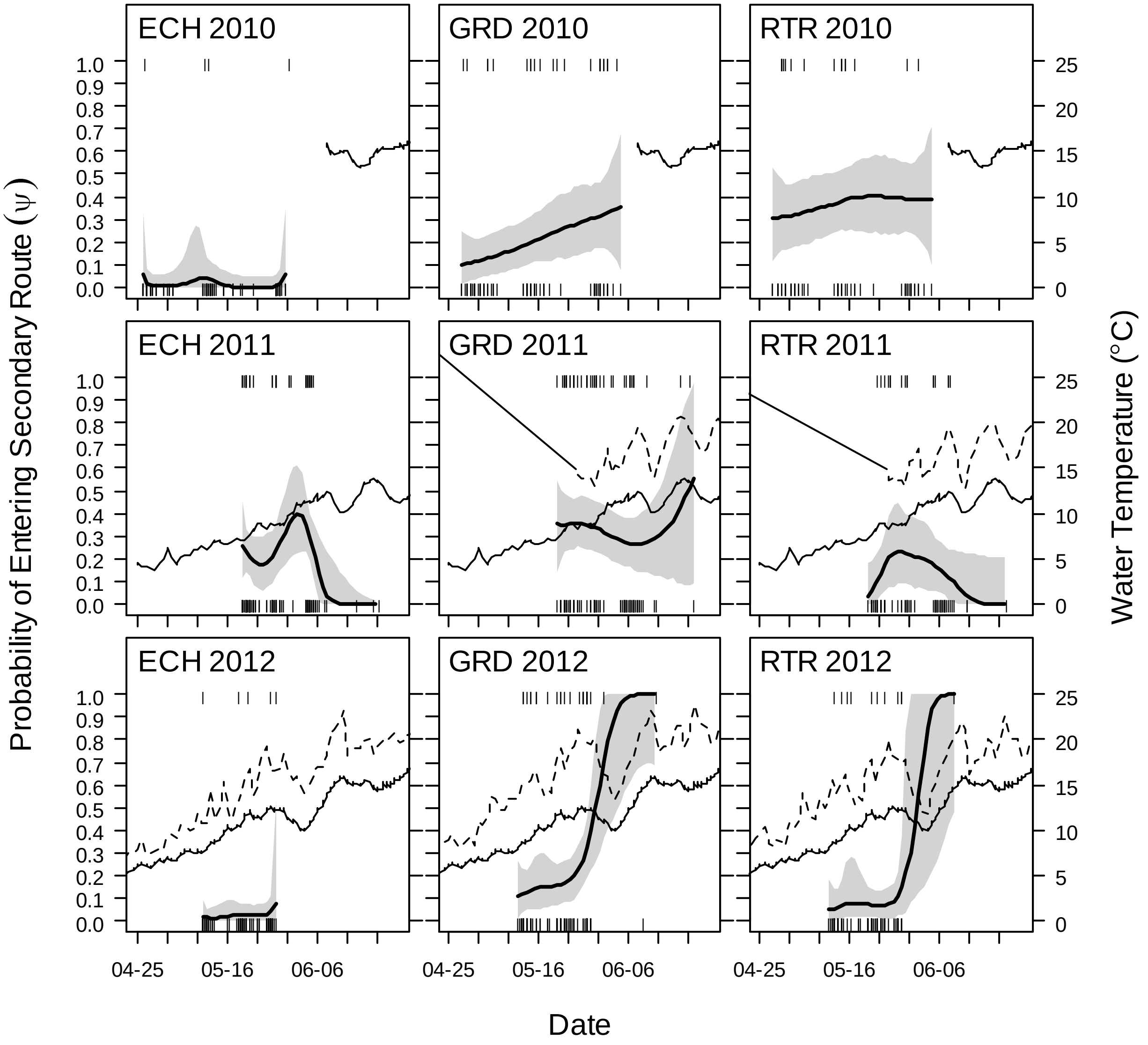

Figure 3.6.—Daily probabilities of entering the Echo (site ECH; left panels), Garden (site GRD; middle panels), and Root (site RTR; right panels), versus remaining in the North Channel, during upstream migration for acoustic-tagged Sea Lampreys in 2010, 2011, and 2012. Heavy solid lines show median posterior probabilities and shaded grey areas represent point-wise 95% HPD intervals (daily resolution) for each parameter. Vertical ticks at 0.0 and 1.0 show observations. Thin solid line shows median daily water temperature in the North Channel just downstream of the Garden River confluence (site GRD) and thin broken lines show median daily water temperature in each tributary. All lines are limited to the range of the associated data.

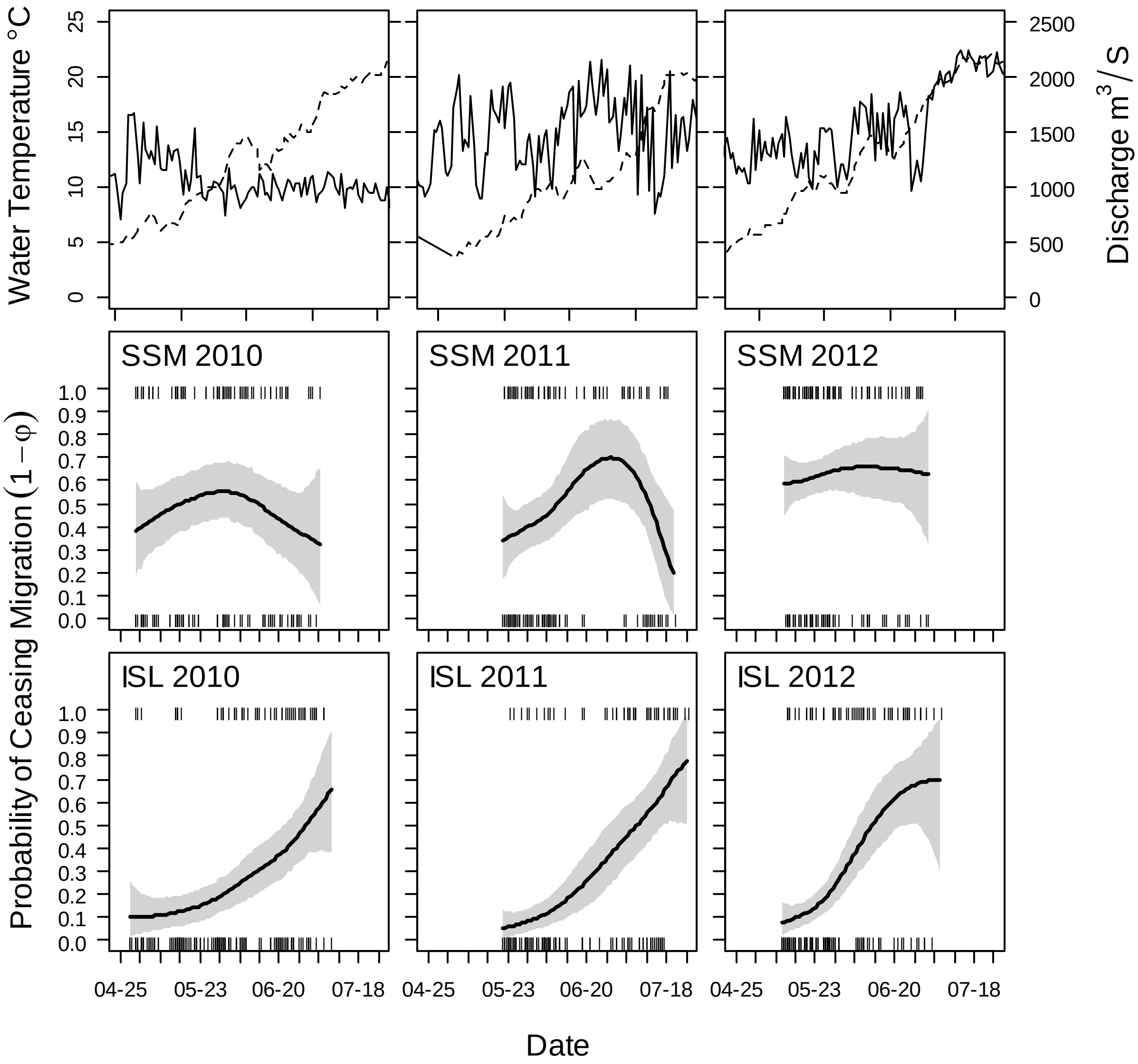

Figure 3.7.—Daily proportions (posterior median: solid line; point-wise 95% HPD: shaded region) of Sea Lampreys that continued migration after arrival at two sites in the upper St. Marys River in 2010, 2011, and 2012.

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