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Survival and metamorphosis of larval sea lamprey (*Petromyzon marinus*) residing in Lakes Michigan and Huron near river mouths

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ABSTRACT

Although population demographics of larval lampreys in streams have been studied extensively, demographics in lake environments have not. Here, we estimated survival and rates of metamorphosis for larval sea lamprey (*Petromyzon marinus*) populations residing in the Great Lakes near river mouths (hereafter termed lentic areas). Tagged larvae were stocked and a Bayesian multi-state tag-recovery model was used to investigate population parameters associated with tag recovery, including survival and metamorphosis probabilities. Compared to previous studies of larvae in streams, larval growth in lentic areas was substantially slower (Brody growth coefficient = 0.00132; estimate based on the recovery of six tagged larvae), survival was slightly greater (annual survival = 63%), and the length at which 50% of the larvae would be expected to metamorphose was substantially shorter (126 mm). Stochastic simulations were used to estimate the production of parasitic stage (juvenile) sea lamprey from a hypothetical population of larvae in a lentic environment. Production of juvenile sea lamprey was substantial because, even though larval growth in these environments was slow relative to stream environments, survival was high and length at metamorphosis was less. However, estimated production of juvenile sea lamprey was less for the lentic environment than for similar simulations for river environments where larvae grew faster. In circumstances where the cost to kill a larva with lampricide was equal and control funds are limited, sea lamprey control effort may be best directed toward larvae in streams with fast-growing larvae, because stream-produced larvae will most likely contribute to juvenile sea lamprey populations.

Introduction

Lampreys (Petromyzontiformes) interest biologists and fishery managers worldwide. Many lamprey species are ecologically and economically important in their native habitats (Docker et al., 2015) and are in decline (Maitland et al., 2015), so their populations are the focus of restoration efforts. In the Great Lakes, sea lamprey (*Petromyzon marinus*) are invasive and damage valuable fishes during their parasitic feeding stage (juvenile stage; Applegate, 1950; Smith and Tibbles, 1980; Madenjian et al., 2003), so populations are controlled primarily by the application of selective pesticides to kill larvae (lampricides; Christie and Goddard, 2003). In both cases, understanding demographics of lamprey populations is beneficial (Close et al., 2002; Jones et al., 2015; Hansen et al., 2016).

Lampreys typically spawn in streams where unidirectional flow and gravel substrate are present (Hardisty and Potter, 1971a; Johnson et al., 2015). After hatching, larvae burrow into soft substrate in streams, where they reside for two or more years prior to metamorphosing into the parasitic feeding stage (parasitic lampreys) or adult stage (non-parasitic lampreys) (Hardisty and Potter, 1971b; Dawson et al., 2015). Larvae can also occupy lake sediments (hereafter termed lentic areas; Heinrich et al., 2003) if they drift out of stream mouths during floods or while dispersing downstream (Hardisty and Potter, 1971b; Potter, 1980; Dawson et al., 2015). In some tributaries to the Great Lakes, the majority of larval sea lamprey in the stream are presumed to be carried to lentic areas (e.g. Mountain Bay; Falls, and Ravine Rivers, Lake Superior; Days River, Lake Michigan; T.B. Steeves, Fisheries and Oceans Canada, personal communication).

Although population demographics of larval lampreys in streams have been studied extensively (Manion and Stauffer, 1970; Purvis, 1980; Morman, 1987; Meeuwig et al., 2007; Mateus et al., 2012), demographics of larval lampreys in lentic areas have not been described. In particular, the contribution of larval lampreys from lentic environments to juvenile and adult populations is not known in sea lamprey or any other lamprey species. Conceivably, growth and survival of larvae in lentic areas could be less than for larvae in streams, because of reduced productivity compared to stream waters. Presumably, the contribution of larvae from lentic areas over time depends on the size structure of the population and growth, survival, and metamorphosis rates.

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Metamorphosing and other large larvae that enter a lentic area from the natal stream are likely to already contain enough stored lipids to complete metamorphosis in the lentic area and, consequently, are less susceptible to the presumed less hospitable conditions of the lentic area. However, whether smaller larvae continue to survive, grow, or metamorphose once they enter the lentic area from the tributary stream is not known.

Information about demographics of larval lampreys in lentic areas would benefit control and restoration by enabling better prioritization of assessment and control actions within these areas. In the Great Lakes where sea lamprey are a nuisance, lentic areas infested with larval sea lamprey are prioritized for lampricide treatment alongside stream-dwelling larval populations by comparing the cost to kill a larva over 100 mm in each population (Hansen and Jones, 2008). Lentic areas ranking high enough are treated with granular Bayluscide (5, 2′-dichloro-4′-nitro-salicylanilide), and 22 such areas were treated in the Great Lakes during 2015 (Sullivan et al., 2016). However, because lampricide control budgets are limited, lampricide treatments to control larvae in lentic areas may not be a good investment if larvae in lentic areas are less likely to survive to the parasitic feeding stage (herein termed juveniles) than stream dwelling larvae. In places where lamprey conservation is a priority, managers may be able to modify flows in regulated rivers to either increase or decrease larval drift into lentic areas, depending upon whether lentic areas are ecological refuges.

Our objective was to estimate survival and metamorphosis rates of larval sea lamprey populations residing in the Great Lakes near river mouths. To accomplish this, we released coded wire tagged (CWT) larval sea lamprey in three lentic areas near stream mouths where larval sea lamprey have been found previously and enumerated recoveries of tagged individuals during both larval and adult stages. Bayesian multi-state tag-recovery models were used to investigate population parameters associated with tag recovery including survival and metamorphosis probabilities.

Materials and methods

Tagging of larval sea lamprey

Larval sea lamprey were coded wire tagged (CWT) and released in three lentic areas that were known to harbor sea lamprey and which had previously been treated with lampricide. Larvae were stocked in two northern Lake Michigan lentic areas, off Hog Island Creek and off Bear River (Petoskey Harbor), and one northern Lake Huron lentic area, off Carp River (Fig. 1; Table 1). The three stocking locations were within 150 km of each other, so likely experienced similar climatic and lake conditions.

A total of 9736 larvae were collected by electrofishing, tagged, and released (Carp River = 3991; Hog Island Creek = 3776; Bear River = 1969). Tags were inserted in the dorsal musculature with a single shot tag injector (Northwest Marine Technologies, Shaw Island, Washington; Bergstedt et al., 1993). All larvae were held in flow-through tanks supplied with water from Lake Huron at ambient temperatures ranging from 12 to 18 °C for five days after tagging to quantify short-term handling mortality and tag loss. Dead larvae were removed from holding tanks and a magnet was used to locate shed tags in the substrate. Tagged larvae were partitioned into five size groups (40–59 mm, 60–79 mm, 80–99 mm, 100–119 mm, ≥120 mm), and each animal was identified by a separate sequential coded wire tag (Table 2). Our intention was to collect larvae from the source stream for stocking in the associated lentic area. This occurred for the Carp

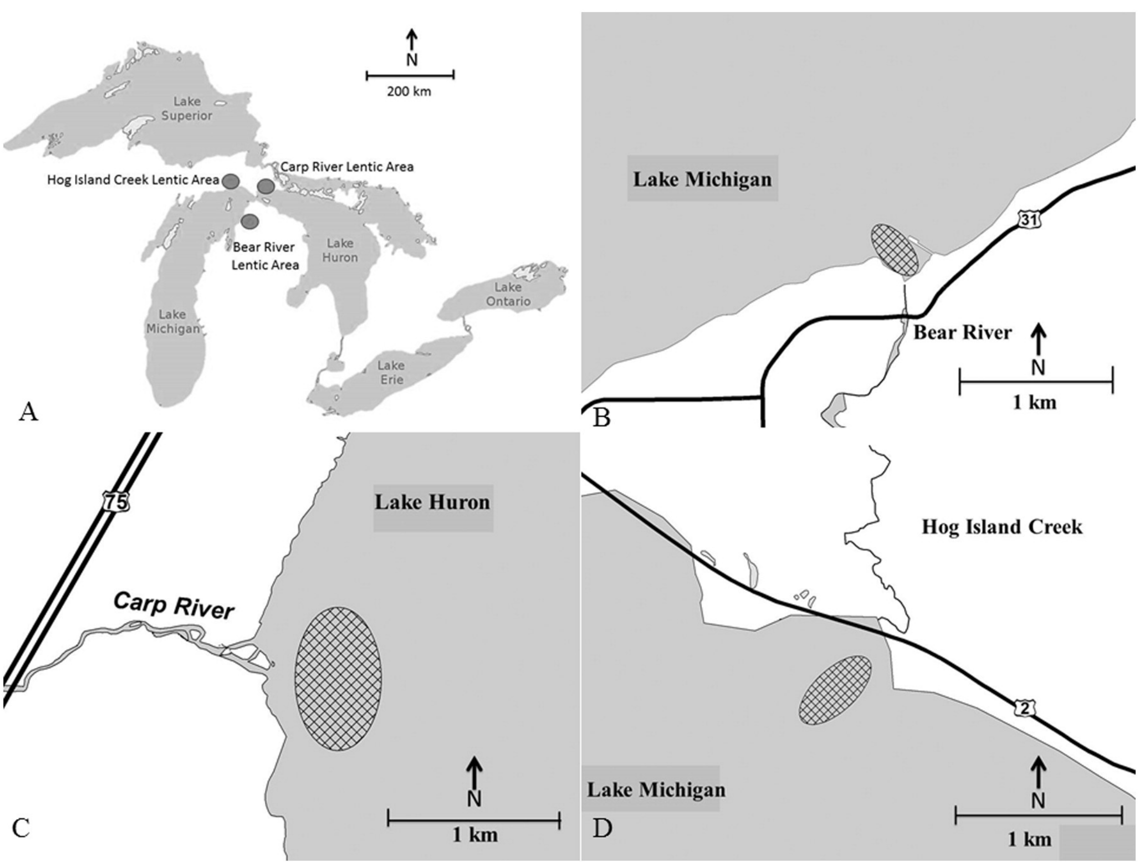

Fig. 1. (A) Locations where coded wire tagged (CWT) sea lamprey larvae were stocked in Lakes Huron and Michigan near river mouths and recovered in the larval and adult stages. (B) Hog Island Creek lentic area. (C) Bear River lentic area. (D) Carp River lentic area. The etched area within each lake is where larval sea lamprey have been found. The tagged larvae were released about 200 m off the mouth of the respective streams inside the etched in area. Nearby roads are illustrated as black lines and named (Highways 2, 31, and 75).

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Table 1
Description of the size, depth, and substrate type of lentic areas located off stream mouths of Great Lakes tributaries where coded wire tagged sea lamprey were released during 2007. Area is the contiguous amount of lentic habitat in which larvae have been previously observed.

Lentic area	Area (ha)	Depth (m)	Substrate
Bear River	1.6	<4	Sand, 0.25 to 1 mm
Carp River	8.9	<4	Sand, 0.25 to 1 mm
Hog Island Creek	3.6	<3	Sand, 0.25 to 1 mm

River, but too few larvae of the proper sizes were available from the other two source streams. Larvae released off Hog Island Creek and Bear River were collected by electrofishing from Platte River (a tributary to Lake Michigan).

The tagged larvae were released approximately 200 m off the mouth of the respective streams, allowing the larvae to distribute themselves in the depositional zones in the lake. We do not know the extent and timing of the normal movement of stream larvae into a lentic area in any year, but the method of release here would appear similar to the results of a flood event that disrupts larval habitat in the stream. Hence, although artificial, the release of tagged larvae in this study was planned to mimic conditions under which stream larvae would normally enter a lentic area.

Recovery of tagged sea lamprey

Larval populations in the study lentic areas were periodically assessed and treated using granular Bayluscide as part of the standard sea lamprey control program (Table 3). During assessments, larvae were captured and inspected to determine if treatment was warranted. As such, during assessments larvae captured were also scanned for CWT and individuals with tags were removed and lengths and weights were measured. Larvae were not scanned for tags following Bayluscide treatments because larvae are typically not collected during treatments and research personnel failed to communicate to sea lamprey control personnel the importance of collecting deceased larvae after treatment and scanning them for CWT. Because CWT larvae released in lentic areas could metamorphose and survive to the adult stage, adult sea lamprey trapped in tributaries to Lakes Huron and Michigan as part of regular adult trapping assessments were also scanned for CWTs from 2008 to 2015 (Mullett et al., 2003; *sensu* Johnson et al., 2014). Knowledge of release site from individual CWTs enabled the assignment of adults to the source lentic area. No tagged sea lamprey were recovered as adults during 2008 because individuals spend between 12 and 18 months in the Great Lakes after metamorphosing before migrating to streams to spawn (Bergstedt and Seelye, 1995). Therefore, the earliest that tagged larvae would have been recovered as adults was 2009.

Estimation model

We used a multistate tag-recovery model (Brownie et al., 1993) similar to that of Johnson et al. (2014) for estimating survival, metamorphosis, and recovery probabilities of lentic sea lamprey. Our different model states corresponded to larval and adult sea lamprey life stages, with the juvenile stage a hidden stage for which survival was confounded with adult recovery probabilities.

Table 2
Number of coded wire tagged larval sea lamprey released in lentic areas located off stream mouths of Great Lakes tributaries during 2007, by size class.

Lentic area	40–59 mm	60–79 mm	80–99 mm	100–119 mm	≥120 mm
Bear River	183	872	751	153	9
Hog Island Creek	239	1376	1635	481	45
Bear River	183	872	751	153	9

The number of tagged sea lamprey recovered was estimated as a function of larval annual survival, larval probability of capture during Bayluscide surveys, larval probability of surviving a Bayluscide treatment, juvenile survival (parasitic stage survival), adult probability of capture, and metamorphosis probability; however, not all of these parameters were estimable based on the study design. We assumed that all larvae in the lentic area were exposed to Bayluscide treatment and larval probability of surviving treatment was 25% (T.B. Steeves, Fisheries and Oceans Canada, personal communication). In general, Bayluscide treatments of lentic areas are less effective than treatment of streams with 3-trifluoromethyl-4-nitrophenol (TFM; 90–95% effective) because larvae have less distance to swim out of the treated area in streams. For sea lamprey tagged during 2007, the expected number of larvae recovered (R^{larval}) of initial length category l, tagged in stream i, and recovered in year ry when streams were sampled by Bayluscide was

$$R^{larval}_{i,l,ry} = N_{i,l} P^{larval}_{i,l,ry} \tag{1}$$

where

$$P^{larval}_{i,l,ry} = \prod_{j=2007}^{ry-1} \left[(1-m_{i,l,j}) S^{larval}_{i} \right] (1-m_{i,l,ry}) \mu_i \qquad \text{for } ry \geq 2008. \tag{2}$$

Here, N is the number of tagged larvae in a category (lentic and length-category specific), P^{larval} is the recovery probability of larvae in lentic areas sampled by Bayluscide, m is the length-dependent probability of metamorphosing, S^{larval} is the annual survival of larval sea lamprey, and μ is the Bayluscide survey probability of capture. If a lentic area was treated with Bayluscide prior to the recovery year, then recovery probabilities were multiplied by 0.25 to account for the probability that tagged individuals survived treatment. The expected number of adults recovered (R^{adult}) of sea lamprey larvae of length category l, tagged in stream i in 2007, and recovered in year y was

$$R^{adult}_{i,l,ry} = N_{i,l} P^{adult}_{i,l,ry} \tag{3}$$

where

$$P^{adult}_{i,l,ry} = \begin{cases} m_{i,l,ry-2} S^{juvenile}_{i} \gamma_i & \text{for } ry = 2009 \\ \prod_{j=2007}^{ry-3} \left[(1-m_{i,l,j}) S^{larval}_{i} \right] m_{i,l,ry-2} S^{juvenile}_{i} \gamma_i & \text{for } ry \geq 2010 \end{cases} \tag{4}$$

where all variables are as previously defined, $S^{juvenile}$ is the overall (not annual) survival of juvenile sea lamprey, and γ is the probability of capture of adults. Because juvenile sea lamprey were not recovered during the course of this study, the $S^{juvenile}$ and γ parameters could not be estimated separately, so the product $S^{juvenile}\gamma$ was estimated instead. As with larval recovery probabilities, a Bayluscide treatment survival rate of 0.25 was incorporated in Eq. (4) if a lentic area was treated at a time that would have affected adult recovery probabilities.

As in Johnson et al. (2014), the probability of larval sea lamprey metamorphosing was modeled as a logistic function of length

$$m_{i,l,ry} = \frac{\exp\left[\beta_0 + \beta_1 \left(\bar{l}_l + \Delta l_{i,ry}\right)\right]}{1.0 + \exp\left[\beta_0 + \beta_1 \left(\bar{l}_l + \Delta l_{i,ry}\right)\right]} \tag{5}$$

where β_0 and β_1 are parameters characterizing the length at which metamorphosis occurs, $\bar{l}$ is the mid-point of length category l, and Δl is expected change in length for a particular recapture year. Changes in length were predicted using the von Bertalanffy growth equation

$$\Delta l_{i,ry} = \left(L_\infty - \bar{l}_l\right)\{1.0 - \exp[-\kappa_i (ry - ty_i) d_i]\} \tag{6}$$

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Table 3
Survey and treatment histories of lentic areas off Bear River, Carp River, and Hog Island Creek. Surveys and treatments were conducted using granular Bayluscide by U.S Fish and Wildlife Service. Numbers in parentheses indicate how many coded wire tagged larval sea lamprey were recovered during the activity. Larval sea lamprey were released during year 0 (2007).

Lentic area	Year 1	Year 2	Year 3	Year 4	Year 5	Year 6	Year 7
Bear River	Survey (3)	Survey	Survey				Survey
Carp River		Survey (2)	Treatment			Treatment	
Hog Island				Survey	Survey (1)		

where L_∞ is asymptotic length, κ is the Brody growth parameter, ry is recapture year, *ty* is tagging year (2007), and *d* is the growing season duration for each of the target streams. For predicting changes in length, L_∞ was set equal to 159 mm (Treble et al., 2008; Jones et al., 2009; Johnson et al., 2014) and growing season length was set equal to 188 days based on entries in the Empiric Stream Treatment Ranking database (Christie et al., 2003). The Brody growth parameter (1/days) was estimated using non-linear least-squares regression based on observed growth differences of recaptured larvae. Because of the low number of recaptures, we did not attempt to estimate lentic area-specific growth models.

The multi-state tag-recovery model was estimated using AD Model Builder (Fournier et al., 2012). We used a Bayesian-based estimation approach, whereby the point estimates of model parameters were highest posterior density estimates (Schnute, 1994). Tag recoveries during larval and adult stages were modeled through a multinomial likelihood. Based on the results of Johnson et al. (2014), a normal probability distribution with a mean of 0.093 and a standard deviation of 0.014 was assumed as an informative prior for the product of juvenile survival and adult probability of recovery given that the studies overlapped in time and that after metamorphosis there is little reason to suspect that juvenile survival would differ between lentic and stream populations. For all other parameters, diffuse uniform priors were specified. Some of the parameters, including S^{larval}, μ, and $S^{juvenile}\gamma$, were estimated as inverse logit functions, which constrained their values between 0.0 and 1.0, while allowing the estimated parameter to occur on the real number line. Similarly, the slope of the maturation function was estimated on a log-scale to constrain the parameter to a positive value. The model was considered to have converged on a solution when the maximum gradient of the parameters with respect to the objective function was $<1.0 \times 10^{-4}$.

To assess uncertainty associated with parameter estimates, posterior probability distributions were obtained by Markov Chain Monte Carlo (MCMC) simulations through a Metropolis–Hastings algorithm in AD Model Builder (Fournier et al., 2012). The MCMC chain was run for 1 million steps sampling every 100th step. The initial 2000 saved steps were discarded as a burn-in period. Convergence of the MCMC chain was evaluated by constructing trace plots for each estimated parameter and derived variable as a visual check to ensure the chain was well-mixed, and by using Geweke (1992) and Heidelberger and Welch (1983) diagnostic tests as formal evaluations of convergence. Additionally, we compared effective sample size of the saved MCMC chain with the actual chain sample size as a method for evaluating autocorrelation among the saved MCMC samples. All MCMC diagnostic measures were conducted in R (R Core Team, 2014) using the "coda" package (Plummer et al., 2006).

Simulating production of juvenile sea lamprey from lentic areas given various lampricide treatment effectiveness levels

Stochastic simulations were used to determine production of juvenile sea lamprey from lentic populations under four lampricide effectiveness levels based on the larval survival and metamorphosis function coefficients estimated from this study. The simulations assumed that a lampricide treatment would occur 2 years after the lentic population was established because it would take one year for the population to be discovered and one year to organize a treatment effort. Annual production of juvenile sea lamprey from a significant dispersal of larvae into a lentic area for up to 8 years after establishment (6 years after treatment) was calculated as

$$N_t^{juvenile} = \begin{cases} \sum_l \left[N_l^{larval} m_{l,t}\right] & \text{for } t = 0 \text{ years} \\ \sum_l \left[N_l^{larval}\left(S^{larval}\right)(1-m_{l,t-1})m_{l,t}\right] & \text{for } t = 1 \text{ years} \\ \sum_l \left[N_l^{larval}(1-\phi)\left(S^{larval}\right)^{t}\prod_{j=0}^{t-1}(1-m_{l,j})m_{l,t}\right] & \text{for } t = 2,3,4,5,6,7,8 \text{ years} \end{cases} \tag{7}$$

where *l*, S^{larval}, and *m* are as previously defined, *t* indexes the number of years after movement into the lentic area, $N^{juvenile}$ is the abundance of juveniles produced after infestation, N^{larval} is the initial abundance of larvae that distributed into the lentic area, and ϕ is the assumed Bayluscide treatment effectiveness. Growth of lentic sea lamprey and probabilities of metamorphosing for the simulations were calculated using Eqs. (5) and (6). Assumed size structure prior to treatment was based on larval assessment data from Lakes Michigan and Huron tributaries prior to treatments (Johnson et al., 2014), because this represents the worst case scenario in which a larval population in a lentic area establishes the year before the stream-resident population was to be treated and because this allows us to compare results directly to Johnson et al. (2014). Specifically, the assumed size structure was: 30–39 mm = 8%; 40–59 mm = 42%; 60–79 mm = 26%; 80–99 mm = 12%; 100–119 mm = 6%; 120–139 mm = 4%; and >139 mm = 2%. Therefore, this simulation was generic to an average Lake Huron or Michigan lentic area and results would vary on an individual basis if differences in length class strength existed. We were not concerned that the assumed proportions at length were not the same as the proportions at length observed in study streams (Table 2) because the simulation is driven by the results of the estimation model, which determined population demographics irrespective of the starting proportions at length in study streams. Simulations assumed initial larval population abundances of 10,000 individuals. We chose 10,000 as our initial abundance in part because this represents a typical lentic population in several of the lentic areas of the Great Lakes (U.S. Fish and Wildlife Service, USFWS, unpublished data). The lack of density-dependent factors in the juvenile production calculations meant that results would scale accordingly to different initial abundances [e.g., initial abundances of 5000 larvae would be expected to result in a 50% reduction in juvenile production (apart from random variation)]. The four TFM treatment effectiveness levels were 0%, 25%, 50% and 75% and were selected to understand the consequences for sea lamprey control if treatment effectiveness was <75%. To account for uncertainty in maturation and larval survival rates, we repeated each scenario simulation 1000 times, drawing a new set of parameters randomly from the joint posterior distribution of parameters from the estimated tag-recovery model.

Results

Tagging mortality, tag loss, and recoveries of larvae

For the period between tagging and release, tagging mortality ranged from 0.47% for Carp River to 0.90% for Hog Island Creek, whereas tag loss ranged from 1.35% for Carp River to 4.96% for Hog Island Creek animals. Shed tags and dead larvae were subtracted from the final count

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of tagged larvae released in each lentic area resulting in the release numbers listed in Table 2.

Granular Bayluscide surveys were conducted following standard sampling protocols/intervals in the study lentic areas (Table 3) and as previously indicated larvae collected during Bayluscide treatments were not routinely scanned for tags, although treatments only occurred in the Carp River lentic area 3 and 6 years after larval release. As a consequence, only six tagged larvae were recovered during the course of the study: two from the Carp River, one from Hog Island Creek, and three from the Bear River. Time at liberty for recovered larvae ranged from 10 months to 5 years. Weight and length change of these six larvae ranged from 0.8 to 4.8 g and −3 to 84 mm, respectively (Table 4). Based on observed length changes of recovered larvae, we estimated a Brody growth coefficient of 0.00132 (SE = 0.00027) for larval sea lamprey in lentic areas.

Recovery of coded-wire tagged adult sea lamprey

Of 9736 larvae tagged in all lentic areas, 169 were recovered as spawning adults (Table 5; Electronic Supplementary Material (ESM) Tables S1, S2, S3). Larvae from each lentic area were collected in the adult stage. Tagged adults were recovered 2 to 7 years after release (2009–2014). No tagged adults were recovered 8 (2015). The number of adults recovered per year resembled a bell shaped curve where recoveries peaked 4 and 5 years after release. Tagged larvae from all size classes were recovered as adults, but generally larger larvae during the year of stocking had a higher probability of adult recovery than smaller larvae. The Carp River lentic area was treated with Bayluscide during 2010, so the 31 adult sea lamprey recovered between 2012 and 2014 that originated from the Carp River lentic area either survived chemical exposure or were no longer in the treatment area.

Estimation model results

The multi-state tag-recovery model converged on a solution despite the small number of tagged larvae recovered. As well, the MCMC simulation for the model converged on a stationary distribution. Examination of trace plots indicated that the chain was well mixed (Fig. 2), and all parameters passed the Geweke (1992) and Heidelberger and Welch (1983) diagnostic tests (Table 6). Effective sample sizes for the parameters ranged from around 7400 to 8000 (Table 6).

Larval survival was estimated to be 62.7% with a 95% highest posterior density interval of 57.8 to 68.7%. Larval recovery probability during Bayluscide surveys was estimated to be 1.65E − 04% with a 95% highest posterior density interval of 5.27E − 04 and 3.05E − 03%. The product of juvenile survival and adult capture probability was estimated to be 8.4% with a 95% highest posterior density interval of 5.7 and 10.0%. The parameters of the metamorphosis function are shown in Table 6. The estimates correspond to a length at which 50% of the larvae would be expected to metamorphose of 126 mm (95% highest posterior density interval of 124 to 129 mm).

Table 5
Number of coded wire tagged sea lamprey recovered as adults by lentic area and year. Larval sea lamprey were released during year 0 (2007). ESM Tables S1 through S3 summarize the size at stocking of individuals that were recovered as adults.

Lentic area	Year 2	Year 3	Year 4	Year 5	Year 6	Year 7	Year 8	Total
Bear River	0	1	5	19	3	3	0	31
Carp River	4	4	37	13	15	3	0	76
Hog Island	0	2	23	28	9	2	0	64

Simulation results

The simulated annual production of juvenile sea lamprey from the hypothetical lentic population of 10,000 individuals was generally bimodal, with peaks during the initial year of discovery and then 4 years after discovery (Table 7). Because Bayluscide treatment was assumed to not occur until year 2, annual production in years 0 and 1 were similar across the levels of treatment effectiveness that were considered. The year 4 peak in production varied from 62 to 132 under a 75% treatment effectiveness to 246 to 530 under a 0% treatment effectiveness. Overall juvenile production was 845 to 1145 for 75% treatment effectiveness, 1072 to 1613 for 50% treatment effectiveness, 1288 to 2068 for 25% treatment effectiveness, and 1542 to 2536 for 0% treatment effectiveness.

Discussion

Annual survival of sea lamprey larvae in lentic areas has not been estimated previously, but our estimate of 63% was slightly higher than most estimates for river dwelling larvae. In a study using the same tagging design and estimation model, except that tagged larvae were stocked into rivers recently treated with lampricide, larval survival was estimated at 57% (Johnson et al., 2014). Annual survival of larvae in Lake Michigan tributaries was estimated at 45% using a management strategy evaluation model (Jones et al., 2009). When that same management model was applied to all five Great Lakes (Irwin et al., 2012), estimated larval annual survival rates ranged from 40% (Lake Erie) to 52% (Lake Ontario). Integrated assessments of the St. Marys River sea lamprey population yielded estimates of larval survival similar to ours (66–91%, Jones et al., 2015). The St. Marys River connects Lakes Superior and Huron, so the chemistry and productivity of the St. Marys River may be similar near river mouths in Lakes Michigan and Huron where we stocked larvae. Survival of larval sea lamprey between ages 1 and 4 held in instream enclosures was very high, (96%; Morman, 1987), perhaps because individuals were protected from predation and environmental factors, such as flooding. The relatively high survival in lentic areas may be because larvae are less vulnerable to floods, icing, and predators.

Growth of larvae in lentic areas has not been estimated previously, but our estimated Brody growth coefficient was lower than estimates for river-dwelling larvae, although it was only derived from the recovery of six tagged larvae. Estimated Brody growth coefficients of larvae stocked in streams recently treated with lampricide ranged from

Table 4
Change in weight and length of tagged larvae released during 2007 and recovered as larvae during 2008, 2009, and 2012 in the lentic area off Bear River, Michigan (Petoskey Harbor), Carp River, Michigan, and Hog Island Creek, Michigan.

Lentic area	Release date	Recapture date	Release weight (g)	Recapture weight (g)	Weight change (g)	Release length (mm)	Recapture length (mm)	Length change (mm)	Length change per year (mm)
Bear River	3-Aug.-07	11-Jun.-08	1.9	2.7	0.8	105	102	-3	-4
Bear River	3-Aug.-07	11-Jun.-08	0.6	1.4	0.8	68	87	19	23
Bear River	3-Aug.-07	11-Jun.-08	1.8	3.7	1.9	100	127	27	2
Carp Lake	26-Jun.-07	26-Aug.-09	1.2	1.7	0.5	86	108	22	10
Carp Lake	26-Jun.-07	26-Aug.-09	0.5	1	0.5	63	95	32	15
Hog Island	18-Jul.-07	6-Sep.-12	0.5	5.3	4.8	56	140	84	16

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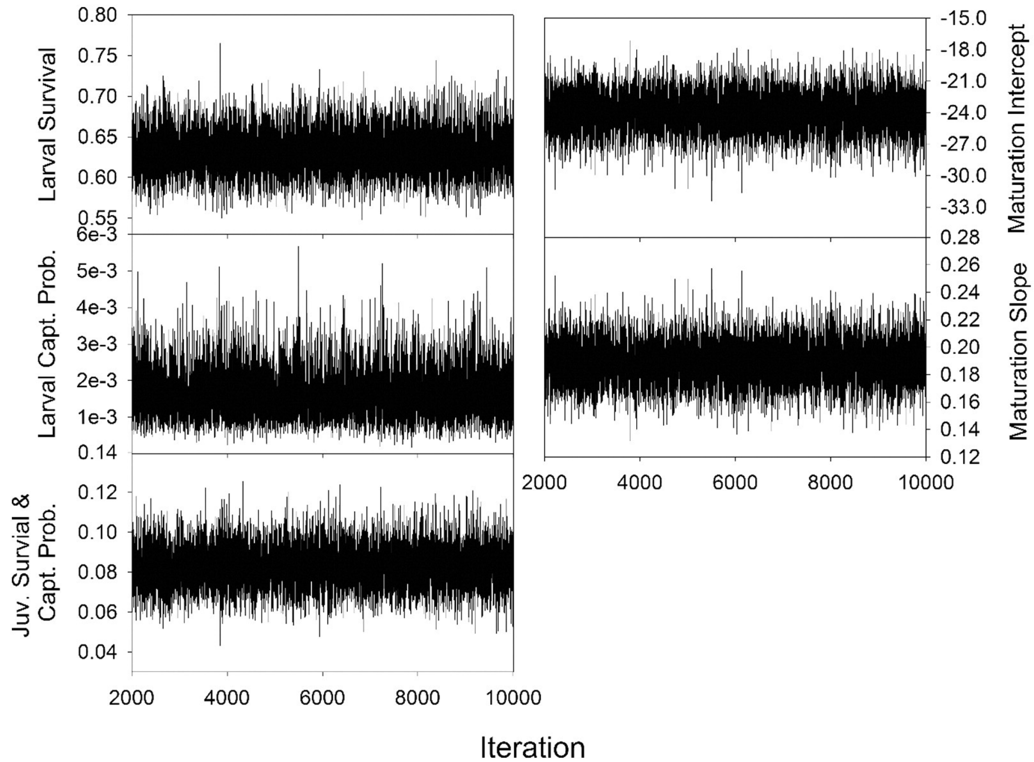

Fig. 2. Trace plots of saved MCMC iterations for larval survival, larval recovery probability during Bayluscide surveys, product of juvenile survival and adult capture probability, and metamorphosis function parameters from the multi-state tag-recovery model fit to the lentic sea lamprey data.

0.00208 to 0.00483 (Johnson et al., 2014), which was two to four times greater than our estimates for larvae residing in lentic areas. Here, the asymptotic larval length was set to 159 mm with 188 growing degree days occurring per year, as in Johnson et al. (2014). Larvae in lentic areas grew slower and required more years to metamorphose than most river dwelling populations, so their higher survival compensated for slower growth. This result is consistent with most fishes; slow growth often correlates with high survival and longer time to maturity (Pauly, 1980).

Low food availability and marginal burrowing habitat could have caused the slow growth observed in lentic areas. Larval lampreys feed on bioseston and abioseston similar to material described as biofilm in streams (Sutton and Bowen, 1994) and prefer to burrow in silty substrate (Yap and Bowen, 2003). More productive streams (high phosphorous, high conductivity) have been found to harbor faster growing larvae (Young et al., 1990) likely because they produce more biofilm. Primary production is relatively low in the upper Great Lakes and has declined in recent decades (Evans et al., 2011). Given the low productivity of Lakes Huron and Michigan and the lack of unidirectional flow in river mouths, biofilms and organic matter may be less abundant and nutritious than in tributaries to these lakes. Furthermore, the lentic areas we studied and most stream mouths in the upper Great Lakes are dominated by sand substrate. Stream dwelling northern brook lamprey (*Ichthyomyzon fossor*) larvae residing in silty depositional areas had higher assimilation efficiencies and condition factors than larvae in sandy areas, although both groups of larvae consumed similar amounts of amino acids and organic matter in their diet (Yap and Bowen, 2003). Therefore, if larvae in lentic areas primarily burrow in sand, they may also have low assimilation efficiencies. Low density larval populations in streams often exhibit fast growth, high survival, and earlier transformation relative to larvae in high density environments (Murdoch et al., 1991; Rodriguez-Munoz et al., 2003; Zerrenner and Marsden, 2005). Because larval density is generally low in lentic environments relative to stream environments (Aaron Jubar, USFWS, personal observation), low quantity and quality of food was likely the cause of the slow growth. Growing degree days in streams and their respective lentic areas are assumed to be similar in the Empiric Stream Treatment Ranking database (Christie et al., 2003). This assumption has not been confirmed, but could be true in some cases because lentic areas, while slower to warm in the spring, would be slower to cool in the fall and winter. If the assumption is true, differences in annual water temperatures were also unlikely the cause of slower larval growth in lentic areas.

Our estimate of the length at which 50% of the larvae were expected to metamorphose was smaller than estimates or observations of mean length at metamorphosis from other larval populations in Great Lakes tributaries (127 mm versus 122–177 mm; Manion and Stauffer, 1970; Purvis, 1980; Morkert et al., 1998; Griffiths et al., 2001; Slade et al., 2003; Johnson et al., 2014). In streams, length at metamorphosis has

Table 6
Highest posterior density estimates and 95% highest posterior density intervals for larval survival, larval capture probability, product of juvenile survival and adult capture probability, and metamorphosis functions parameters from the multi-state tag-recovery model fit to the lentic sea lamprey data. Also shown are P-values for the Geweke (1992) and Heidelberger and Welch (1983) diagnostic tests for posterior distribution convergence for estimated parameters and the effective sample size (ESS) for the saved chain.

Parameter	Estimate	95% HPD interval	Geweke *P*-value	HW *P*-value	ESS
Larval survival	0.627	0.578–0.687	0.916	0.212	8000
Larval capture prob.	1.653E − 03	5.265E − 04 – 3.046E − 03	0.444	0.185	8000
Juv. survival & adult capture prob.	0.084	0.061–0.104	0.281	0.279	8000
Metamorphosis intercept	−23.886	−27.757 – −20.232	0.589	0.656	7594
Metamorphosis slope	0.186	0.158–0.221	0.568	0.547	7543

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Table 7
Simulated annual production of juvenile sea lamprey from a hypothetical lentic population assuming an initial abundance of 10,000 individuals at time of discovery across different levels of Bayluscide treatment effectiveness. Reported are the 2.5 and 97.5 quantiles in annual juvenile production from 1000 simulations for each treatment effectiveness. The simulations assumed that Bayluscide treatment would occur 2 years after discovery of the lentic population to allow time for treatment planning. Year 0 is the year of discovery.

Time since discovery	Assumed Bayluscide effectiveness			
	75%	50%	25%	0%
Year 0	431–512	430–512	430–512	431–510
Year 1	155–209	154–210	155–210	154–210
Year 2	39–61	78–123	117–184	156–246
Year 3	50–92	99–183	147–274	196–367
Year 4	62–132	122–260	185–398	246–530
Year 5	51–118	101–237	152–357	202–496
Year 6	18–49	36–101	56–152	71–197
Year 7	2–9	4–19	6–28	8–38
Year 8	0–1	0–2	0–3	0–4

been found to be inversely related to larval density (Purvis, 1980; Treble et al., 2008). Furthermore, stream dwelling larvae have been found metamorphosing at smaller sizes in productive streams with fast larval growth rates, and at larger sizes in streams with low productivity (Griffiths et al., 2001). Accordingly, the short length at metamorphosis in this study could be considered surprising because of low larval density and slow growth rates in our lentic areas. However, Purvis (1979) found that among six Lake Superior tributaries, the mean length at metamorphosis increased from 140 mm to 166 mm as larval density decreased after their first ever lampricide treatment. Therefore, we speculate that our results are consistent with a hypothesis that under highly competitive conditions, when food and silty burrowing habitat are limiting, larvae metamorphose at smaller sizes relative to environments with fast growth and high condition factors. According to this hypothesis, larvae in lentic areas may metamorphose at smaller size because food and habitat is always limiting, regardless of population density.

Our estimated product of juvenile survival and adult capture probability (8.4%; adult recovery rates) was similar to previous studies on stream dwelling larvae in Lakes Huron and Michigan. Swink and Johnson (2014) captured outmigrating juvenile sea lamprey in the fall and spring, injected them with CWTs, released then in a northern Lake Huron tributary, and recovered tagged sea lamprey in the adult stage. Recovery rate in the adult stage (product of juvenile survival and capture probably) was 8% and recapture probability was not related to season of release or size at release. Therefore, even though metamorphosed sea lamprey from lentic areas were shorter on average than most stream dwelling populations, we expect that they would have similar survival rates in the juvenile stage. In a similar study where tagged larvae were released in tributaries to Lakes Huron and Michigan, estimated adult recovery rate ranged from 7 to 9% (Johnson et al., 2014). Assuming that lake-wide adult abundance estimates are accurate (Mullett et al., 2003), CWT tag-recovery data from this study (adults captured between 2009 and 2014), Swink and Johnson (2014; adults captured between 1999 and 2001), and Johnson et al. (2014; adults captured between 2006 and 2012) suggests that the probability of a recently metamorphosed sea lamprey surviving to the adult stage in northern Lakes Huron and Michigan is around 40%. Assuming that survival was constant during this period, this would equate to an annual survival of 65%, which is similar to the estimate Jones et al. (2015) found when modeling population demographics of sea lamprey in the St. Marys River.

The potential contribution of juvenile sea lamprey from untreated lentic environments appears less than the juvenile contribution from untreated river environments where larvae grow faster. In Johnson et al. (2014), the production of juvenile sea lamprey from a population of 10,000 larvae with the same starting conditions was simulated in streams with fast and slow larval growth (see Table 5 of Johnson et al., 2014 where the starting population was 1,000,000 and then the lampricide treatment removed 99% leaving 10,000 survivors). Total juvenile production from those larval populations over 6 years was estimated to be between 2280 and 4183 for rivers with fast growth and 455–994 for rivers with slow growth, whereas in this study, juvenile production from a lentic population over 8 years with the same starting conditions was 1464–2598 (see Table 7 when Bayluscide effectiveness equaled 0%). As such, given the same abundance and size distribution of larvae in three different habitats, control effort would be better focused on streams with fast larval growth, because those larvae are most likely to contribute to the juvenile population. For the same reasons, if the cost of lampricide control in the three habitats was equal, but resources were such that they all could not be treated with lampricide in a given year, sea lamprey control effort would be best directed toward the larvae in the fast growth stream, followed by the lentic area, and, lastly, the slow growth stream. At present, lentic areas infested with larval sea lamprey are considered for lampricide treatment alongside stream-dwelling populations of larvae by comparing the cost to kill a larva over 100 mm in each population (Hansen and Jones, 2008) without consideration for the probability that a larva in a population will contribute to the juvenile population. We conceptualize that differences in survival of larvae to the juvenile stage may be important for control agents to consider when prioritizing lampricide treatment options under limited budget scenarios. A sea lamprey can only die from one cause, so if a sea lamprey would have died of natural causes before inflicting damage to the fishery, then killing it might waste lampricide that could better be used on larvae that would more likely contribute to the juvenile population. Our simulations show that lentic areas and slow growth streams can still produce thousands of juvenile sea lamprey, so sea lamprey control will be most successful if lentic areas and slow growth streams are assessed and treated regularly, especially when efficiencies are gained by treating several areas in a geographic region with the same treatment crew and when the opportunity to kill multiple age classes occurs.

When lampricide effort is directed at lentic populations, our simulation shows that juvenile production from that population is reduced. However, the timing of the treatment seems important because, given our starting larval population size structure and because larval growth slowed after arriving in the lentic area, production of juvenile sea lamprey is highest the year the population is established (when larvae from multiple year classes drift from the stream into the lentic area). In our simulation, we assumed that Bayluscide treatment occurred two years after the population established; one year to identify the infestation and one year to treat it. If treatment occurred the year the population was established, juvenile production would be reduced even further. An interesting observation from our study was that 31 adult sea lamprey recovered from the Carp River lentic area survived the 2010 Bayuscide treatment. Larvae that survived the Carp River lentic treatment could have done so because they distributed widely after release and were not in the treatment area or because they were in the treatment area, but the Bayluscide did not yield the expected 75% kill rate. Additional research to better describe how larvae distribute in lentic areas and how Bayluscide treatment efficacy varies would help to determine the reason for survival of sea lamprey larvae in lentic areas.

Assuming our results are applicable to other lamprey species, in places where conservation of lamprey populations is desired, lentic areas may be habitats with lower growth and survival if the larvae were displaced from a fast growth stream, but could serve as a refuge if they were displaced from a slow growth stream. Depending on the circumstance, managers may want to focus more attention to management tactics that either decrease or increase larval drift into lentic areas. In regulated rivers, modifying flow regimes may influence drift rates. In natural rivers, increasing or decreasing the prevalence of backwaters and sediment traps may be ways to influence drift during high flow events. Additional research seems warranted to describe the length frequency, survival, and metamorphosis of other lamprey species in lentic environments, especially species like the Vancouver lamprey

(*Entosphenus macrostomus*) that regularly spawn in lentic areas (Beamish, 1987; Johnson et al., 2015).

In conclusion, we conducted the first evaluation of survival and metamorphosis of larval sea lamprey stocked into lentic areas near stream mouths and found that indeed small larvae introduced into lentic areas, grow, metamorphose, and contribute to the juvenile population. Larval growth in these environments was slow relative to some stream environments, but survival was high and the length at which metamorphosis occurred was less than most stream environments, so production to the juvenile stage occurred and control of these populations seems warranted. However, given the same cost to kill larvae over 100 mm in a fast growth stream and lentic area, effort may be better spent treating the fast growth stream because those larvae appear most likely to contribute to the juvenile population. Our study only evaluated three lentic areas, and production almost certainly varies among lentic areas. Additional research would improve understanding of how larval lamprey size, survival, and metamorphosis vary among lentic areas, how broadly larvae distribute in lentic areas, and how Bayluscide treatment efficacy varies among lentic areas.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.jglr.2016.09.003.

References

Applegate, V.C., 1950. Natural history of the sea lamprey (*Petromyzon marinus*) in Michigan. U.S. Fish Wild. Serv. Spec. Sci. Rep. Fish. Serv. 55, p. 237

Beamish, R.J., 1987. Status of the lake lamprey, *Lampetra macrosto*, in Canada. Can. Field. Nat. 101, 186–189.

Bergstedt, R.A., Seelye, J.G., 1995. Evidence for lack of homing by sea lampreys. Trans. Am. Fish. Soc. 124, 235–239.

Bergstedt, R.A., Swink, W.D., Seelye, J.G., 1993. Evaluation of two locations for coded wire tags in larval and small parasitic-phase sea lampreys. N. Am. J. Fish. Manag. 13, 609–612.

Brownie, C., Hines, J.E., Nichols, J.D., Pollock, K.H., Hestbeck, J.B., 1993. Capture–recapture studies for multiple strata including non-Markovian transitions. Biometrics 49, 1173–1187.

Christie, G.C., Goddard, C.I., 2003. Sea lamprey international symposium (SLIS II): advances in the integrated management of sea lampreys in the Great Lakes. J. Great Lakes Res. 29 (Suppl. 1), 1–14.

Christie, G.C., Adams, J.A., Steeves, T.A., Slade, J.W., Cuddy, D.W., Fodale, M.F., Young, R.J., Kuc, M., Jones, M.L., 2003. Selecting Great Lakes streams for lampricide treatment based on larval sea lamprey surveys. J. Great Lakes Res. 29 (Suppl. 1), 152–160.

Close, D.A., Fitzpatrick, M.S., Li, H.W., 2002. The ecological and cultural importance of a species at risk of extinction, Pacific lamprey. Fisheries 27, 19–25.

R Core Team, 2014. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Dawson, H.A., Quintella, B.R., Almeida, P.R., Treble, A.J., Jolley, J.C., 2015. The ecology of larval and metamorphosing lampreys. In: Docker, M.F. (Ed.), Lampreys: Biology, Conservation, and Control. Springer, pp. 75–138.

Docker, M.F., Hume, J.B., Clemens, B.J., 2015. Introduction: a surfeit of lampreys. In: Docker, M.F. (Ed.), Lampreys: Biology, Conservation, and Control. Springer, pp. 1–34.

Evans, M.E., Fahnenstiel, G., Scavia, D., 2011. Incidental oligotrophication of North America's Great Lakes. Environ. Sci. Techol. 45, 3297–3303.

Fournier, D.A., Skaug, H.J., Ancheta, J., Ianelli, J., Magnusson, A., Maunder, M.N., Nielsen, A., Sibert, J., 2012. AD model builder: using automatic differentiation for statistical inference of highly parameterized complex nonlinear models. Optim. Methods Softw. 27, 233–249.

Geweke, J., 1992. Evaluating the accuracy of sampling-based approaches to the calculation of posterior moments. In: Bernado, J.M., Berger, J.O., Dawid, A.P., Smith, A.F.M. (Eds.), Bayesian Statistics 4. Oxford University Press, pp. 169–193.

Griffiths, R.W., Beamish, F.W.H., Morrison, B.J., Barker, L.A., 2001. Factors affecting larval sea lamprey growth and length at metamorphosis in lampricide-treated streams. Trans. Am. Fish. Soc. 130, 289–306.

Hansen, G.J.A., Jones, M.L., 2008. A rapid assessment approach to prioritizing streams for control of Great Lakes sea lampreys (*Petromyzon marinus*): a case study in adaptive management. Can. J. Fish. Aquat. Sci. 65, 2471–2484.

Hansen, M.J., Madenjian, C.P., Slade, J.W., Steeves, T.B., Almeida, P.R., Quintella, R., 2016. Population ecology of the sea lamprey (*Petromyzon marinus*) as an invasive species in the Laurentian Great Lakes and imperiled species in Europe. Rev. Fish Biol. Fish. http://dx.doi.org/10.1007/s11160-016-9440-3 (online).

Hardisty, M.W., Potter, I.C., 1971a. The general biology of adult lampreys. In: Hardisty, M.W., Potter, I.C. (Eds.), The Biology of Lampreys vol. 1. Academic Press, London, pp. 127–206.

Hardisty, M.W., Potter, I.C., 1971b. The behavior, ecology, growth of larval lampreys. In: Hardisty, M.W., Potter, I.C. (Eds.), The Biology of Lampreys vol. 1. Academic Press, London, pp. 85–125.

Heidelberger, P., Welch, P.D., 1983. Simulation run length control in the presence of an initial transient. Oper. Res. 31, 1109–1144.

Heinrich, J.W., Mullett, K.M., Hansen, M.J., Adams, J.V., Klar, G.T., Johnson, D.A., Christie, G.C., Young, R.J., 2003. Sea lamprey abundance and management in Lake Superior, 1957 to 1999. J. Great Lakes Res. 29 (Suppl. 1), 566–583.

Irwin, B.J., Liu, W., Bence, J.R., Jones, M.L., 2012. Defining economic injury levels for sea lamprey control in the Great Lakes basin. N. Am. J. Fish. Manag. 32, 760–771.

Johnson, N.S., Swink, W.D., Brenden, T., Fodale, M.F., Slade, J.W., Steeves, T.B., Jones, M.L., 2014. Survival and metamorphosis of low-density populations of larval sea lampreys (*Petromyzon marinus*) in streams following lampricide treatment. J. Great Lakes Res. 40, 155–163.

Johnson, N.S., Buchinger, T.J., Li, W., 2015. Reproductive ecology of lampreys. In: Docker, M.F. (Ed.), Lampreys: Biology, Conservation, and Control. Springer, pp. 265–303.

Jones, M.L., Irwin, B.J., Hansen, G.J.A., Dawson, H.A., Treble, A.J., Liu, W., Dai, W., Bence, J.R., 2009. An operating model for the integrated pest management of Great Lakes sea lamprey. Open Fish Sci. J. 2, 59–73.

Jones, M.L., Brenden, T.O., Irwin, B.J., 2015. Re-examination of sea lamprey control policies for the St. Marys River: completion of an adaptive management cycle. Can. J. Fish. Aquat. Sci. 72, 1538–1551.

Madenjian, C.P., Cochran, P.A., Bergstedt, R.A., 2003. Seasonal patterns of growth, blood consumption, and effects on host by parasitic-phase sea lampreys in the Great Lakes: An individual-based model approach. J. Great Lakes Res. 29, 332–346.

Maitland, P.S., Renaud, C.B., Quintella, B.R., Close, D.A., Docker, M.F., 2015. Conservation of native lampreys. In: Docker, M.F. (Ed.), Lampreys: Biology, Conservation, and Control. Springer, pp. 375–428.

Manion, P.J., Stauffer, T.B., 1970. Metamorphosis of the landlocked sea lamprey, *Petromyzon marinus*. J. Fish. Res. Board Can. 27, 1735–1746.

Mateus, C.S., Rodriguez-Munoz, R., Quintella, B.R., Alves, M.J., Almeida, P.R., 2012. Lampreys of the Iberian Peninsula: distribution, population status, and conservation. Endanger. Species Res. 16, 183–198.

Meeuwig, M.H., Puls, A.L., Bayer, J.M., 2007. Survival and tag retention of Pacific lamprey larvae and macrophthalmia marked with coded wire tags. N. Am. J. Fish. Manag. 27, 96–102.

Morkert, S.B., Swink, W.D., Seelye, J.G., 1998. Evidence for early metamorphosis of sea lampreys in the Chippewa River, Michigan. N. Am. J. Fish. Manag. 18, 966–971.

Morman, R.H., 1987. Relationship of density to growth and metamorphosis of caged larval sea lampreys, *Petromyzon marinus* (L.), in Michigan streams. Trans. Am. Fish. Soc. 30, 173–187.

Mullett, K.M., Heinrich, J.W., Adams, J.V., Young, R.J., Henson, M.P., McDonald, R.B., Fodale, M.F., 2003. Estimating lake-wide abundance of spawning-phase sea lampreys (*Petromyzon marinus*) in the Great Lakes: extrapolating from sampled streams using regression models. J. Great Lakes Res. 29 (Suppl. 1), 240–252.

Murdoch, S.P., Beamish, F.W.H., Docker, M.E., 1991. Laboratory study of growth and interspecific competition in larval lampreys. Trans. Am. Fish. Soc. 120, 653–656.

Pauly, D., 1980. On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. J. Cons. int. Explor. Mer 39, 175–192.

Plummer, M., Best, N., Cowles, K., Vines, K., 2006. CODA: convergence diagnosis and output analysis for MCMC. R News 6, 7–11.

Potter, I.C., 1980. Ecology of larval and metamorphosing lampreys. Can. J. Fish. Aquat. Sci. 37, 1641–1657.

Purvis, H.A., 1979. Variations in growth, age at transformation, and sex ratio of sea lamprey reestablished in chemically treated tributaries of the Upper Great Lakes. Great Lakes Fish. Comm. Tech. Repo. 35, p. 36p

Purvis, H.A., 1980. Effects of temperature on metamorphosis and the age and length at metamorphosis in sea lamprey (*Petromyzon marinus*) in the Great Lakes. Can. J. Fish. Aquat. Sci. 37, 1827–1834.

Rodriguez-Munoz, R., Nicieza, A.G., Brana, F., 2003. Density-dependent growth of sea lamprey larvae: evidence for chemical interference. Funct. Ecol. 17, 403–408.

Schnute, J.T., 1994. A general framework for developing sequential fisheries models. Can. J. Fish. Aquat. Sci. 51, 1676–1688.

Slade, J.W., Adams, J.V., Cuddy, D.W., Weise, J.G., Young, R.J., Christie, G.C., Fodale, M.F., Heinrich, J.W., Weisser, J.W., Wuinlan, H.R., 2003. Techniques and methods for assessment of larval sea lampreys in the Great Lakes. J. Great Lakes Res. 29 (Suppl. 1), 137–151.

Smith, B.R., Tibbles, J.J., 1980. Sea lamprey (*Petromyzon marinus*) in Lakes Huron, Michigan, and Superior: history of invasion and control, 1936–78. Can. J. Fish. Aquat. Sci. 37, 1780–1801.

Sullivan, P., Adair, R., Woldt, A., 2016. Sea lamprey control in the Great Lakes 2015. Great Lakes Fishery Commission Annual Report, Ann Arbor, MI.

Sutton, T.M., Bowen, S.H., 1994. Significance of organic detritus in the diet of larval lampreys in the Great Lakes basin. Can. J. Fish. Aquat. Sci. 51, 2380–2387.

Swink, W.D., Johnson, N.S., 2014. Growth and survival of sea lampreys from metamorphosis to spawning in Lake Huron. Trans. Am. Fish. Soc. 143, 380–386.

Treble, A.J., Jones, M.L., Steeves, T.B., 2008. Development and evaluation of a new predictive model for metamorphosis of Great Lakes larval sea lamprey (*Petromyzon marinus*) populations. J. Great Lakes Res. 34, 404–417.

Yap, M.R., Bowen, S.H., 2003. Feeding by northern brook lamprey (*Ichthyomyzon fossor*) on sestonic biofilm fragments: habitat selection results in ingestion of a higher quality diet. J. Great Lakes Res. 29 (Suppl. 1), 15–25.

Young, R.J., Kelso, J.R.M., Weise, J.G., 1990. Occurrence, relative abundance, and size of landlocked sea lamprey (*Petromyzon marinus*) ammocoetes in relation to stream characteristics in the Great Lakes. Can. J. Fish. Aquat. Sci. 47, 1773–1778.

Zerrenner, A., Marsden, J.E., 2005. Influence of larval sea lamprey density on transformer life history characteristics in Lewis Creek, Vermont. Trans. Am. Fish. Soc. 134, 687–696.