Articles

Environmental and Biological Factors Influence Migratory Sea Lamprey Catchability: Implications for Tracking Abundance in the Laurentian Great Lakes

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Abstract

Sea Lamprey Petromyzon marinus population trends in the Great Lakes are tracked by trapping migratory adults in tributaries and using mark-and-recapture techniques to estimate abundance. Understanding what environmental and biological factors influence Sea Lamprey capture in tributaries is crucial to developing efficient trapping methods and reliable abundance estimates. We analyzed data from trapping sites located on eight Great Lakes tributaries using Cormack–Jolly–Seber models and examined how water temperature, discharge, sex, and length influenced Sea Lamprey apparent survival and capture probability. Sea Lamprey apparent survival was negatively associated with water temperature in all tributaries. Additionally, the odds of small Sea Lamprey (≤ 45 cm) remaining available to capture were 39% less (95% CI: 63% decrease–1% increase) than large (> 45 cm) lamprey odds. We used these observed relationships to investigate if bias in abundance estimates using the pooled-Petersen estimator and Jolly–Seber models was expected to be similar across trapping locations or influenced by variable environmental conditions and biological traits. Pooled-Petersen abundance estimates had a positive bias when we generated data sets from simulated populations with empirical relationships between environmental characteristics and catchability. The degree of bias depended upon changes in stream warming patterns and was not consistent among trapping locations. Jolly–Seber models using data from either weekly batch-marked or uniquely marked individuals generated abundance estimates with low bias when data quality was high, but performed poorly in scenarios with few recaptured Sea Lamprey. This research can promote improved Sea Lamprey monitoring efforts by providing insight into the reliability of the pooled-Petersen abundance estimator as a tool for tracking Sea Lamprey populations and demonstrating the limitations of adopting more robust methods when data are sparse.

Keywords: abundance estimation; invasive species; population monitoring; Sea Lamprey

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Sea Lamprey Petromyzon marinus are an anadromous fish that expanded from their native range in the Atlantic Ocean into the Laurentian Great Lakes after natural barriers to fish migration between the Great Lakes and the Atlantic Ocean were bypassed by navigational canals (Sullivan et al. 2003). During their parasitic juvenile phase, Sea Lamprey damage fish populations that drive ecologically important trophic interactions and support Great Lakes fisheries valued at US $7 billion (American Sportfishing Association 2008). Sea Lamprey populations in the Great Lakes are controlled by structures that prevent spawning adults from accessing quality spawning and rearing habitat and by applying lampricide to streams containing larval Sea Lamprey (Smith and Tibbles 1980).

Natural resource managers within the Sea Lamprey Control Program (SLCP) track trends in migratory Sea Lamprey population abundance by annually conducting mark-and-recapture tagging studies on 29 Great Lakes tributaries (Mullett et al. 2003). The SLCP develops an index of abundance for each Great Lake basin by combining in-stream estimates from tributaries within each basin. A reliable index can be used to measure Sea Lamprey control effectiveness and guide future control effort, but variable catchability of migratory Sea Lamprey could mask abundance trends and lead to incorrect interpretations of Sea Lamprey control success in the Great Lakes. For our purposes, Sea Lamprey catchability refers to all of the processes that contribute to capture in assessment traps conditional on movement into the mouth of a river with an assessment site. Exploring biological and environmental factors that contribute to catchability of Sea Lamprey during upstream spawning migrations could improve assessment methods for migratory Sea Lamprey (Jones 2007) and guide development of efficient trapping programs (McLaughlin et al. 2007).

A potential driver of variable Sea Lamprey catchability is modified behavior in response to changing environmental cues. Sea Lamprey behavior is influenced by river discharge; migrating Sea Lamprey locate tributary entrances by detecting the river plume (Vrieze et al. 2011) and river discharge is positively related to Sea Lamprey movement within streams (Almeida et al. 2002). Though lamprey are poor swimmers at high currents (Beamish 1974), their tendency to use lower-velocity habitats during upstream migration (Holbrook et al. 2015) likely allows them to successfully migrate upstream during high-discharge events. Furthermore, Sea Lamprey were more likely to encounter traps during high-discharge events compared with low-discharge events downstream of a hydrogenerating station (Rous 2014). In addition to discharge, temperature influences migratory Sea Lamprey behavior. Applegate (1950) documented that Sea Lamprey migratory activity peaked at 10–18°C and temperatures above this range inhibited migratory activities. Similarly, daily catches of Sea Lamprey at trapping sites, an indicator of migratory activity, had a dome-shaped association with water temperature within Lake Ontario tributaries with peaks at 15°C (Binder et al. 2010). Water temperature is also associated with Sea Lamprey spawning behaviors; nest building typically does not occur until water temperatures reach 15°C (Manion and Hansen 1980). Finally, migratory adult Sea Lamprey diel activity patterns, light avoidance, and rheotaxis were directly influenced by temperature regimes in a laboratory setting (Binder and McDonald 2008).

In addition to environmental factors, biological traits associated with behavior and swimming ability could be important drivers of Sea Lamprey catchability. Swimming performance of Sea Lamprey tends to increase with size (Beamish 1974; McAuley 1996). Additionally, length was an important predictor of Pacific Lamprey Entosphenus tridentatus passage success through fishways on the Columbia River (Keef er et al. 2009), indicating that larger individuals were more adept at navigating through difficult hydraulic conditions. Differences between male and female Sea Lamprey behaviors could also lead to gender-based variability in catchability. Specifically, male and female lamprey differ in nest-building activity, arrival at spawning grounds (Manion and Hanson 1980), behavioral response to pheromones released by spermating male Sea Lamprey (Buchinger et al. 2015), and standing metabolic rate (Madenjian et al. 2014).

Behavioral heterogeneity related to changing environmental conditions and individual biological traits can influence the performance of abundance estimators. Currently, Sea Lamprey abundance is estimated using the pooled-Petersen abundance estimator, which generates abundance estimates from migratory Sea Lamprey mark-and-recapture data sets with similar accuracy and precision as more complicated Schaefer or Bayesian P-spline estimators (Harper et al. 2018). However, Jolly–Seber (JS) models are robust to temporal variation and differences in catchability associated with measured individual covariates and could lead to more robust abundance estimates compared with those from the pooled-Petersen estimator (Velez-Espino et al. 2016). Furthermore, using individual marks rather than weekly batch marks (which are currently used by the SLCP for annual abundance assessment) could provide more robust data for abundance estimation using JS models.

Our primary objective was to provide insight into the efficacy of estimating migratory Sea Lamprey abundance using the pooled-Petersen and JS abundance estimators and thereby promote improved monitoring efforts. Additionally, we investigated relationships between environmental and biological factors to guide development of effective trapping protocols for migratory Sea Lamprey. We used empirical Sea Lamprey catchability parameter estimates from multiple trap sites throughout the Great Lakes basin to simulate how the accuracy and precision of Sea Lamprey abundance estimates could vary temporally and among trap sites. We developed simulation scenarios to address three questions relating to the performance of the pooled-Petersen abundance estimator, JS models using mark-and-recapture data from batch-marked lamprey, and JS models using data from uniquely identifiable lamprey: 1) do environmental...
effects on catchability affect bias in Sea Lamprey abundance estimates? 2) Do individual effects on catchability affect bias in Sea Lamprey abundance estimates? 3) Does bias vary among SLCP trapping sites? We predicted that abundance estimates from JS models would outperform pooled-Petersen estimates in terms of accuracy and that adopting uniquely identifiable tags would improve precision and accuracy compared with using batch marks.

Methods

Field methods and study area

We analyzed migratory Sea Lamprey mark-and-recapture data collected at eight long-term assessment sites during 2012–2018. These sites were located on the Bad, Bois Brule, Tahquamenon, Manistique, Peshtigo, Manistee, St. Joseph, and Black rivers (Figure 1). We checked traps four to five times per week for the duration of the Sea Lamprey migration (March–June, but start and end dates varied by latitude). We determined the sex of all captured Sea Lamprey, checked for marks, applied a week-specific fin clip to a subset of unmarked lamprey (marking rates varied by site), and recorded the fin-clip type of captured, previously marked lamprey to infer marking week. We transported newly marked lamprey downstream of the sampling location and removed released-and-recaptured Sea Lamprey from the stream and euthanized them.

In addition to week-specific fin clips, we marked Sea Lamprey captured in the Bois Brule River with uniquely identifiable tags during 2017–2018 and recorded the total length (cm) of all released individuals. During 2017 we used t-bar anchor tags and implanted internal half-duplex passive integrated transponder tags (32 mm, 0.8 g, Oregon RFID) in 2018. We adopted passive integrated transponder tags in 2018 because tag loss rate for t-bar anchor tags during 2017 was 15%. We did not examine potential effects of passive integrated transponder tag implantation on Sea Lamprey behavior and survival, but passive integrated transponder tags have been used successfully in other studies for monitoring movement of juvenile (Miehls et al. 2019) and adult (Castro-Santos et al. 2016) Sea Lamprey. We assigned fin-clipped individuals recovered without a tag a release date on the basis of the week-specific fin clip and by matching length and weight measurements with released individuals.

Assessment sites were integrated with barriers to Sea Lamprey migration located 2 to 49 km upstream from river confluences with the Great Lakes. We released marked Sea Lamprey captured in the Bois Brule, Tahquamenon, Manistique, Peshtigo, St. Joseph, and Black rivers near the mouth of the river of capture, whereas we released those captured in the Bad and
Manistee rivers 10 km and 24 km upstream from the river mouth, respectively.

Trap operators recorded stream temperature by using a handheld thermometer each time they lifted a trap and we obtained stream discharge measurements from U.S. Geological Survey gauging stations located upstream of the trapping sites. We calculated mean discharge during 2012–2018 Sea Lamprey trapping seasons for each river. We calculated mean weekly discharge anomaly for each stream as the percent deviation of mean weekly discharge from overall 2012–2018 mean discharge. We adopted this approach to facilitate comparisons among streams by converting discharge measurements to a similar scale. We recorded stream temperature and water level in the Bois Brule River with a Hobo U20 water level data logger deployed immediately downstream of the trap site that recorded data at 30-min intervals.

Mark-and-recapture data analysis

Cormack–Jolly–Seber models (Lebreton et al. 1992) were developed to investigate the influences of biological and environmental factors on migratory Sea Lamprey apparent survival and capture probability. Both parameters contribute to overall catchability; capture probability is the weekly probability of being captured given a lamprey is available to capture and apparent survival dictates how long a Sea Lamprey that has entered a tributary remains available to capture. The processes contributing to apparent survival are permanent emigration, permanent cessation of upstream migration due to onset of spawning behavior, and mortality, but we were unable to investigate how specific process contributed to overall apparent survival rates using available mark–recapture data sets from SLCP long-term assessment sites. For the weekly batch-mark data set, we constructed individual capture histories from mark-and-recapture data on the basis of the week of release and recapture. Using this method, we removed lamprey that we marked and recovered during the same week from the analysis (treated as losses upon capture) because the release and recovery occurred during the same time step. We created individually marked Sea Lamprey capture histories on the basis of day of release and recapture. We censored recaptured lamprey for the remaining weeks after recovery because we euthanized all recaptured individuals and did not release them.

We modeled capture probability and apparent survival as either a linear function of Julian week, mean weekly stream temperature, or mean weekly river discharge anomaly. For the Bois Brule River data, we used mean water level instead of discharge anomaly because discharge data were unavailable. We did not include multiple environmental predictors in models of capture probability or apparent survival because of high covariance in some streams (r > 0.5). We considered sex and total length (cm) biological covariates, but we only included length in the individually marked lamprey analysis because length information was not available for the batch-marked fish. We converted length to a categorical covariate; we considered lamprey large (> 45 cm) or small (≤ 45 cm) individuals on the basis of total length at capture. For the Bois Brule River data set, the most saturated models contained an environmental variable (Julian week, stream temperature, or discharge), length category, and sex. For the batch-marked data set containing data from the seven remaining rivers, the most saturated models included an environmental variable (Julian week, stream temperature, or discharge), a covariate for sex, and stream-specific associations between environmental and biological covariates and catchability. We considered all reduced models with fewer biological variables (225 models for the Bois Brule data set and 49 for the batch-mark data set) and conducted model selection using Akaike information criterion corrected for small sample size (AICc). We considered models with ΔAICc < 2 most supported by the data (Burnham and Andersen 2003). We developed and analyzed all models in R version 3.6.1 (R Core Team 2017) using the RMark package (Laake 2013) to interface with program MARK (White and Burnham 1999). We provide environmental data (Table S1, Supplemental Material), capture histories (Table S2, Supplemental Material), and R code (Table S3, Supplemental Material) to demonstrate the methodology and data used to investigate Sea Lamprey capture probability and apparent survival using SLCP long-term assessment data.

Abundance estimator evaluation

We evaluated abundance estimators by comparing known Sea Lamprey population abundances with estimated values. We generated simulated capture histories and summary statistics (total number marked and recaptured) by developing process and observation models for migratory Sea Lamprey on the basis of assumed values and empirical data. The process model consisted of migratory Sea Lamprey timing of arrival at monitored tributaries and apparent survival. Sea Lamprey migration and daily trapping effort lasted 10 wk and we simulated arrival times (days) as random deviates from a truncated normal distribution (mean = 14, SD = 14, minimum = 1, maximum = 69). After arrival on day tᵢ, the probability of remaining available to capture until tᵢ+1 was daily apparent survival rate φᵢ. The observation model sampled Sea Lamprey that had arrived to the tributary and remained available to capture with daily capture probability pᵢ. Upon capture, the model was programmed to either remove or mark and release unmarked lamprey (marking rate = 0.5). At-large marked lamprey were then susceptible to capture at the same daily capture probability as unmarked lamprey. The model removed all captured marked lamprey from the population.

We simulated individual lamprey trajectories as stochastic processes from their arrival date through the
end of the migration period (day 70) by drawing random deviations for \( \Phi \) and \( p \) from binomial distributions. We developed multiple models of apparent survival and capture probability that included associations with environmental and individual covariates. For each underlying process model we simulated 500,000 individual lamprey and compiled data sets \( (n = 250) \) by randomly sampling 5,000 individuals from this pool of simulated trajectories.

We converted all data sets to capture histories with either a daily time step or a weekly time step to mimic data available from uniquely marked or batch-marked lamprey. For the weekly time-step capture histories, we treated lamprey that we captured, marked and released, and recaptured during the same week as losses on capture. We did not simulate model selection and assumed that the correct underlying model for capture probability and apparent survival was selected and that we measured environmental and individual covariates without error. We analyzed all data sets using the POPAN formation of the JS model (Schwarz and Arnason 1996). We conducted analyses with Program MARK (White and Burnham 1999) and the RMark package (Laake 2013) for R version 3.4.1 (R Core Team 2017). We also estimated abundance using the pooled-Petersen estimator (Schwarz and Taylor 1998)

\[
N = \frac{n_1n_2}{m_2}
\]

where \( N \) is estimated abundance, \( n_1 \) is the total number of unmarked lamprey captured, \( n_2 \) is the number marked, and \( m_2 \) is the number of captured marked individuals. We calculated standard errors following Seber (1982). We compared abundance estimation methods (JS individual marks, JS batch marks, and pooled-Petersen) by calculating percent root mean-square error (%RMSE), percent bias, and coefficient of variation (CV) for each simulated data set and reporting means and standard-deviations of these metrics for each simulation type.

**Scenario 1. Variable rates of water temperature increase.** For these simulations we assumed that Sea Lamprey apparent survival was associated with water temperature and that daily capture probability remained constant \( (p = 0.03) \). Daily apparent survival was 0.98 at 9°C, decreased as water temperature increased, and reached 0.72 at 18°C. We considered three types of stream warming: constant warming, early warming, and delayed warming. In all instances, water temperature was 9°C at the outset of the spawning run and peaked at 18°C (Figure 2). We increased temperature by week rather than by day so that both JS evaluations (weekly and daily time step) were evaluated assuming the correct underlying process model.

**Scenario 2. Length-based apparent survival.** We used the constant warming condition from scenario 1 for these simulations, but we also included a length-based effect on apparent survival. We developed models with either a moderate length effect (small lamprey daily apparent survival of 0.70 at 18°C) or a large length effect (small lamprey daily apparent survival of 0.66 at 18°C). Large lamprey daily apparent survival at 18°C was 0.75 for both models. We based length effect size on the mean and upper 95% confidence interval [CI] bound for the estimated effect of length on apparent survival in the Bois Brule River (see “Results”). We used a 50:50 large : small population ratio for all simulations.

**Scenario 3. Geographic variability.** We used apparent survival and capture probability parameter estimates from Cormack–Jolly–Seber models to simulate Sea Lamprey populations representative of those sampled at SLCP long-term assessment sites located on the Bad, Tahquamenon, Manistique, Peshtigo, Manistee, St. Joseph, and Black rivers. We used environmental data from 2017 (mean weekly discharge anomaly and stream temperature) to generate capture probability and apparent survival values. In addition to comparing estimator performance among sites assuming a constant population size, we examined how number of recaptured individuals influenced the quality of abundance estimates at each site. We generated data sets for each site (30 per site and number of recaptures) with a specified number of recaptured individuals (10, 30, 50, 70, 90, 110) by randomly sampling individuals until the population contained the appropriate number of recaptured individuals. Using this approach, population size was variable among sites but we could compare abundance estimates for different streams with data sets containing the same number of recaptures. We plotted percent RMSE and percent bias against number of recaptures to identify relationships

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**Figure 2.** Water temperature warming patterns (early, constant, and late) used in Sea Lamprey *Petromyzon marinus* spawning run simulations.
Table 1. Model selection results for Cormack–Jolly–Seber models estimating capture probability \( p \) and apparent survival \( \Phi \) for Sea Lamprey Control Program long-term assessment site data set (2012–2018). We modeled parameters as a linear function of water temperature (\( \text{temp} \)), river discharge, or trapping week (time). All models included interactions between trap site \( (n = 7) \) and other environmental and biological covariates. We present results for the 10 most supported models. \( \Delta \text{AIC}_C \) = Akaike information criterion corrected for small sample size.

<table>
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<tr>
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<th>( \Delta \text{AIC}_C )</th>
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<td>138.96</td>
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between abundance with quality and these metrics and to determine if associations were consistent across trap sites. Finally, we calculated mean annual catchability \( (q = n_1/N) \) for each site model to determine if this metric was associated with abundance estimator performance.

Results

Environmental and biological associations with Sea Lamprey capture probability and apparent survival

For the weekly batch-mark data set, the Cormack–Jolly–Seber model most supported by the data included associations between water temperature and apparent survival, sex and apparent survival, and river discharge and capture probability (Table 1). Sea Lamprey apparent survival was strongly negatively associated with water temperature for all sites except for the Manistee River, where a substantial portion of the odds ratio 95% CI for the effects of water temperature on apparent survival included positive values (Figure 3). We observed a strong negative association between water temperature and apparent survival in the Bois Brule River as well; a 1°C increase in water temperature was associated with a 34% (95% CI: 26–42%) decrease in the weekly odds of remaining available to capture. The influence of river discharge was less consistent among trapping sites. Capture probability declined as discharge rate increased at all trapping sites except for the Manistique and Manistee rivers, where we observed the reverse relationship (Figure 3). For the Bois Brule River, models including river discharge were not strongly supported by the data, but capture probability was strongly positively associated with water temperature (Table 2). A 1°C increase in water temperature was associated with an 18% (95% CI: 3–35%) increase in the odds of being captured. Sex was not a strong predictor of Sea Lamprey catchability, but there was evidence that male Sea Lamprey apparent survival was higher than female apparent survival in some streams (Figure 3). Finally, in the Bois Brule River Sea Lamprey size was a strong predictor of catchability. Larger lamprey tended to have higher apparent survival than smaller ones, though a model with length influencing capture probability rather than apparent survival had similar support (Table 2). Using the model most supported by the data for inference, the odds of small Sea Lamprey (\( \leq 45 \text{ cm} \)) remaining available to capture were 39% less (95% CI: 63% decrease–1% increase) than large (\( > 45 \text{ cm} \)) lamprey odds.

Abundance estimator evaluation

None of the abundance estimators explored provided unbiased abundance estimates across all simulation scenarios, but estimates from JS models tended to be robust to environmental variability and site-specific differences in catchability when data quality was high. Models consistently had low bias (< 10%) as the number of recaptured individuals exceeded 100 and fewer recaptures were required to generate abundance esti-
mates with low bias when annual catchability was high ($q > 0.50$). However, JS models performed poorly when few animals were recaptured. Abundance estimates were biased and magnitude and direction of bias was not consistent among data type (weekly batch mark and individual) and site model.

Abundance estimates from the pooled-Petersen estimator were positively biased in all simulations. Estimates were less biased in scenarios where stream temperatures increased rapidly and remained high for the duration of the migration period compared with scenarios with constant or delayed stream warming. Furthermore, bias was not consistent across catchability models developed using empirical apparent survival and capture probability parameters from seven SLCP trapping locations. As number of recaptures increased, bias stabilized at some positive value and did not converge toward 0. Finally, when we captured a large proportion of the population ($q > 0.8$), the pooled-Petersen estimator performed well (bias < 10%).

Table 2. Model selection results for Cormack–Jolly–Seber models estimating capture probability $p$ and apparent survival $\Phi$ for Sea Lamprey Petromyzon marinus released in the Bois Brule River during 2017–2018. We modeled parameters as a linear function of water temperature (temp), water level (WL), or trapping week (time). Sex and length (> 45 cm large, ≤ 45 cm small) were individual categorical covariates. We present results for the 10 most supported models. $\text{AIC}_c = \text{Akaike information criterion}$ corrected for small sample size.

<table>
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Figure 4. Mean (± SD) percent root mean-square error (%RMSE), percent bias (%Bias), and coefficient of variation (CV) for abundance estimated with Jolly–Seber models and uniquely marked animals (JS), weekly batched marked animals (JS wk), and the pooled-Petersen abundance estimator (PP). We simulated Sea Lamprey Petromyzon marinus spawning runs ($n = 250$) for three water temperature warming patterns (early, constant, late) and two scenarios with length-based apparent survival (mod = constant warming with moderate length effect; high = constant warming with large length effect).

Though changes in environmental conditions influenced estimator performance, the addition of length-based apparent survival had minimal effect on abundance estimates. Influence on JS abundance estimates was negligible and percent RMSE for the pooled-Petersen estimates declined slightly as we added length-based heterogeneity to the constant warming scenario and increased the effect size.

Abundance estimates from individually marked animals using the JS model were the least biased in all scenarios (Figure 4). Estimates from weekly batch-mark data had a substantial negative bias in the early warming scenario, but estimates improved in the constant and late warming scenarios. Length-based apparent survival did not substantially influence percent bias for JS models. The pooled-Petersen estimate had a positive bias in all scenarios (> 10%) and this increased as the timing of warming shifted from early to late in the migration period. However, the addition of length-based apparent survival caused bias to decline, though this effect was small. Mean percent bias for pooled-Petersen abundance estimates was 14.2% in the constant
warming scenario and 11.7% in the constant warming scenario with a strong length-based effect on apparent survival.

The pooled-Petersen estimator generated abundance estimates with the lowest CV in all scenarios (Figure 4). All estimators were less precise in the early warming scenario, but the CV of JS estimates from weekly batched marked data was higher than the other estimators (Figure 4). In the other scenarios all abundance estimates were precise (CV < 11). However, the precision of abundance estimates from JS models declined in simulations with length-based apparent survival.

**Geographic variability in abundance estimator performance.** The relative performance of abundance estimators was not consistent among trap sites. Mean percent RMSE for the JS estimator using weekly batch-mark data was lower than the other estimators for the Bad, Tahquamenon, and Manistique rivers, though the spread of percent RMSE for each site was high and mean values were within one standard deviation of each other (Figure 5). Pooled-Petersen abundance estimates had the highest mean percent RMSE for the Manistique, Peshtigo, St. Joseph, and Black rivers simulation models. Percent bias varied by trap site as well; JS abundance estimates using batch-marked data were the least biased for the Bad, Tahquamenon, and Manistique rivers and estimates from the pooled-Petersen estimator and JS model using individually marked animals were similarly biased high for these sites. Jolly–Seber abundance estimates using both data types had low bias (< 10%) for the Manistique, Peshtigo, St. Joseph, and Black rivers. Precision varied considerably by site as well, though pooled-Petersen abundance estimates had the lowest CV for all trapping site models. Differences in CV were driven by differences in annual catchability among sites. Annual catchability was high for the Manistique River (q = 0.84) and Peshtigo River (q = 0.79) trap site models, intermediate for the St. Joseph River (q = 0.36) and Black River (q = 0.37) models, and low for the Bad River (q = 0.14), Manistique River (q = 0.11), and Tahquamenon River (q = 0.10) models.

Though percent bias of abundance estimates from JS models varied considerably by site when we held population size constant among sites, we did not observe this pattern in simulations that held number of recaptured individuals constant among sites and allowed population size to vary. Abundance estimates from JS models had low bias (0% ± 10%) for all models as the number of recaptured individuals approached 100 (Figure 6). However, the percent bias of pooled-Petersen abundance estimates did not become less biased as the number of recaptures was increased (Figure 6). Rather, percent bias remained at a relatively constant level that varied by site. For example, for data sets with 110 recaptures, abundance estimates were nearly unbiased for the Manistique River model and > 20% biased for the Bad River model.

![Figure 5](http://meridian.allenpress.com/jfwm/article-pdf/11/1/68/2511793/i1944-687x-11-1-68.pdf)

**Figure 5.** Mean (± SD) percent root mean-square error (%RMSE), percent bias (%Bias), and coefficient of variation (CV) for abundance estimated with Jolly–Seber models and uniquely marked animals (JS), weekly batched marked animals (JS wk), and the pooled-Petersen abundance estimator (PP). We simulated Sea Lamprey Petromyzon marinus spawning runs (n = 250) using empirical capture probability and apparent survival parameters from seven Sea Lamprey Control Program assessment sites (Bad = Bad River; Tahq = Tahquamenon River; Manistique = Manistique River; Peshtigo = Peshtigo River; St. Joe = St. Joseph River; Black = Black River).

**Discussion**

Of the environmental and biological factors considered, stream temperature was the strongest driver of migratory Sea Lamprey apparent survival. This finding suggests that upon entering a stream, the duration of time Sea Lamprey exhibit migratory behavior is negatively related to water temperature. The likely mechanism causing the duration of upstream migration to become shorter at higher temperatures is the onset of spawning behaviors at elevated water temperature (Manion and Hansen 1980). Alternatively, migratory Sea Lamprey may emigrate from streams at higher rates as stream temperature increases. However, although migratory Sea Lamprey emigration rates can be high in some Lake Superior tributaries (Kelso and Gardner 2000), it is unclear if emigration rates tend to be positively associated with stream water temperature. Before our research the influence of stream temperature on Sea Lamprey abundance estimation bias had not been examined, though the effects of stream temperature
Bias in the pooled-Petersen estimator related to environmental and site-specific differences was caused by a violation of the equal catchability assumption between marked and unmarked individuals. When this assumption is not met, the proportion of marked individuals that are recaptured (i.e., estimated overall capture probability) will not be an unbiased estimator of capture probability for the unmarked population (Seber 1982). Though we used the same daily capture probability and apparent survival rates for both marked and unmarked individuals in our simulations, the mean entry time of the population of marked individuals was always later than the unmarked population mean entry time because unmarked individuals had to be captured before they could be released as a marked individual. Later entry timing reduced the length of time marked individuals were available to capture compared with unmarked individuals because apparent survival rates tended to be lower later in the migration period due to the negative association with water temperature. This

Figure 6. Median percent bias for abundance estimated with Jolly–Seber models and uniquely marked animals (JS), weekly batched marked animals (JS wk), and the pooled-Petersen abundance estimator (PP). We simulated Sea Lamprey *Petromyzon marinus* spawning runs (*n* = 30) using empirical capture probability and apparent survival parameters from seven Sea Lamprey Control Program assessment sites and with number of recaptures equal to 10, 30, 50, 70, 90, and 110.
lower catchability of marked individuals caused the positive bias we observed in the pooled-Petersen estimator. The degree to which overall catchability of marked individuals differed from unmarked individuals varied substantially among simulation scenarios (corresponding to degree of positive bias in the pooled-Petersen estimator) and depended upon capture and apparent survival rates and how these rates varied over the course of the trapping season. For example, the pooled-Petersen estimator had low bias for scenarios with high annual trapping efficiency ($q > 0.8$) because entry timing of marked and unmarked individuals was similar due to high capture rates. This is consistent with the findings of Velez-Espino et al. (2016), who noted that the performance of the pooled-Petersen estimator improved as sampling rate increased.

Neither of the estimators evaluated was ideal for tracking Sea Lamprey abundance. The pooled-Petersen estimator was influenced by variable environmental conditions and not consistent among trapping locations. Our simulations demonstrated that estimating migratory Sea Lamprey abundance using JS models is a good alternative to the pooled-Petersen estimator when data quality are high. However, mark-and-recapture studies conducted at some SLCP annual assessment sites regularly have low data quality ($< 10$ recaptures) because of small numbers of migrating Sea Lamprey, inefficient traps, high loss rates between release sites and capture locations (lamprey emigrating from the system or migrating up a different tributary and spawning), or a combination of these factors. Thus, JS models applied ubiquitously across time-series data from the 29 SLCP assessment sites in the Great Lakes Basin would not generate reliable indices to Sea Lamprey abundance. Using aggregated data for estimating abundance when data are limited for specific strata could be useful for improving the performance of the JS estimator when data quality are low.

The reliability of abundance estimates for individual sampling units with sparse data can be improved by using aggregated data to model catchability while estimating abundance separately among sampling units (Litt and Steidl 2010). With regard to SLCP long-term assessment site data sets, sampling units would be annual estimates for a particular stream and mark-and-recapture data for the time series could be aggregated to model catchability. Specifically, the relationship between catchability parameters and water temperature, discharge data, or both could be constrained across years and trap catch for individual years would then be used to estimate yearly abundance. However, if Sea Lamprey catchability is strongly driven by unmeasured covariates that vary substantially from year to year rather than measured covariates, then abundance estimates using this approach could be substantially biased.

Abundance estimates from batch-marked Sea Lamprey were comparable with estimates from individually marked animals in most simulation scenarios; however, estimates from batch-marked Sea Lamprey were consistently lower and, in some instances, more biased. Particularly, there was a large discrepancy between estimates in the early stream warming scenario. The necessity to censor marked animals that were recaptured during the week of release in the batch-mark analysis likely caused the JS estimator to perform differently on the basis of marking type. Thus, in scenarios in which a large proportion of marked animals is expected to be caught during the week of release, adopting uniquely identifiable tags would likely improve abundance estimates obtained with JS models. In addition to not having to censor Sea Lamprey captured during the week of release, using uniquely identifiable tags allows for environmental covariates to be examined on a daily time step, rather than weekly. This would allow for fine-scale environmental changes such as daily change in water temperature, which is associated with Sea Lamprey trap catch rate (Binder et al. 2010), to be included in analyses of Sea Lamprey catchability. Furthermore, individual heterogeneity in catchability can be modeled when Sea Lamprey are uniquely marked. We determined that the effect of length on apparent survival observed in the Bois Brule River, though substantial, did not have a large effect on abundance estimates assuming a population ratio of 50:50 large : small individuals. However, larger length effects, variability in population structure over time, or a combination of these factors could result in biased Sea Lamprey abundance estimates if length is not modeled appropriately.

Applying uniquely identifiable marks to Sea Lamprey would allow researchers to tap into the wealth of mark-and-recapture models developed to account for heterogeneity in capture probability and improve abundance estimation (Otis et al. 1978; Lebreton et al. 2009), but the quality of the data collected at some of the SLCP long-term assessment sites restricts use of some of these modeling techniques. Future tagging studies in the Great Lakes with sufficient sample sizes to estimate Sea Lamprey abundance using JS models or other maximum-likelihood approaches would be improved by adopting individual marks rather than weekly batch marks, though trade-offs associated with increased handling time on survivability, tag effects on Sea Lamprey behavior (Holbrook et al. 2016), and tag loss should be considered.

Examining trade-offs between using simple estimators with low data quality requirements and more complex estimators would help identify the most effective method of generating Sea Lamprey abundance indices, the primary means of gauging Sea Lamprey suppression efforts. An important aspect of this question is how often gaps in reliable abundance estimates occur because of insufficient data and the method used to fill in these gaps (e.g., pool data, interpolate, etc.). Additionally, potential sampling biases introduced by the single-trap mark-and-recapture study design implemented at SLCP long-term assessment sites (Harper et al. 2018), poor data quality, or both of these factors could reduce the reliability of abundance estimates from mark-and-recapture data collected at these sites and trap catch may be a more reliable index to abundance. Improvements to traps at SLCP long-term assessment sites have been made since the beginning of the monitoring program; if catch data were used to track abundance rather than mark-and-recapture techniques these data would need
to be standardized to account for changes in trapping efficiency over time (Wilberg et al. 2009). Simulation could be used to compare how well basinwide Sea Lamprey population growth and trends in abundance can be tracked using indices generated from different abundance estimators or trap catch and methods for filling in missing values (e.g., Peel et al. 2015). Building on our investigations into the mechanisms driving Sea Lamprey catchability, this work would guide natural resource managers toward the best analytical techniques for tracking Sea Lamprey abundance in the Great Lakes using mark-and-recapture data collected by the SLCP since 1980 and provide a measure of confidence for how accurately SLCP assessment data can track basinwide Sea Lamprey populations in the Great Lakes.

**Supplemental Material**

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**Table S1.** Mean weekly stream temperature and discharge data collected during 2012–2018 from Sea Lamprey Control Program long-term assessment sites that comprised the environmental data we used to investigate associations between Sea Lamprey *Petromyzon marinus* catchability and environmental covariates in the Great Lakes Basin. Trap operators collected stream temperature data during collections and river discharge measurements are data from U.S. Geological Survey gauging stations.

Found at DOI: [https://doi.org/10.3996/022019-JFWM-013.S1](https://doi.org/10.3996/022019-JFWM-013.S1) (25 KB CSV).

**Table S2.** Capture histories for Sea Lamprey *Petromyzon marinus* captured at Sea Lamprey Control Program long-term assessment sites during 2012–2018. We used these data to investigate Sea Lamprey catchability in the Great Lakes Basin using Cormack-Jolly-Seber models. We constructed capture histories on the basis of week of release and recapture, as identified by week-specific fin clips applied to all released Sea Lamprey.

Found at DOI: [https://doi.org/10.3996/022019-JFWM-013.S2](https://doi.org/10.3996/022019-JFWM-013.S2) (80 KB CSV).

**Table S3.** R code for running Cormack-Jolly-Seber (CJS) models using Sea Lamprey *Petromyzon marinus* mark-and-recapture and time-varying river discharge and temperature data from seven rivers located in the Great Lakes Basin. We used this modeling approach to investigate associations between Sea Lamprey catchability and environmental predictors in the Great Lakes Basin.

Found at DOI: [https://doi.org/10.3996/022019-JFWM-013.S3](https://doi.org/10.3996/022019-JFWM-013.S3) (3 KB R).

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**References**


Holbrook CM, Bergstedt R, Adams NS, Hatton TW, McLaughlin RL. 2015. Fine-scale pathways used by adult Sea Lampreys during riverine spawning migra-


