UNCERTAINTY IN ESTIMATING SEA LAMPREY (*Petromyzon marinus*) ABUNDANCE IN GREAT LAKES TRIBUTARIES

By

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ABSTRACT

Great Lakes tributaries are selected for lampricide treatment with a simulation model that uses sampling information on habitat and lamprey density to estimate larval lamprey abundance and forecast metamorphosed lamprey production. I examined the effect of water depth and temperature, larval size and density, and stream conductance on the efficiency of the primary device for sampling sea lamprey larvae, a DC backpack electrofisher. A higher proportion of larvae of all sizes were collected per unit sampling effort when sample sites were shallower, contained fewer larvae, and were in streams of lower specific conductance ($P<0.001$). Additionally, larvae were more likely to be included in a sample as the total length increases. Temperature did not affect the efficiency of sampling larvae in this study. The results have implications for the development of a sampling protocol that uses a single-pass electrofishing technique to estimate the number of sea lamprey larvae in a stream. This estimate is critical to determining the abundance of larvae with the potential to metamorphose as parasitic lamprey the following year, and, consequently, the prioritization of streams for chemical treatment.

I used mark-recapture estimates made at the time of lampricide treatment to test the accuracy of the model forecasts. I also used Monte Carlo methods with the simulation model to examine the effects that propagation of uncertainty in the input parameters had on the outputs of the model. The model had poor predictive utility, as the estimates of lamprey production did not fall within the 95% confidence intervals of the mark-recapture estimates. The estimates were also highly variable, and were sensitive to correlations within the sampling data. The results indicate the model structure, the input data, and model parameters require calibration for the model to be used as a predictive tool.

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I will miss being a part of the 'Jones lab'; the quintessential Fisheries and Wildlife Department lab perched high in our windowless ivory tower on the third floor. Thanks for helping to keep everything in perspective by working and laughing at the appropriate times. And let us never forget the 'flow chart'.

Finally, for my wife Lisa, who made the same journey at the same time, although in a different place:

"Come to the moon,
I hope to see you soon,
Half a million miles isn't far to go
You know I need you so,
I hope you still need me.
Come to the moon."   J. Buffett, M. Utley, and W. Jennings 1984

TABLE OF CONTENTS

List of Tables

List of Figures

Thesis Introduction

The sea lamprey (*Petromyzon marinus*) is a primitive, parasitic fish species, indigenous to the Atlantic coasts of North America and Europe (Beamish 1980). It is a highly adaptable species, as evidenced by its ability to shift from an anadromous to a completely freshwater life history (Emery 1985, Smith 1971). Freshwater populations of sea lampreys were reported in the St. Lawrence River, Lake Champlain, and the Finger Lakes of New York prior to 1920 (Pearce et al. 1980, Scott and Crossman 1973). Sea lampreys may have been present in the Laurentian Great Lakes as early as 1835, when a spawning-phase sea lamprey is described in Duffins Creek, a Lake Ontario tributary (Lark 1971), although this identification is controversial (Smith 1995). If sea lampreys were present in Lake Ontario in the early 1800's, a population of large and abundant piscivores combined with degraded or inaccessible spawning habitat likely limited the effect of the sea lamprey on the freshwater fish community (Eshenroder and Burnham-Curtis 1999, Christie and Kolenosky 1980). Sea lampreys did not enter the upper Great Lakes until the mid-1930's, after the 1929 modification of the Welland Canal allowed sea lampreys to bypass Niagara Falls (Eshenroder and Burnham-Curtis 1999). The first sea lamprey was observed in Lake Erie in 1931 (Pearce et al. 1980); by 1947, spawning runs of sea lampreys were confirmed in all of the upper Great Lakes (Smith and Tibbles 1980).

Although physically smaller, freshwater populations of sea lampreys exhibit the same life history characteristics as their Atlantic counterparts (Scott and Crossman 1973, Applegate 1950). In the spring, semelparous adults migrate into tributaries where they build nests in gravel riffles, then spawn. The eggs incubate within the nest for 18-21 days, and the emergent larvae are passively carried downstream to depositional areas, where they burrow into the substrate. The larval stage lasts for approximately 5 years, during which the lampreys filter-feed on biofilm and other organic matter (Sutton and Bowen 1994) until they attain sufficient length and energy stores to metamorphose to the parasitic juvenile stage and migrate downstream to the lake population (Holmes and Youson 1998). In their parasitic stage, sea lampreys feed on the blood, body fluids, and tissue products of host species (Farmer 1980). In the Great Lakes, hosts include all but the smallest of teleosts, but lampreys preferentially select larger, cold-water species (Farmer and Beamish 1973), which are often commercially valuable. Combined with fishing pressure on these species, the parasitic sea lamprey has been at least partially credited with the demise of commercially and ecologically important fish stocks in the Great Lakes (Eshenroder 1992, Coble et al. 1990, Smith and Tibbles 1980).

In 1955, the Great Lakes Fishery Commission (GLFC) was established to co-ordinate a control program for sea lampreys in the Great Lakes (Smith 1971). Early control efforts focused on limiting the reproductive potential of the spawning phase of the sea lamprey with mechanical and electrical barriers installed below spawning areas in streams (Smith et al. 1974). These methods had limited success (Smith 1971). The development of a selective chemical, 3-triflouromethyl-4-nitrophenol (TFM), to control stream-dwelling larval populations re-directed control efforts towards limiting the recruitment of parasitic-phase lampreys to the lake population (Smith and Tibbles 1980). TFM was first applied to lamprey natal streams on Lake Superior in 1958, followed by Lakes Michigan and Huron in 1960, Lake Ontario in 1971, and Lake Erie in 1986, resulting in significant declines in sea lamprey abundance (Dustin et al. 1990, Smith and Tibbles 1980).

Initially, streams were selected for TFM treatment based upon the established frequency of TFM application (e.g. every four years), and on a qualitative assessment of the size structure and abundance of larval sea lamprey populations that had re-established since the last treatment (Weise and Rugen 1987). Streams were scheduled for treatment when biologists subjectively estimated that a significant portion of the larval population in the stream would metamorphose to the parasitic stage the following year. This method of stream selection emphasized the maximum reduction in the overall abundance of parasitic sea lampreys recruited to the lake population.

Since 1982, the GLFC has implemented a more holistic approach to sea lamprey control, establishing targets for lamprey abundance that balance the ecological, social, and economic impacts of control efforts (Koonce et al. 1993, Great Lakes Fishery Commission 1992). One goal of this approach is to utilize concepts from the integrated pest management of insects to develop alternative control strategies that reduce the dependency on TFM for control of the sea lamprey in the Great Lakes (Great Lakes Fishery Commission 1992, Sawyer 1980). A decision support system was developed to assess the outcomes of various lamprey control options, including optimizing the selection process for streams that will receive the reduced TFM treatment efforts (Koonce et al. 1993, Koonce and Locci-Hernandez 1989). Within this system, information about lamprey populations and stream treatment costs allows a cost-benefit approach to prioritizing streams for treatment, where treatment is recommended for those streams that prevent the largest number of metamorphosed lampreys from being recruited to the lake population for each treatment dollar spent. The use of kill-per-unit-cost criteria in stream rankings provides better control of sea lamprey populations than does the previous method of maximizing kill (Jones et al. 1987).

The kill-per-unit-cost criterion requires quantitative estimates of the potential parasitic lamprey production for each stream considered for TFM treatment. The logistics of treatment scheduling and applying TFM to the selected suite of streams requires that parasitic production estimates be made and the streams prioritized at least six months prior to the prospective treatment date. Consequently, lamprey control personnel are required to forecast the parasitic lamprey production from data gathered the year prior to proposed treatment, one year prior to the anticipated onset of metamorphosis in the larval lamprey population.

Lamprey control biologists with Fisheries and Oceans Canada and the U.S. Fish and Wildlife Service (the control agents) as well as the GLFC have developed a computer-based simulation model, the Empiric Stream Ranking System (ESTR), to estimate larval lamprey populations and predict juvenile lamprey production from annual survey data. The ESTR model combines the information from the annual sampling of larval lamprey densities and nursery habitat abundance in Great Lakes tributaries with biological rate information, such as growth and metamorphosis, estimated from archival data. Using this information, ESTR produces a deterministic estimate of the number of larval lampreys within each stream in the year of sampling, and forecasts the number of parasitic lampreys expected to leave the tributary the year after sampling (Appendix A).

In conjunction with the prediction model, a sampling protocol has been established to provide consistent and statistically valid information about larval lamprey abundance in candidate streams (Slade et al in review, Fodale et al. 2001, unpublished manuscript).

Prior knowledge of stream morphology allows sampling to be divided between deep and shallow water techniques. Sampling in water over 1 metre in depth is accomplished using either a bottom-release toxicant or a specialized deep-water electrofishing device (Slade et al, *in review*). In water less than 1 metre deep, backpack electrofishing gear is used as the sampling tool. In both techniques, the protocol prescribes using standardized effort to estimate larval lamprey density in a number of randomly located, measured plots, as well as quantifying the availability of larval nursery habitat from transects located perpendicular to stream flow at the sample site. The catch from each plot is corrected by a measure of sampling effectiveness, and plot density is calculated as the corrected catch divided by the plot area. The mean density of larval lampreys within the stream is estimated as the total number of lampreys collected divided by the total area sampled. The ESTR model uses mean density along with the estimated area of available larval nursery habitat to estimate larval lamprey abundance in each candidate stream.

Backpack electrofishing accounts for 84% of the plot-specific density estimates collected by the control agents each year. Following the protocol, surveyors determine the larval lamprey densities within the available larval nursery habitat at randomly selected sites along the river. Two plots, between 5 and 15 square metres in area, are measured and marked within suitable larval habitat. A single pass of electrofishing, at the rate of 1.5 minutes per square metre of plot area, is used to collect as many lampreys as possible from the plots. The corrected electrofishing catch is used to estimate the mean larval density within the stream reach, which is multiplied by the estimated amount of available habitat to estimate the larval lamprey population.

Initial studies estimated that backpack electrofisher sampling collects approximately 48% of the lamprey larvae initially present within a sample plot, under all sampling conditions (Steeves et al. in review). The control agents recognize that there will be variability in sampling effectiveness due to plot-specific sampling conditions, such as water depth or larval lamprey density, and that this variability will affect the catchability of larval lampreys. In turn, this will affect the estimates of larval and parasitic lamprey abundance forecast by the ESTR model, as well as the order of streams produced by the ranking procedure. Quantitative knowledge of the causes of this variability would allow more accurate estimates of larval lamprey density to be obtained.

In Chapter 1 of this thesis, I investigate the influence that water depth, conductivity, temperature, lamprey density, and lamprey length have on the proportion of lampreys that are collected using backpack electrofishing gear. I illustrate the effects of environmental variability on lamprey population estimates, and make recommendations regarding the incorporation of the results into the ESTR model.

Once estimates of the larval lamprey population and potential parasitic lamprey production are calculated using the ESTR model, the streams are ranked based on the number of parasitic sea lampreys removed for each treatment dollar spent. As the cost of TFM treatment prohibits treating all streams that will produce parasitic sea lampreys each year, the control agents and the GLFC collectively agree on a subset of streams that are the most cost-effective to treat. The inclusion of a stream on the TFM treatment schedule is a decision process that balances the benefits of treating the suite of streams to reduce the recruitment of parasitic lampreys to the lake population with the cost of not treating the remaining streams that will also produce parasitic lampreys.

The ESTR model produces deterministic estimates by design, and treatment decisions are based on estimates of lamprey abundance without quantitative information regarding their inherent uncertainty. However, treatment decisions include subjective evaluation of the uncertainty in the ESTR forecasts, where informed experience and prior knowledge of the effectiveness of larval lamprey sampling and lamprey distribution affects the degree that the control agents are willing to accept the ESTR abundance estimates. This implicit recognition of uncertainty in the predictive capability of the ESTR model influences the decision to include streams on the treatment list the following year.

Uncertainty in the ESTR model stems from multiple sources. First, the accuracy of the forecasts of larval and metamorphosed lamprey abundance produced by the ESTR model has never been verified. Forecasts of abundance are evaluated against expected measures of abundance given prior experience with the stream-specific lamprey population and examination of the current sampling information. Verification of the ESTR model estimates would increase the confidence that the control agents have in the prioritized stream list. Second, there is uncertainty in the structure of the ESTR model, in terms of the parameters used in the model as well as in the structural assumptions regarding how the parameters are linked within the model. These uncertainties may, in turn, affect the accuracy of the ESTR model forecasts. The quantitative specifications of the ESTR model are based on current understanding of lamprey biology and stream sampling methodologies. Archival data were used to calculate the required sampling intensity for density and habitat measures, as well as for the rate parameters of growth, length of growing season, and probability of metamorphosis (Appendix A). These quantitative components are continually being revised as new information refines or reshapes the understanding of lamprey population dynamics. Quantitative knowledge of the variability in the components could be used to direct research towards those components that would best reduce the overall uncertainty in the ESTR model, and allow more accurate estimates to be obtained.

In Chapter 2 of this thesis, I examine the accuracy of the ESTR model estimates of larval and metamorphosed lamprey abundance. First, I examine the accuracy of the ESTR model forecasts of metamorphosed sea lampreys produced by a stream by comparing model forecasts with independent mark-recapture population estimates of larval and parasitic lampreys made at the time of treatment. Second, I use Monte Carlo methods to assess the possible contribution of errors in the input variables to uncertainty in the ESTR model forecast. The analyses illustrate the influence that each variable in the ESTR model has on uncertainty in the estimates of larval and parasitic lamprey abundance. Influential model inputs and relationships are identified, and recommendations are made to improve those components that will most reduce the uncertainty around the ESTR model estimates.

Sampling sea lamprey (*Petromyzon marinus*) larvae in wadeable Great Lakes tributaries.

INTRODUCTION

Information about the presence and abundance of sea lamprey larvae in Great Lakes tributaries has been used, both qualitatively and quantitatively, to determine a streams potential production of parasitic sea lampreys. Many techniques have been investigated to gather this information, including dredges, chemical application (for example, rotenone and DDT), and remote-operated submersible vehicles equipped with electrofishing electrodes (Weise and Rugen 1987). One of the earliest methods used for detecting larval sea lamprey presence was to use a shovel to remove larval habitat from the streambed and deposit it on shore, collecting the larvae as they emerged from the drying sediment (Weise and Rugen 1987). This method was used in conjunction with visual inventories of stream characteristics, sampling areas of suitable larval nursery habitat in close association with spawning gravel and lamprey nests (Loeb and Hall 1952). Most of these early techniques had detrimental side effects, such as altering the physical and chemical properties of the stream, or negatively impacting non-target organisms.

Electrofishing had been used to collect aquatic biological samples as early as 1863 (Vibert 1967), but was not used for larval lamprey collection until 1947, when a 110 volt alternating current generator was used to sample lampreys in the Ocqueoc River, Michigan (Applegate 1950). In 1969, a direct current backpack electrofisher was developed specifically for sampling larval sea lampreys (Weise and Rugen 1987). The backpack electrofisher had the advantage of greater portability and ease of use than previous methodologies for sampling larval lampreys in Great Lakes tributaries (Smith et al 1974). This method of sampling was limited to water less than 1 m deep, but reduced the unintentional physical, chemical, and biological effects on the stream environment.

Initially, backpack electrofishing was used to determine the relative abundance, size structure, and distribution limits of lamprey larvae in wadeable portions of streams. Streams were selected for treatment with the selective larvicide 3-triflouromethyl-4-nitrophenol (TFM) when subjective assessments of larval sea lamprey population structure, based on modal length examination, indicated that a portion of the larval lampreys sampled were expected to reach 120 mm, a size where metamorphosis was likely (Smith et al 1974, Weise and Rugen 1987). Samples of larvae for modal analysis were taken from areas of the stream that were easily accessible and known to harbour high numbers of larval lampreys (Weise and Rugen 1987). While this subjective approach was convenient, it was not statistically rigorous, and comparable quantification of larval abundance among streams was difficult (Smith et al 1974, Weise and Rugen 1987).

In 1990, the Great Lakes Fishery Commission adopted a policy to reduce dependency on TFM (Great Lakes Fishery Commission 1992). This reduction has been accomplished in part through more stringent controls on the amount of larvicide applied to a stream, and through a more judicious selection of the streams that receive TFM treatment each year. In support of this policy, the focus of larval lamprey sampling has changed from a qualitative approach to a quantitative assessment of lamprey populations, where a systematic and repeatable method of sampling provides estimates of lamprey abundance that are comparable among streams. These estimates are incorporated into a predictive model, the Empiric Stream Ranking System (ESTR), that uses known treatment and manpower costs to rank the streams for potential lampricide treatments, based on an evaluation of the cost-effectiveness of eliminating the lamprey population in each stream (G. Christie, Great Lakes Fishery Commission, Ann Arbor, MI, personal communication).

Up to 100 Great Lakes tributaries require quantitative assessment each year. Backpack electrofishing is the standard sampling methodology for waters less than 1 metre deep, and accounts for approximately 84% of the annual sampling completed by both the U.S. Fish and Wildlife Service (USFWS) and Fisheries and Oceans Canada (DFO) lamprey control agents each year. Given the number of streams to sample and the reliance on backpack electrofishing as the sampling tool, a rapid, systematic, single-pass technique is required to complete the quantitative sampling. Slade et al. (*in review*) describe a systematic technique for sampling larval sea lampreys within a stream. The technique prescribes sampling sea lamprey larvae from measured and staked plots, 5 to 15 m^2 in area, in the wadeable portions of streams, using a direct current (DC) backpack electrofisher. The observed density of larvae collected during a single-pass episode of backpack electrofishing is corrected by a measure of gear efficiency to estimate the density of larvae prior to electrofishing. The corrected densities are combined with estimates of larval habitat, rates of growth, and probability of metamorphosis in the ESTR model, to estimate a stream's capacity to produce parasitic lampreys the following year. TFM treatment is scheduled for those streams that prevent the largest number of metamorphosed sea lampreys from being recruited to the parasitic lake population for each treatment dollar spent.

The ESTR model relies on accurate measures of electrofishing effectiveness to estimate the abundance and size structure of larval lampreys within a stream. Previous estimates of first pass sampling efficiency for larval lampreys have ranged from 13% (Sea Lamprey Control Centre, Sault Ste. Marie, ON, unpublished data) to 70% (Marquette Biological Station, Marquette, MI, unpublished data). Morkert (1987) reported a recapture of 21% of marked larvae, and Daugherty and Dahl (1986) recovered between 50 and 85% (mean 69%) of a known number of larvae in a single pass using backpack electrofishers.

Since the ESTR model population estimates are sensitive to the specification of sampling efficiency, the control agents initiated a study in 1996 and 1997, to obtain a systematic estimate of first-pass electrofisher efficiency in three streams encompassing the range of conductivity found in Great Lakes tributaries (Steeves et al *in review*). In this study, experimental plots were measured and electrofished in three streams following the methodology described in Slade et al (*in review*). Techniques were developed to determine the number of lamprey larvae remaining within the plot after electrofishing was completed. Plot abundance prior to electrofishing was calculated as the sum of the electrofishing catch and the number of lampreys remaining after electrofishing. Sampling efficiency for the experimental plots was estimated as the electrofishing catch divided by the initial plot abundance. The study pooled the data from the three streams, and estimated backpack electrofisher sampling efficiency as 0.48, or 48% of initial plot abundance. This value was incorporated into the ESTR model, and is currently used as the estimate of sampling efficiency for backpack electrofishing gear.

It is unlikely that this estimate of electrofishing efficiency is consistent among all lamprey-producing streams. External variables such as conductivity (Pusey et al. 1998, Hill and Willis 1994), stream width (Kennedy and Strange 1981), fish size (Zalewski 1985), density (Coble 1992), and temperature (Regis et al. 1981) have been reported to affect capture efficiency in teleosts. Further, laboratory studies have determined that the response of larval lampreys to electrical stimuli can vary depending upon water conductance and temperature, substrate composition, and orientation of electrical field (Weisser 1994, Hintz 1993). Sea lamprey larvae are sampled across a wide range of water depths, temperatures, and conductivities throughout the Great Lakes basin, with each combination of conditions contributing to potential variability in the proportion of larvae collected. Inaccurate population estimates could result from applying a fixed value for electrofishing efficiency to samples collected under varying sampling conditions. This could affect the placement of streams on the stream ranking list, allowing parasitic lampreys to escape to the lake population from streams that should have ranked higher on the treatment schedule. Refining the estimate of sampling effectiveness using backpack electrofishing gear would help to calibrate the ESTR model and provide more accurate estimates of larval lamprey abundance and account for among-site differences in sampling conditions that may affect efficiency.

The objectives of this study are:

1) examine the effects of water conductivity and temperature, plot depth and larval density on the effectiveness of sampling sea lamprey larvae using backpack electrofishing gear
2) estimate the effect of length on sampling effectiveness with backpack electrofishers

MATERIALS AND METHODS

Data Collection

Six Great Lakes tributaries, Salem, Proctor's, Lynde, and Watson's creeks, and the Sturgeon and Batchawana rivers (Figure 1) were selected to encompass the range of water conductivity found in streams throughout the Great Lakes. To examine the effects of larval density and lamprey length on collecting efficiency, these streams were selected with the additional criteria that larval densities could exceed 5 larvae·m^{-2} and that multiple year-classes of lamprey larvae were present (Table 1).

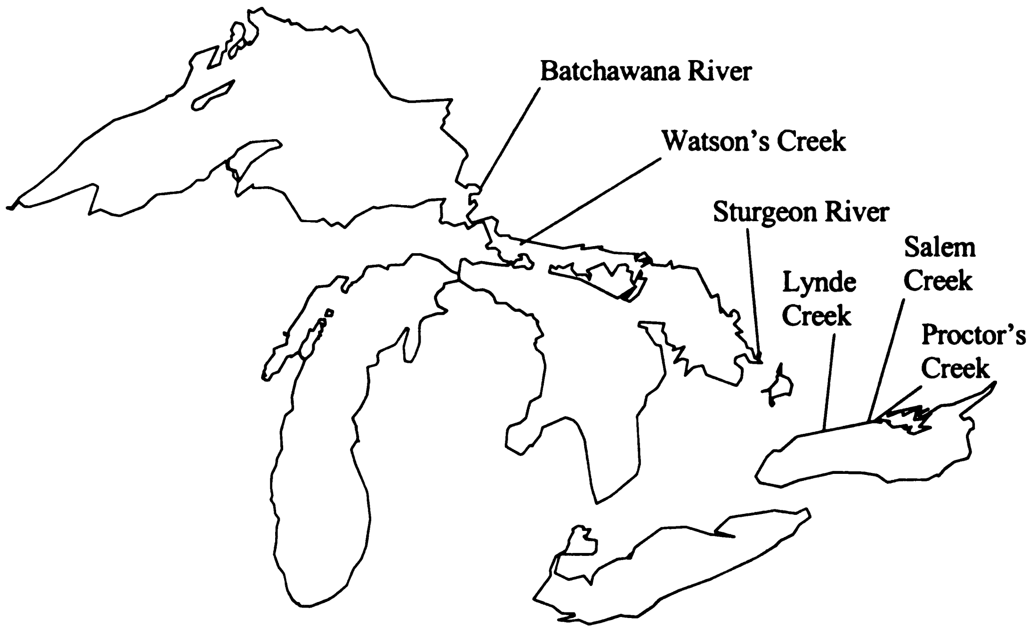


Figure 1. Location of electrofisher effectiveness study streams around the Great Lakes Basin.

I measured plots within preferred (Type 1) larval habitat, defined as a combination of sand, fine organic matter, and detritus or aquatic vegetation, in each stream. Plots were measured to the nearest 0.1 m in each dimension and stakes were inserted at the corners. Sample plots were electrofished following the standardized methods and electrofisher settings used by the sea lamprey control agents for quantitative sampling: a single-pass of electrofishing at the rate of 1.5 minutes·m^{-2}, 125V, 3 pulses-per-second (pps) slow, 30 pps fast, and 25% duty cycle (Slade et al., *in review*). As many lampreys as possible were collected from within the measured sample site during the allotted time. Immediately after electrofishing, the plots were enclosed in 7 thread per cm screening. Electrofished larvae collected from each plot were anesthetized, measured to total length, and marked with a tail clip. All marked larvae were released into the respective plots and watched to ensure that each lamprey burrowed into the substrate within plot boundaries.

Table 1. Characteristics of the streams used in the electrofishing effectiveness study. Data from Fisheries and Oceans Canada and U.S. Fish and Wildlife Service.

Stream	Lake	Drainage (km^2)	Mean Annual Discharge (m^3s^{-1})	Alkalinity (mg/L as $CaCO_3$)	Conductivity (µmhos)	Number of Lamprey Age Classes
Batchawana River	Superior	1190	23.20	21	50	3
Watson's Creek	Huron	6.5	0.65	54	100	2
Sturgeon River	Huron	103	1.29	168	285	2
Lynde Creek	Ontario	106	0.91	213	525	3
Salem Creek	Ontario	52	0.55	183	450	3
Proctor's Creek	Ontario	27	0.78	220	460	3

Immediately after the marked larvae had successfully burrowed, the substrate within the plot was evacuated to a depth of 12 cm using a modified suction dredge (Bergstedt and Genovese 1994). This device pumps water through a tapered orifice, creating a high-velocity jet stream within a flow eduction tube. This produces a strong vacuum within a flexible intake pipe, allowing sites to be excavated without passing the excavated materials through the pump. Substrate, detritus, and larvae are transported through the intake and filtered through a 1mm aperture mesh bag. The substrate from each plot was sorted and larvae removed, identified to species, examined for marks, measured, and preserved in 10% formalin solution.

Data Analysis

The electrofishing and dredge capture data were used to estimate electrofishing efficiency in each of the sample plots. Efficiency is defined as the proportion of the sea lamprey larvae in a plot captured by a single unit of electrofishing effort, as described above. If the dredge technique captured all the larvae in a plot that remained after electrofishing, efficiency could be simply calculated as the ratio of electrofishing catch to electrofishing+dredge catch. Failure to recapture all of the marked larvae that were released back into the plots after electrofishing, however, would suggest that the dredge technique was not 100% effective. Some portion of the marked larvae were not recaptured in the majority of the plots, so an alternative method was required to estimate electrofishing efficiency. I applied the data on recovery of marked larvae in the dredge to a mark-recapture model to estimate the initial abundance of larvae in the plot.

Application of the mark-recapture method to the dredge data was complicated by evidence that dredge catchability is affected by larval size. In general, it appears that smaller larvae are less vulnerable to capture than larger animals. To compensate for this unequal catchability, I divided the larval catches into 5 length bins (0-80mm, 81-100mm, 101-120mm, 121-140mm, and >140mm). Modified Petersen estimates (Seber 1982) were calculated for each increment, as:

$$\hat{N}_i = \frac{(M_i + 1) * (C_{Di} + 1)}{(R_i + 1)} - 1$$

where: $\hat{N}_i$ = abundance of larvae in length bin i

M_i = the number of marked lampreys released, corresponding to electrofishing catch

C_{Di} = the number of lampreys in length bin i examined for marks, corresponding to the dredge catch

R_i = the number of marked larvae in C_{Di}

The proportion of larval lampreys captured in each bin was estimated as:

$$\hat{p}_i = \frac{C_{Ei}}{\hat{N}_i}$$

where: C_{Ei} = electrofishing catch in length bin i

$\hat{N}_i$ = the estimated abundance in bin i for each plot, i = 1-5

I used a multiple logistic regression model (Collett 1991, Hosmer and Lemeshow 1989) to estimate the effect of larval length (X_1), log(density) (X_2), water temperature (X_3), conductivity (X_4),, and depth (X_5) on the proportion of lampreys captured in each length bin as:

$$\hat{p}_i = \frac{1}{(1+\exp(-(\beta_0+\beta_1 X_1+\beta_2 X_2+\beta_3 X_3+\beta_4 X_4+\beta_5 X_5+\text{interaction terms})))}$$

This model can be linearized by a logit transformation as:

$$\text{logit}\left(\hat{p}_i \big/ (1-\hat{p}_i)\right) = \beta_0+\beta_1\cdot X_1+\beta_2\cdot X_2+\beta_3\cdot X_3+\beta_4\cdot X_4+\beta_5\cdot X_5+\text{interaction terms}$$

To estimate the effect of larval length I calculated the mean length of the larvae caught by electrofishing in each length bin for each individual plot, instead of simply using the mid-point length for each bin. To estimate the effect of density, I used the mark-recapture estimate of initial plot abundance divided by the measured plot area. Initial plot abundance was estimated as the sum of the individual length bin estimates in each plot. The distribution of the density calculations in the data was skewed, indicating a log-transformation of the density data in the logistic model could improve the model fit (Kay and Little 1987). A Chi-square test (Neter et al. 1996, Hosmer and Lemeshow 1989) was used to compare the –2*log likelihood (called 'deviance' in logistic regression) of the model fit for density and its $\log_e$-transformation against a constant-only logistic model. The difference in deviance between fitting a constant-only model and a logistic regression on density is 63.61, while that for a regression on $\log_e$(density) is 115.54, both approximating a Chi-square distribution on 254 degrees of freedom. Log_e(density) was deemed a better predictor of capture proportion, and was used as an explanatory variable in the model fitting procedure (Collett 1991).

The assumption of homogeneous variances for the dependent variable, $\hat{p}_i$, is not valid for these data. The variance of $\hat{N}_i$ is inversely related to the number of lampreys recaptured, R_i, in the second sampling period of a mark-recapture estimate (Krebs 1999). The number of lampreys recaptured will vary among length increments within a plot, as well as among plots within and among rivers, resulting in non-homogeneous variance in $\hat{N}_i$ and subsequently $\hat{p}_i$. Because the assumption was violated, I used a weighted logistic regression model (Neter et al. 1996, Collett 1991, Hosmer and Lemeshow 1989) where the weighting factor was the inverse of the variance of the capture proportion for each length increment. This weight was calculated as (Appendix B, Equation B.7):

$$\mathrm{var}(\hat{p}_i) = \frac{\left(M_i^{\,2} \cdot \frac{R_i}{(R+1)^2} \right)}{\hat{N}_i^{\,2}}$$

Model fitting procedures followed those outlined in Collett (1991) and Hosmer and Lemeshow (1989). The variables identified as significant using Wald's Chi-square test were examined for appropriate scale in the logit, and for interaction terms that were both statistically significant and biologically meaningful. Outliers were identified using Pearson residuals, analogous to Studentized residuals in least-squares regression (Hosmer and Lemeshow 1989). The final model of electrofisher effectiveness was selected using a likelihood ratio goodness-of-fit test.

Data analyses were done using the S-Plus (MathSoft 2000) software package.

RESULTS

Between 6 and 19 plots were sampled in each of the study streams, with the length of lampreys captured in electrofishing comparable to the length of lampreys measured in the dredge catch (Table 2a). The plots that were electrofished represent the range of depth, density, and conductivity commonly encountered in wadeable Great Lakes tributaries (Table 2b). The sampling dates in this study precluded electrofishing across the range of temperatures typical of a field season, between April and October each year (Table 2b).

A scatterplot of the logit of capture proportion shows that capture proportion increases as the length of larvae increases (Figure 2). Scatterplots of the logit of capture proportion for each length bin versus the site specific variables show a decrease in capture proportion as larval lamprey density and water conductivity increase (Figure 3). Water temperature and plot depth does not appear to affect the capture proportion of lamprey larvae.

Table 2a. Sample site information in streams selected for electrofisher efficiency study.

Stream	Sample Dates (1998)	Number of Plots	Plot Size (m^2) (min - max)	Conductivity (μmhos) (min - max)	Depth (m) (min - max)	Temperature (°C) (min - max)
Watson's Cr.	29/05 - 05/06	6	5.0 - 5.0	70 - 130	0.15 - 0.6	10 - 17.5
Sturgeon R.	10/06 - 15/06	14	5.0 - 5.0	275 - 300	0.1 - 0.7	12 - 15
Lynde Cr.	17/06 - 23/06	14	4.7 - 5.1	495 - 550	0.1 - 0.4	19 - 21
Batchawana R.	02/07 - 17/07	19	4.5 - 5.1	49 - 56	0.2 - 0.8	18 - 22
Salem Cr.	06/08 - 10/08	17	4.5 - 5	440 - 462	0.1 - 0.5	18 - 20
Proctor's Cr.	11/08 - 14/08	14	5.0 - 5.1	442 - 470	0.15 - 0.4	16 - 20

Table 2b. Catch and estimated abundance in streams selected for electrofisher efficiency study

Stream	Electrofishing Catch			Dredge Catch			Estimated Plot
	Total Catch	Catch by Plot (min - max)	Length (min - max)	Total Catch	Catch by Plot (min - max)	Length (min - max)	Abundance (min - max)
Watson's Cr.	294	2 - 91	21 - 187	255	4 - 126	21 - 108	7 - 207
Sturgeon R.	134	1 - 17	34 - 135	50	1 - 19	28 - 121	2 - 37
Lynde Cr.	78	1 - 11	50 - 143	38	2 - 13	44 - 154	2 - 17
Batchawana R.	920	16 - 91	24 - 182	482	25 - 101	23 - 173	36 - 141
Salem Cr.	408	5 - 56	31 - 162	761	12 - 251	27 - 154	13 - 359
Proctor's Cr.	146	1 - 29	39 - 149	74	2 - 27	42 - 149	4 - 37

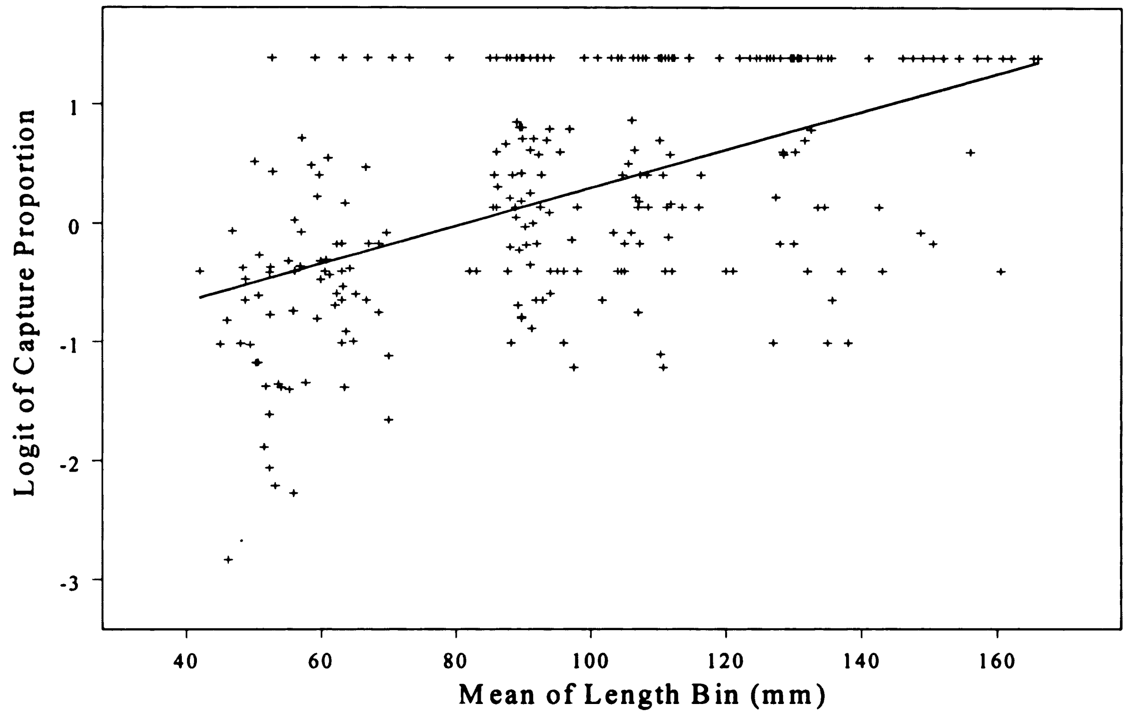


Figure 2. The logit of the capture proportion $\log\left(\hat{p}_i / 1-\hat{p}_i\right)$ versus the mean length of larvae within each length bin.

Individually fitting each explanatory variable to a logistic model of capture proportion indicates that each significantly reduces the model deviance (Table 3). Based on these univariate results, all variables are included in the initial multivariate model. In the multivariate model the effect of temperature, after adjusting for all other terms in the model, was not significant (Table 4). As well, the intercept term does not significantly improve the model fit, and was removed from the model.

After determining the significant main effects, each of six potential interaction terms was individually fit to the model. Three of the interaction terms significantly improved the fit of the model (Table 5). All three terms combined with the main effects model significantly reduce the model deviance.

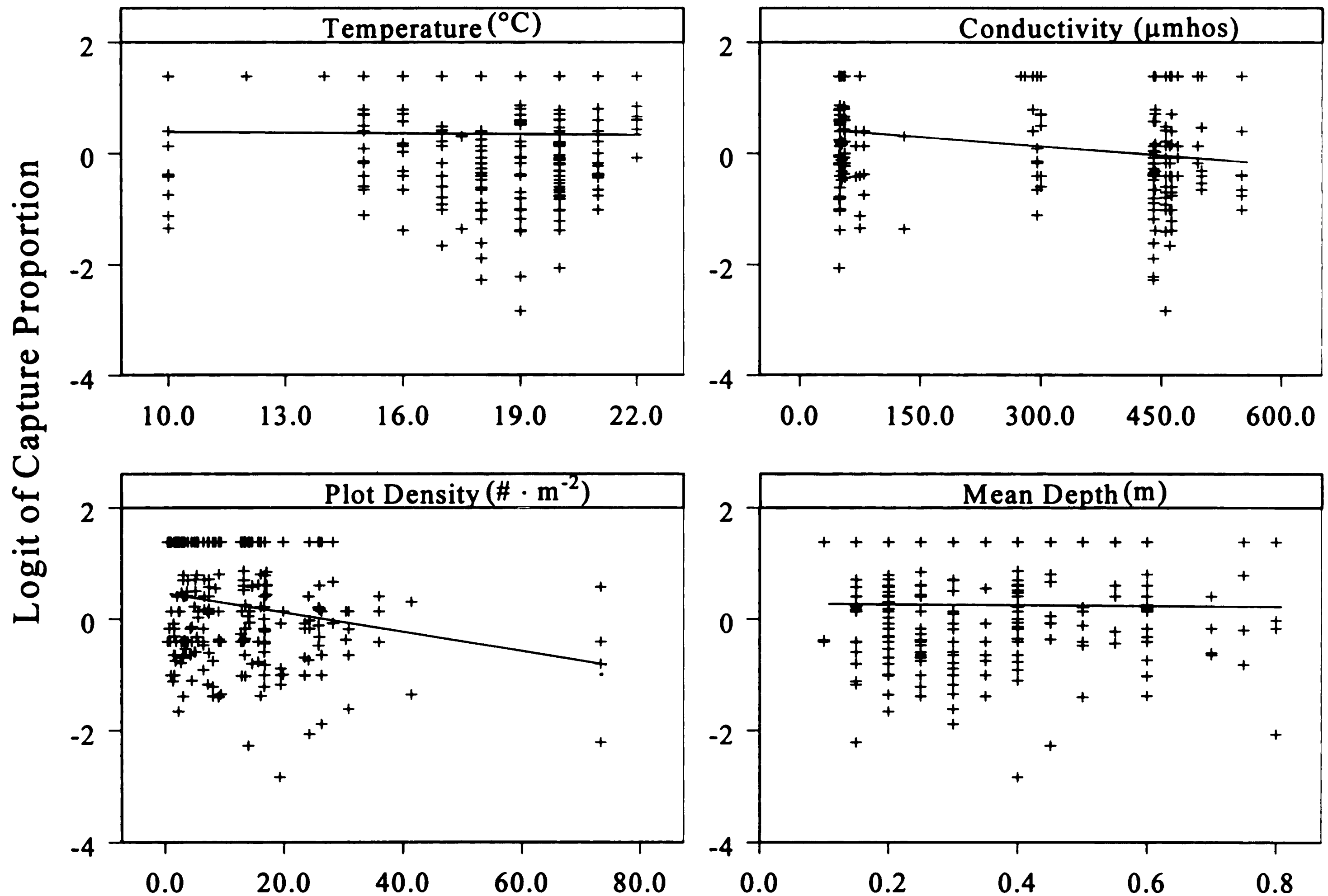


Figure 3. Scatterplots of the logit of capture proportion, $\log\left(\hat{p}_i \big/ 1-\hat{p}_i\right)$, of initial plot abundance versus temperature, conductivity, plot density, and mean depth. The line in each chart is the best linear fit for the data.

Table 3. Logistic regression models of capture proportion versus the individual explanatory variables.

Variable	β	S.E. (β)	Residual Deviance	d.f	Model χ^2	p-value
NULL	---	---	2472.58	259	---	---
Mean Length	0.0264	0.001	1755.14	258	644.38	< 0.0001
log(Density)	-0.463	0.0229	2044.29	258	407.53	< 0.0001
Conductivity	-0.002	0.0001	2035.86	258	433.09	< 0.0001
Temperature	-0.043	0.0074	2441.96	258	34.39	< 0.0001
Mean Depth	-0.503	0.1149	2453.55	258	19.18	0.00001

Table 4. Parameter estimates for multivariate logistic regression of length, density, conductivity, temperature and depth on electrofishing capture efficiency.

Variable	β	S.E. (β)	Wald χ^2	p-value
Intercept	0.3618	0.2105	2.95	0.086
Mean Length	0.0209	0.0011	367.65	< 0.0001
log(Density)	-0.426	0.0261	266.23	< 0.0001
Conductivity	-0.003	0.0001	1011.24	< 0.0001
Temperature	0.0158	0.0181	0.76	0.38
Mean Depth	-1.58	0.1515	108.71	< 0.0001

Residual Deviance: 1023.7 on 254 df

Table 5. Possible interactions to be added to the main effects logistic model.

Variable	β	S.E. (β)	Residual Deviance	d.f	Model χ^2	p-value
Main Effects (excluding temperature and intercept terms)	---	---	1027.5	256	---	---
Mean Length x log(Density)	-0.00338	0.0026	0.28	255	1.69	0.194
Mean Length x Conductivity	-0.00002	0.0000049	14.26	255	16.66	0.00016
Mean Length x Mean Depth	0.001	0.0047	0.046	255	0.045	0.829
log(Density) x Conductivity	-0.0006	0.0001	35.35	255	36.00	< 0.0001
log(Density) x Mean Depth	-0.1889	0.1434	1.73	255	1.74	0.188
Conductivity x Mean Depth	-0.0041	0.00083	24.84	255	24.40	< 0.0001

Pearson residuals were used to identify 3 potential outliers in the data, corresponding to length bins within sites 3, 54, and 57. Since estimates of abundance for length bins within the same plot are not independent, the data for all length bins within each plot were removed when examining the influence of the outliers. The deletion of plots 3 and 57 did not improve the model fit. Deletion of plot 54 reduced the residual deviance of the logistic model from 982.18 to 926.20. Lamprey density in plot 54 was estimated to be 71.8 larvae·m^{-2}, which is quite large compared to the densities typically encountered when sampling for lamprey larvae. This plot was deleted from the data set. The logistic model of electrofisher sampling proportion therefore included the 4 main effects as well as the 3 interaction terms (Table 6). Although the parameter estimate for conductivity was no longer significant, it was retained in the model due to its interaction with other variables.

Table 6. Final parameter estimates for logistic regression model of length, density, conductivity, temperature and depth on electrofishing capture efficiency.

Variable	β	S.E. (β)	Wald χ2	p-value
Mean Length	0.0225	1.77 x 10-3	161.04	< 0.0001
log(Density)	-0.3322	4.16 x 10-2	63.68	< 0.0001
Conductivity	0.00043	4.03 x 10-4	1.12	0.289
Mean Depth	-0.8843	1.79 x 10-1	24.40	< 0.0001
Mean Length x Conductivity	-0.000013	5.29 x 10-6	6.15	0.013
log(Density) x Conductivity	-0.000133	5.54 x 10-5	5.76	0.016
Mean Depth x Conductivity	-0.0068	9.54 x 10-4	50.27	< 0.0001

Residual Deviance: 579.8 on 253 df

DISCUSSION

Sampling conditions have been found to affect the sampling efficiency of electrofishing.gear for a variety of species, depending upon the sampling strategy (Bohlin et al. 1989), type of gear (Bergstedt and Genovese 1994, Weddle and Kessler 1993), and species sought (Fievet et al. 1999, Pusey et al. 1998, Strange et al. 1989). Sampling efficiency using backpack electrofishing gear was significantly affected by several variables in this study. Effectiveness increased ($P<0.001$) as the length of the larvae increased, but declined ($P<0.001$) as larval density, water depth, and conductivity increased. Although temperature is known to affect both conductivity (Weisser 1994, Bohlin et al. 1989) and larval response to electrical stimulus (Hintz 1993), the temperature range in this study (10 - 22°C) did not appear to influence sampling effectiveness.

The results of this study are consistent with previous studies examining the relationship between teleost size and electrofishing efficiency (Fievet et al. 1999, Anderson 1995, Bohlin et al. 1989, Zalewski 1985, Reynolds 1983, Sullivan 1956), yet contrasts with laboratory experiments on larval lampreys (Hintz 1993). In the laboratory experiment, the emergence rate of smaller size classes (65-69 mm) was greater than that of larger size classes (75-89mm) under constant voltage gradients and water conductivity at 15 and 20°C (Hintz 1993). However, the laboratory experiment was conducted in clear aquaria, designed to permit observation of all emergent lampreys. The capture of lamprey larvae under field conditions is quite different, where larvae that emerge from the substrate may not be seen and, of those that are observed, immobilization and successful capture are not guaranteed. As well, due to their size, large larvae are more likely to be seen once they have emerged, increasing the probability that they will be captured in field sampling conditions. Successful capture of lamprey larvae includes inducing lampreys to emerge from their burrows, followed by observation of the free-swimming larvae, immobilization, and capture. The effect of increased size may be more important than the effect of increased emergence rate for successfully capturing emergent larvae under field conditions.

My study also showed that increased density of larval lampreys reduced the observed capture proportion (Figure 4). Electrofishing an area of high larval density results in the simultaneous emergence of multiple larvae. Capture success for an operator faced with increasing larval lamprey density is similar to a Type II functional response in predator-prey interactions (Holling 1959). The rate of capture of the operator increases as lamprey density increases, until physical limitations prohibit the operator from collecting all of the larvae that emerge. In high density plots some larvae will escape initial capture. Of the portion that escape, some will swim either out of the plot or to areas of the plot already sampled, and thus remove themselves from potential capture. The larvae that re-burrow in the unsampled plot area are more susceptible to narcosis from further electrical stimuli (Pusey et al. 1998, Cross and Stott 1975), and may not emerge for a second capture opportunity.

Increasing depth in the sampling plots was found to decrease electrofishing efficiency (Figure 5). Bohlin et al. (1989) summarize the potential for an increase in electrofishing efficiency in shallow water when electrofishing for teleosts, where the effectiveness of the electrical field changes at the water-air and water-substrate boundaries. Typically, the current lines of an electrical field are uniform between electrofishing electrodes, with the voltage gradient smoothly decreasing as distance from the electrode increases. However, the current lines are compressed at the water/air interface, resulting in increased electrofisher efficiency near the water surface. A fish that encounters the electrical field while near the surface of the water is more likely to be immobilized due to this effect. Conversely, stream sediment is usually higher in specific conductance than the surrounding water. This results in the current lines of an electrical field being attracted into the sediment and reducing the capture efficiency for fish that are encountered close to the substrate. When electrofishing for burrowed lamprey larvae, the increased conductance of the substrate may increase the probability of stimulating lamprey larvae to emerge, assuming that the level of stimulus remains below that required to induce galvanonarcosis. When this occurs in shallower water, the larvae are more likely to be observed and immobilized for capture due to the increased visibility and efficiency of the electrical field near the water surface. Together, the effects of increased emergence, increased visibility, and a more effective electrical field increase the sampling effectiveness of backpack electrofishers in shallow water.

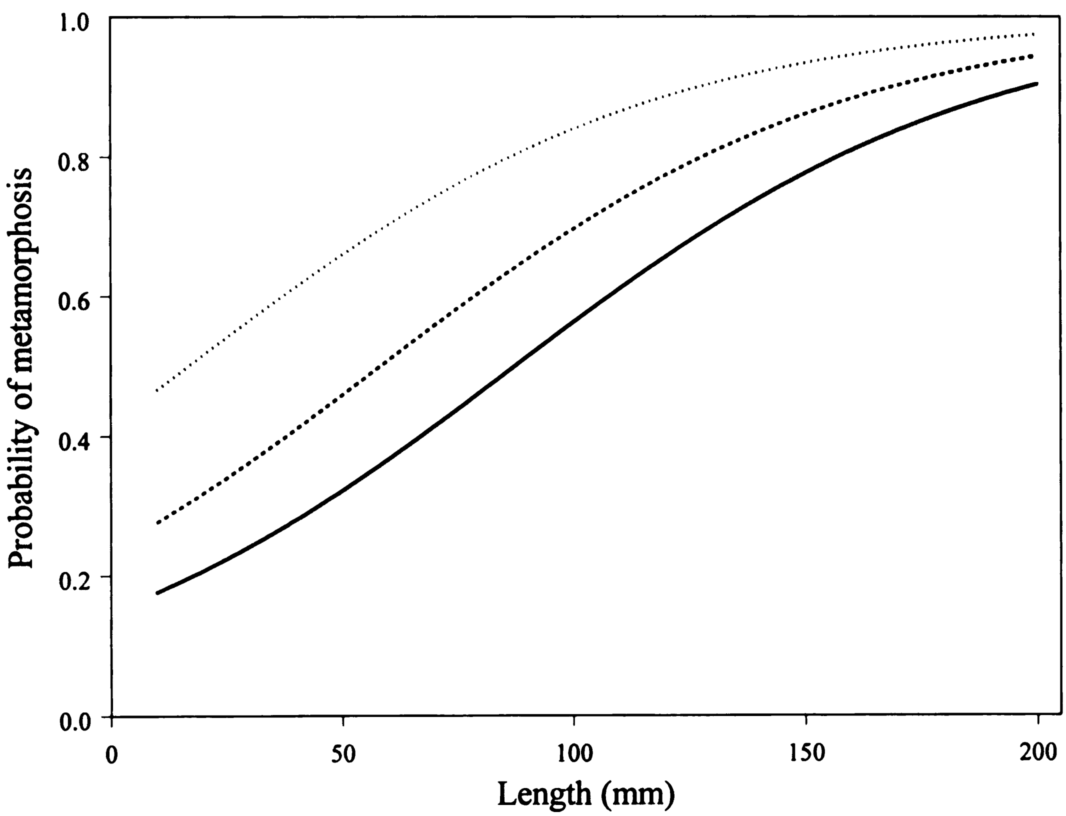


Figure 4. The effects of density on capture proportion, conditioned on length. Capture proportion decreases as density increases from 0.5 larvae·m^{-2} (dotted line) to 5 larvae·m^{-2} (dashed line) and 25 larvae·m^{-2} (solid line). Conductivity and depth are fixed at 200 μmhos and 0.3m, respectively.

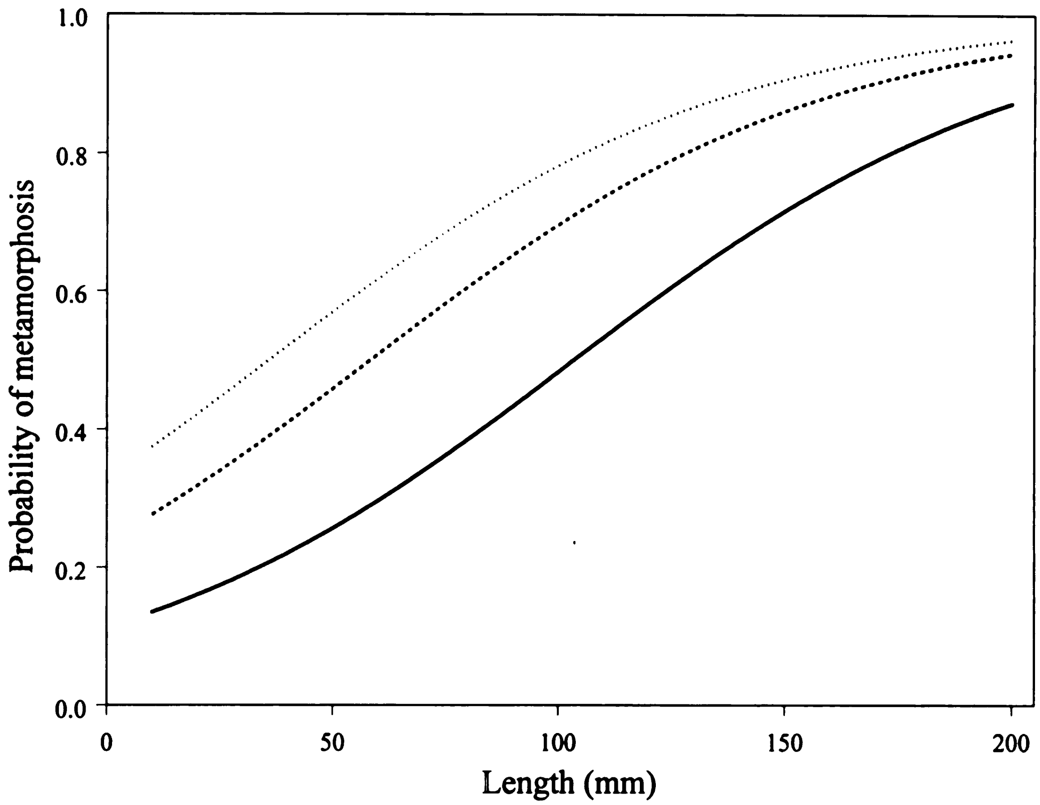


Figure 5. The effects of depth on capture proportion, conditioned on length. Capture proportion decreases as depth increases from 0.1m (dotted line) to 0.3m (dashed line) and 0.8m (solid line). Conductivity and lamprey density are fixed at 200 μmhos and 5 larvae·m^{-2}, respectively.

The effects of conductivity on electrofishing efficiency are represented as interaction terms with the other environmental variables in the study, but, in general, increases in water conductivity result in lower electrofishing efficiency (Figure 6). Increasing conductivity results in a smaller electrical field surrounding the electrodes with a higher current density between the electrodes (Bohlin et al. 1989, Reynolds 1983). Given the sedentary nature of lamprey larvae, the electrical field in high conductivity water may not have the current density required to elicit an emergence response until the electrodes are very close to the burrowed larva. Depending upon the speed the electrodes are being passed over the substrate, the larval burrow may be located between the electrodes before the larva has the opportunity to emerge. Once this occurs, the current density may be so large as to induce galvanonarcosis in the individual, and prohibit a response to the stimulus (Regis et al. 1981).

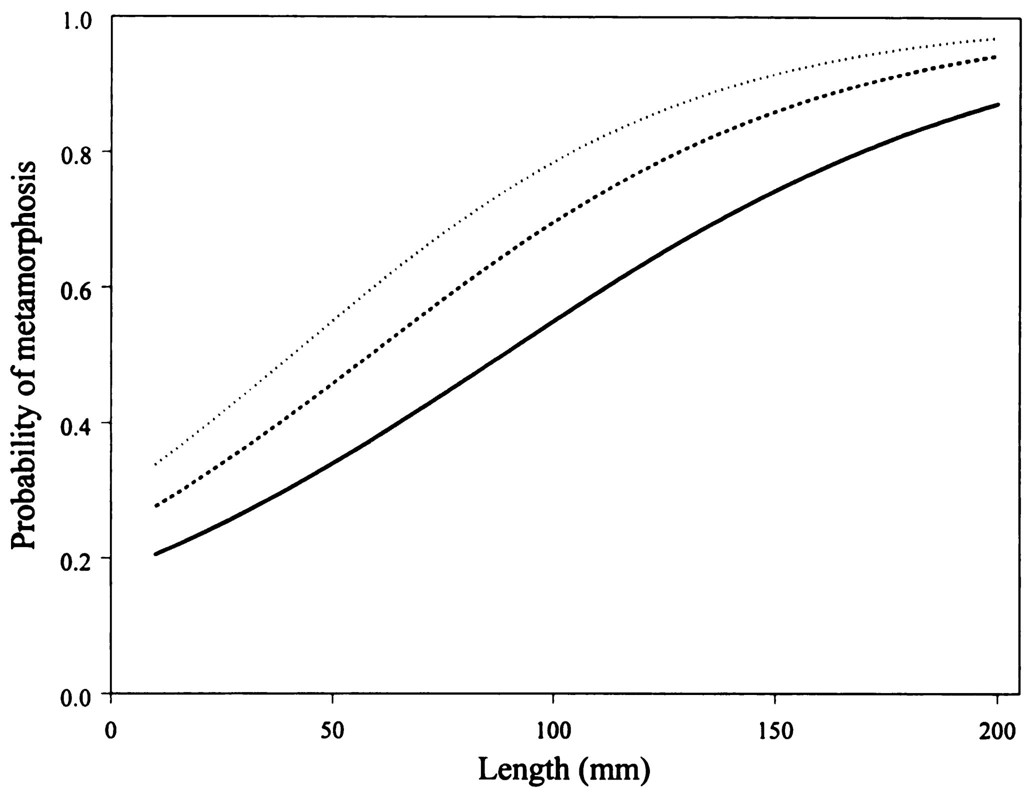


Figure 6. The effects of conductivity on capture proportion, conditioned on length. Capture proportion decreases as conductivity increases from 50 μmhos (dotted line) to 200 μmhos (dashed line) and 400 μmhos (solid line). Lamprey density and water depth are fixed at 5 larvae·m^{-2} and 0.3m, respectively.

Similar to the effects of density and depth, the effect of conductivity on capture efficiency can be offset as the length of the larvae increases. In this case, a much smaller current density is required to produce a physiological response to electrofishing as the length of a fish increases (Bohlin et al. 1989, Zalewski 1985). Therefore, although the generated electrical field is smaller and less effective at higher conductivities, larger lampreys have a higher probability of responding to the stimulus while the electrodes are further away, increasing their likelihood of being captured. The presence of the interaction term in the logistic model indicates that these effects are also not consistent across the range of conductivities and larval lengths examined in this study.

The variables selected for investigation in this study are readily measured using equipment that is easily portable for field use. Although some of the environmental variables significantly reduced the deviance of the logistic model, there are other factors that influence electrofishing effectiveness. Perhaps the most important of these is electrofishing experience (Hardin and Connor 1992). For example, the density at which an operator becomes limited in the ability to capture larval lampreys during the first pass of electrofishing will vary depending upon physical ability and electrofishing experience (Hardin and Connor 1992). While the sampling protocol specification of electrofishing at 1.5 minutes$\cdot m^{-2}$ is intended to minimize the differences in catch due to experience, veteran electrofishing personnel will tend to have a more refined capture technique, enabling them to collect a higher proportion of lampreys on the first pass. Density estimates from samples collected by experienced personnel would be systematically higher than those made by less experienced crewmembers, resulting in biased population estimates. One solution to this problem would be to assess the sampling efficiency of each individual under a variety of sampling conditions, creating an efficiency model for each field person. However, the time required to replicate this study for individual field crewmembers makes this an impractical solution. Perhaps the best solution to reduce the potential bias in population estimates is to ensure that each stream is assessed by multiple crewmembers representing a range of electrofishing experience. Although this would increase the variability in the sampling data, it would also reduce the potential sampling bias of individual crewmembers in selecting sample plots. This would result in more comparable estimates of mean stream density and larval lamprey abundance.

Other variables that influence electrofishing effectiveness include turbidity, vegetative cover, water colour, water surface conditions, glare, fatigue, and even biting insects. With the exception of turbidity, none of these variables are easily quantifiable, but may be incorporated as categorical variables in future studies. Turbidity can be quantified using Secchi disc readings, and the effects of turbidity could be quantified in future studies.

The logistic regression incorporates the effects of the sampling conditions and lamprey density into a prediction of capture success given the size of the lamprey. An hypothetical example can be used to illustrate how the larval and parasitic population estimates are affected by using the logistic model of electrofisher efficiency model to adjust the observed catch when sampling a larval population across the range of survey conditions examined in the study (Figure 7). Assume that two different streams are sampled and the same number and size structure of lampreys are obtained in each collection. Then assume that the two streams represent, respectively, optimal sampling conditions of low water depth, larval density, and stream conductivity (stream A) and the worst sampling conditions, where all sampling attributes have high values (stream B). Since the observed catch is the same for each stream, the fixed efficiency of 48% would estimate the larval population, and the potential number of parasitic individuals, to be the same for each stream. If the cost of treatment is comparable for both streams, it would be equally cost-effective to treat either. Incorporating the effects of environmental variables into the population estimate yields very different population estimates for the two streams. As we are less effective at sampling larvae under the extreme sampling conditions of stream B, the observed catch represents a much lower proportion of the true population. Consequently, the population estimate of larvae and the potential production of parasitic individuals will be larger than that of stream A. If the cost of treating either stream is still the same, it becomes more beneficial to treat stream B, as more potential parasitic lampreys will be removed for each dollar spent.

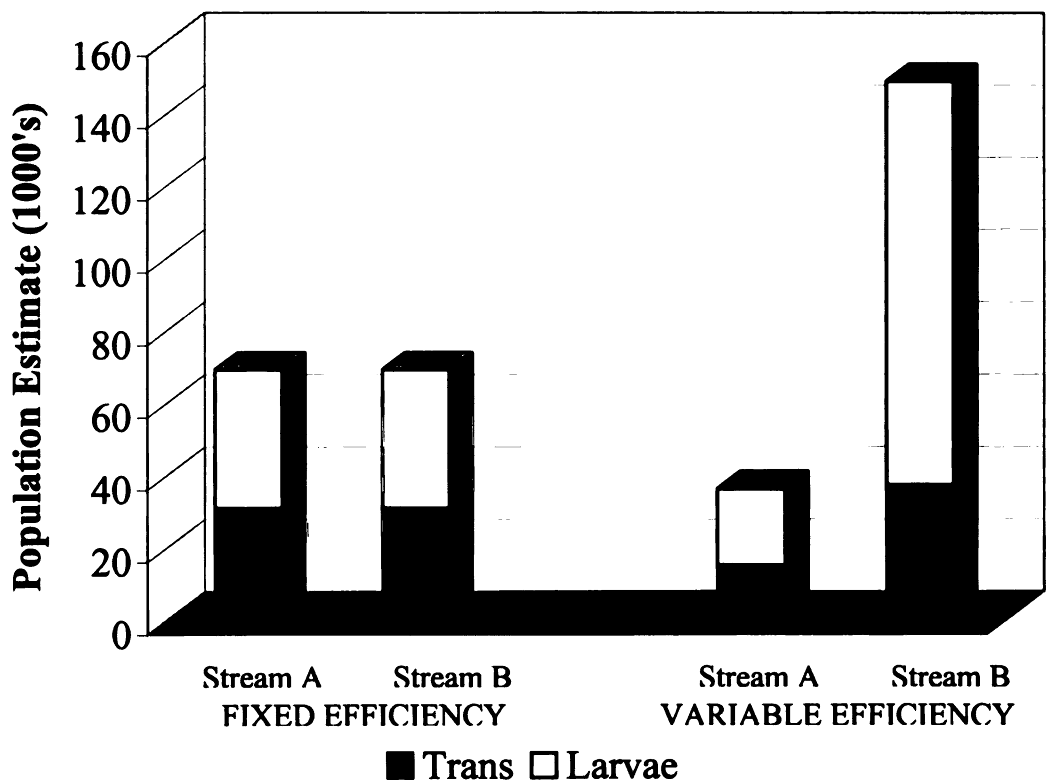


Figure 7. A comparison of the consequences of fixed versus variable efficiency on estimates of sea lamprey populations. Stream A represents optimal sampling conditions: Conductivity=50 μmhos, Density=0.5 larvae m^{-2}, Mean Depth=0.1 m; stream B represents extreme sampling conditions: Conductivity =550 μmhos, Density =20.0 larvae m^{-2}, Mean Depth =0.8 m.

Since accounting for environmental variables can have large effects on population estimates, I recommend that Sea Lamprey Control managers incorporate the current logistic estimate of electrofisher efficiency into the Empiric Stream Ranking model. Incorporation of the model should be done with the understanding that the model reflects the sampling efficiency of one individual, uses fixed electrofisher settings, and that investigation of the other variables mentioned could further refine the understanding of sampling effectiveness using backpack electrofishers.

Estimates of available larval habitat range from 500 to 800,000 square metres in tributaries of the Great Lakes. From a management perspective, an estimated difference of 0.1 larvae m^{-2} can affect both the overall population estimate and estimate of parasitic production derived by the Empiric Stream Ranking model, particularly in large streams. Since streams are prioritized for treatment based on the cost of eliminating the potential parasitic population, a change in estimated density of 0.1 larvae m^{-2} could make the difference between TFM treatment the following year or deferral to a later date, allowing parasitic lampreys to escape to the lake population. Refining our understanding of how environmental variables influence the effectiveness of sampling lamprey larvae using backpack electrofishing gear will enable the control agents to more accurately estimate the larval lamprey population of a stream. This will result in more accurate estimates of parasitic lamprey production, and a more cost-efficient application of treatment efforts to control sea lampreys in the Great Lakes.

Uncertainty in the estimation of sea lamprey (*Petromyzon marinus*) populations in Great Lakes tributaries.

INTRODUCTION

"All models are wrong. Some models are useful." George Box

Sea lampreys in the Great Lakes are currently controlled using an integrated approach, combining biological, physical, and chemical techniques (Great Lakes Fishery Commission 1992). While biological (e.g. sterile male release) and physical (e.g. low-head barriers, mechanical traps) methods have the potential to reduce the reproductive success of sea lampreys, chemical control, with the selective lampricide 3-trifluoromethyl-4-nitrophenol (TFM), remains the primary tool used to reduce sea lamprey populations (Great Lakes Fishery Commission 1992, Smith and Tibbles 1980). The controlled application of TFM to Great Lakes tributaries kills larval lampreys in their natal streams (Smith and Tibbles 1980), before they have the opportunity to metamorphose to the parasitic stage (Potter 1980).

Presently, the cost of TFM prohibits treating all streams that will produce parasitic sea lampreys each year. This has led the U.S. Fish and Wildlife Service, Fisheries and Oceans Canada (the control agents) and the Great Lakes Fishery Commission (GLFC) to evaluate and prioritize which Great Lakes tributaries should receive treatment. Using information about the cost of stream treatment as well as sampling information on lamprey populations in each candidate stream, the control agents apply a cost-benefit approach to selecting streams for treatment. Streams where the control agents anticipate the largest number of parasitic sea lampreys will be killed for each treatment dollar spent receive the highest prioritization for treatment.

A computer-based simulation model, the Empiric Stream Ranking (ESTR) system (Appendix A), is used to assist with the stream ranking process. The model uses sampling data collected by assessment crews from approximately 100 streams each year. In wadeable streams, the control agents begin by randomly selecting 6-10 points in each stream where the river may be easily accessed, from a pool of all access points available for the stream. At each access point the crews measure 12 transects perpendicular to stream flow and subjectively categorize the stream substrate along each transect as preferred (Type 1), secondary (Type 2), or not usable (Type 3) by larval sea lampreys. Two sample plots between 5 and $15m^2$ are measured within the areas of preferred habitat, and backpack electrofishers are used to determine the density of larval lampreys within the Type 1 habitat. This typically results in 72 habitat transects, 12 electrofished plots, and 100 or more lamprey larvae captured per stream, but can vary depending upon stream- and site-specific conditions. These data are used as inputs to the ESTR model to estimate the areas of available larval habitat and mean lamprey density. These estimates are then used to provide a single estimate of larval sea lamprey abundance per stream (Appendix A).

The ESTR model also uses the length data from the larval sampling to forecast the number of lampreys in the sample expected to metamorphose the following year (Appendix A). Larval length in the fall of the year is used as an indicator of the potential of the larva to metamorphose the following year (Potter 1980, Holmes and Youson 1994). Lamprey larvae are collected throughout the field season in the year prior to expected metamorphosis, requiring the control agents to estimate the amount the larvae will increase in length by the fall of the current season. This additional growth is estimated as the product of an average daily growth rate and the number of days between collection and the end of the growing season. The additional growth is added to the measured length of each larva to estimate fall length. The ESTR model uses this estimated fall length as an input to a geographically defined, length-dependent logistic model that estimates the probability of metamorphosis for each larva in the sample. The ESTR model then calculates the proportion of the sample expected to metamorphose. This same proportion is applied to the estimate of larval lamprey abundance to forecast the number of larval lampreys expected to migrate to the lake population the year after sampling.

Due to uncertainties in the input data as well as the driving variables of sampling efficiency, lamprey density in Type 2 habitat, growth, and probability of metamorphosis, the forecasts of larval and metamorphosed lampreys are also uncertain quantities. Although not quantified, perceived uncertainties in the ESTR predictions currently play a qualitative role in determining the final stream treatment list. Based on experience and informed knowledge, biologists from the U.S. Fish and Wildlife Service and Fisheries and Oceans Canada (the control agents) as well as the Great Lakes Fishery Commission subjectively assess the ESTR forecasts of parasitic lamprey production. Review of the stream-specific sampling information that is the basis for the ESTR prediction is compared with information regarding the streams' historical productivity, and the stream is scheduled for treatment when the informed opinions of the biologists agree with the ESTR prediction. Quantification of the uncertainty in the ESTR model predictions would allow the control agents to assess the magnitude and potential consequences of their stream treatment decisions.

In this chapter I examine the sources of uncertainty associated with the ESTR model forecasts. The first is the accuracy of the ESTR model predictions. Although the ESTR model has been used to prioritize streams for TFM treatment since 1995, the accuracy of model forecasts has never been verified by direct comparison with observations at the time of TFM treatment. Consequently, the control agents tend to use subjective judgement about the accuracy of the estimates to help establish the stream treatment list. To determine the accuracy of the ESTR model forecasts, I compared the model estimates with mark-recapture estimates of larval and metamorphosed lamprey abundance made during TFM treatment. Verifying the accuracy of the ESTR forecasts will enhance confidence in the ESTR model as a decision tool for the stream ranking procedure. The collection of data to compare predicted and observed parasitic lamprey production in the verification process will also enable the control agents to assess any systematic biases in the ESTR model.

A second source of uncertainty stems from uncertainty in the model inputs and their propagation to the ESTR model outputs. The ESTR model components, by design, are deterministic and do not reflect the underlying variability in their values. Values for the parameters and constants within the ESTR model were initially derived from analyses of historical data compiled by the control agents, and from analogous studies that paralleled the purpose of the ESTR model (e.g. Simonson et al 1994). I re-parameterized the ESTR model using the data sources initially used to develop the model as well as incorporating more recent data that provided a measure of the variability in the input data. To examine the propagation of input uncertainty, I combined the re-specified model with a Monte Carlo simulation procedure to quantify the uncertainty in the model outputs, as well as to determine which of the input variables contributed most to the uncertainty in model output (Kleinjen 1996, McKay 1995). The effects of the input variables are examined for nine representative streams to determine relative importance within the simulation model.

The objectives of this chapter are to:

1) provide an independent estimate of larval and metamorphosed lampreys at the time of TFM treatment to compare with ESTR model predictions
2) quantify the uncertainty in the ESTR model predictions of metamorphosed lampreys
3) determine the model variables that contribute most to prediction uncertainty

MATERIALS AND METHODS

Study streams

Nine streams were selected for both Petersen mark-recapture estimates of metamorphosed lamprey production, and to provide input data for simulation modeling (Table 7, Figure 8). These streams were selected from the list of streams scheduled for TFM treatment after mid-July in either 1998 or 1999. This timing was necessary to ensure that external signs of metamorphosis were readily visible on the lampreys and that sufficient time was available to capture, mark, release and recapture lampreys from each stream.

Mark-recapture population estimates

I used the survey data collected the year prior to treatment, initially used as inputs to the ESTR model, to estimate a target of larvae to mark and recapture in each stream. The desired precision for the mark-recapture population estimate was ±10%, and I estimated the target sample sizes from Figure 6 in Robson and Regier (1964).

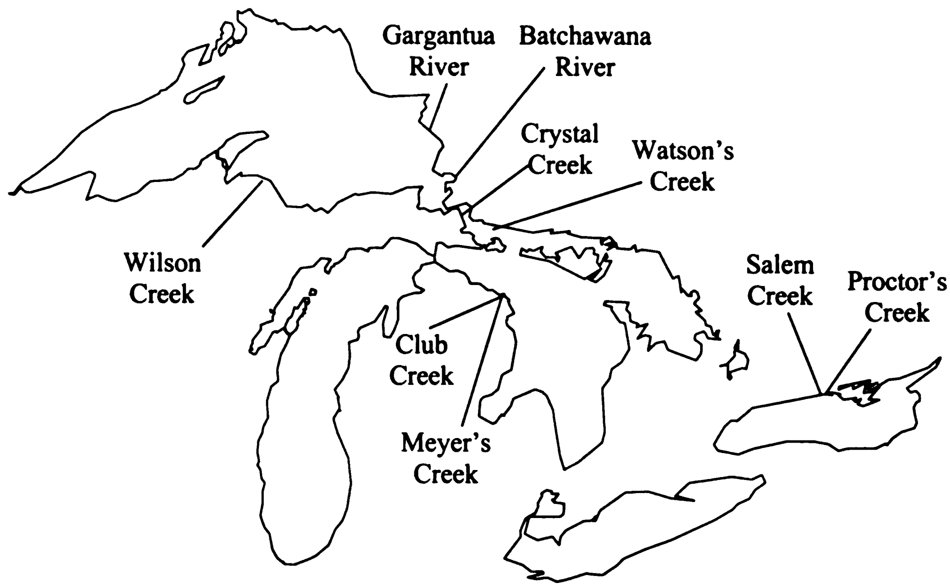


Figure 8. Location of the study streams for the verification and validation of the ESTR model.

Table 7. Characteristics of the study streams used in the simulation model.

Stream	Lake	Drainage (km^2)	Mean Annual Discharge (m^3s^{-1})	Alkalinity (mg/L $CaCO_3$)	Conductivity (μmhos)
Batchawana River	Superior	1190	23.2	21	50
Club Creek	Huron	2.3	0.7*	178	360
Crystal Creek	Huron	89	0.30*	16	54
Gargantua River	Superior	97	0.25*	20	20
Meyer's Creek	Huron	0.5	0.12*	140	250
Proctor's Creek	Ontario	27	0.78	220	460
Salem Creek	Ontario	52	0.55	183	450
Watson's Creek	Huron	6.5	0.65	54	100
Wilson Creek	Superior	3.8	0.10	62	140

*Mean discharge during TFM treatments

In the year of treatment I collected lamprey larvae from each stream using backpack electrofishing gear, marked them by removing a portion of non-vascular tissue at the end of the caudal fin, and released them in the approximate area of capture. All collections for marking were made at least two weeks prior to TFM treatment. Lampreys were recaptured either during TFM treatment or within 24 hours after treatment, using stationary fyke nets or actively collecting with hand dip nets. The recaptured larvae were identified to genus, examined for marks and for external signs of metamorphosis.

Population size (N) was estimated for each stream using the bias-corrected Petersen estimator (Seber 1982):

$$\hat{N} = \frac{(M+1)\cdot(C+1)}{(R+1)} - 1$$

where: M = number of individuals marked

C = total number of individuals in treatment collection

R = number of marked individuals in the treatment collection

with variance:

$$V(\hat{N}) = \frac{(M+1)^2\cdot(C+1)\cdot(C-R)}{(R+1)^2\cdot(R+2)}$$

Four of the eight streams selected for the mark-recapture study contained populations of indigenous lamprey species. Larvae of these species can be difficult to differentiate from sea lamprey larvae while electrofishing or collecting during treatment, but can be easily identified using morphometric characteristics after the collecting effort is completed. I marked all lampreys collected by electrofishing and retained all lampreys encountered during treatment. The proportion of the overall population estimate that were sea lampreys was assumed to be the same as the proportion in the treatment collection:

$$\hat{N}_{SL} = \hat{N}\cdot\frac{C_{SL}}{C}$$

where: $\hat{N}_{SL}$ = the estimated number of sea lampreys;

$\hat{N}$ = the Petersen population estimate of all lampreys;

C_{SL}= number of lampreys in the treatment collection that are sea lampreys; and

C = total number of individuals in the treatment collection

Similarly, the number of metamorphosed sea lampreys in each population was estimated as:

$$\hat{N}_T = \hat{N} \cdot \frac{C_T}{C}$$

where: $\hat{N}_T$ = the estimated number of metamorphosed sea lampreys;

$\hat{N}$ = the Petersen population estimate;

C_T= the number of lampreys in the treatment collection that are;

metamorphosed sea lampreys; and

C = the total number of individuals in the treatment collection

The variance of the estimators of population proportions was calculated as:

$$V(\hat{N}_x) = \left(\hat{N}\right)^2 \cdot V(\frac{C_x}{C}) + V(\hat{N}) \cdot \left(\frac{C_x}{C}\right)^2$$

where: $V\left(\hat{N}_x\right)$ = the variance of the proportion interest, either T or SL as appropriate

$\hat{N}$ = the Petersen population estimate;

$V(\hat{N})$ = the variance of the Petersen population estimate;

$V(\frac{C_x}{C}) = \frac{\frac{C_x}{C} \cdot (1 - \frac{C_x}{C})}{C}$, the variance of the proportion of interest, with

C_x = the number of larvae in the treatment collection equal to T or SL as appropriate

C = the total number of individuals in the treatment collection

Confidence intervals for the estimates were calculated using the normal approximation:

$$\left(\hat{N}_x\right) \pm 1.96 \cdot V\left(\hat{N}_x\right)$$

I assumed that the mark-recapture estimate provided an unbiased estimate of lamprey abundance at the time of TFM treatment. I plotted the estimates of larval and metamorphosed lamprey abundance from the ESTR model versus the mark-recapture estimates to compare the relative accuracy of the ESTR forecasts. I considered the ESTR model estimates of abundance accurate if the plotted points fell along a replacement line having a slope of 1.

Monte Carlo Simulation Model Parameterization

A Monte Carlo simulation procedure was developed in the S-Plus programming language (MathSoft Inc. 2000) to examine the influence of uncertainty in the ESTR model parameters and on the model's prediction of parasitic-phase sea lamprey production. In most cases parametric distributions were not easily fit to the input data, so the simulation model sampled directly from the input data using resampling procedures (Davison and Hinkley 1997). Values for each of the input variables were selected, with replacement, from the data during each iteration of the simulation model. The simulation model calculated larval and metamorphosed lamprey abundance from the selected values after each iteration.

The parameters for electrofishing efficiency, lamprey density in Type 2 habitat, growth, and probability of metamorphosis are deterministically specified in the ESTR model (Appendix A). To examine the effects of uncertainty in these parameters on the overall uncertainty in the model outputs, a measure of variability was assigned to each, as outlined in the appropriate sections below. The measure of variance was based on historical data or, in the case of electrofisher efficiency, on the model developed in Chapter 1.

Habitat and Catch Resampling

The data to describe habitat, electrofishing catch, and lamprey length for each of the 9 study streams were obtained from the control agents. To preserve the potential spatial correlation that may be present among these variables in a stream, the hierarchy of access points, habitat transects, plots sampled and observed catch were resampled using a nested bootstrap approach (Figure 9).

Each stream has sampling data from S access points. For each iteration of the simulation model, the access point data was randomly sampled S times, with replacement. Each access point has data for T habitat transects and P electrofishing plots. For each randomly selected access point, T transects and P plots were selected with replacement from the habitat and plot data specific to the access point. Each electrofishing plot has length information for L total lampreys captured within the plot. For each plot P selected from site S, L lengths were randomly selected with replacement from the plot-specific length information. The resampled transect and electrofishing data were used to estimate available habitat and larval lamprey density as outlined in Appendix A.

Electrofisher Effectiveness

The logistic model of electrofisher effectiveness (Chapter 1) was incorporated into the simulation model. The logistic equation models probability of capture of lamprey larvae as a function of stream conductivity, sampling depth, larval size, and initial density of larvae within the plot. However, initial larval density is unknown in the data collected using the quantitative sampling protocol. An iterative procedure was developed that estimated initial plot density and incrementally adjusted this density within the logistic

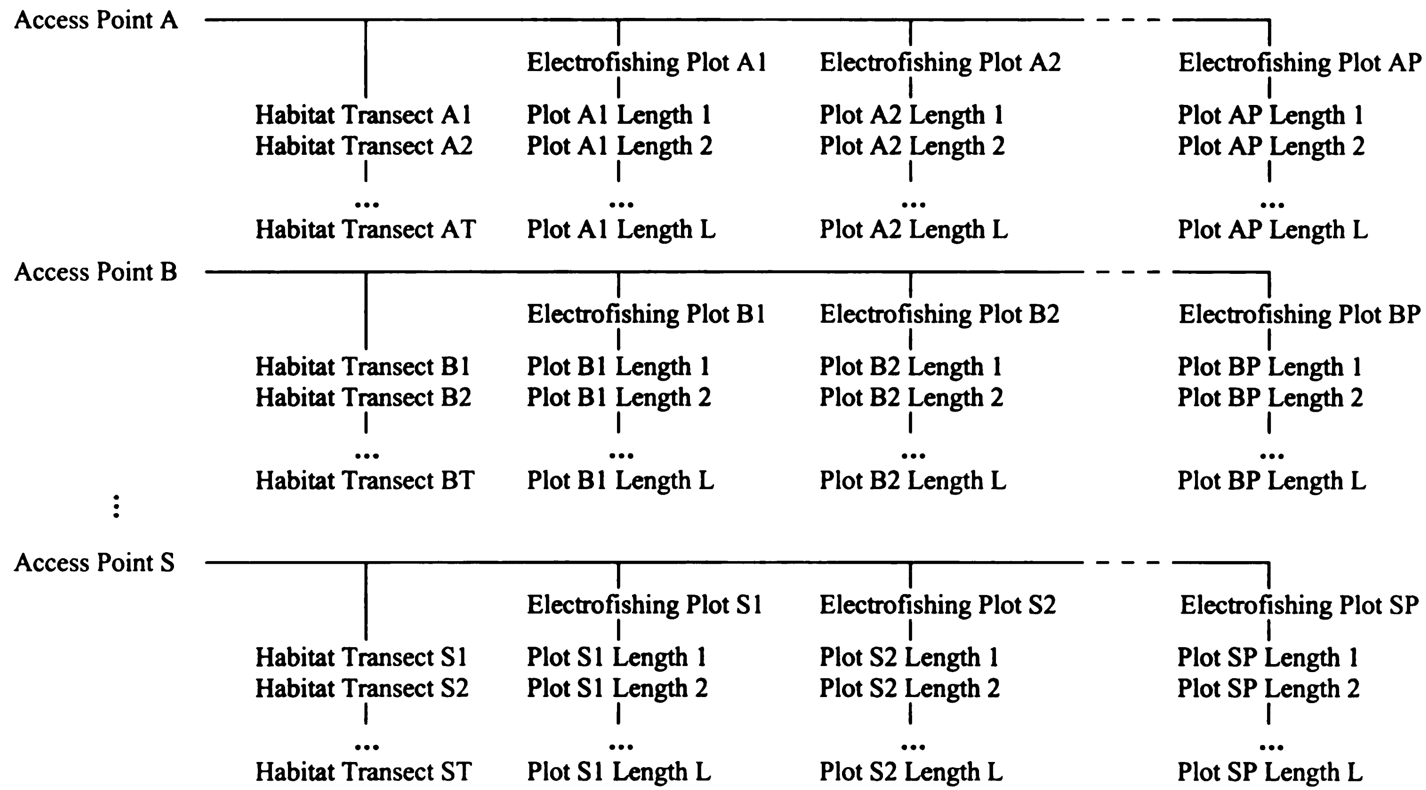


Figure 9. Hierarchy of stream site, electrofishing plot, and capture data used in the simulation model. During each model iteration the access points were randomly sampled S times, with replacement. For each access point selected, the associated habitat transects were randomly sampled T times with replacement, and the electrofishing plots were randomly sampled P times, with replacement. For each electrofishing plot sampled, the plot-specific length data were randomly sampled L times, with replacement.

model until the predicted catch, given the site specific variables and length of observed lampreys, was equal to the observed catch. The iteration procedure is stopped when the difference between the predicted and observed catch, given estimated density, is less than 1×10^{-5}.

Variability in electrofisher sampling effectiveness for each length bin is estimated as:

$$\mathrm{var}(EF) = X'_h s^2\{\beta\} X_h \qquad \text{(Neter et al. 1996, p 603)}$$

where: $s^2\{\beta\}$= the approximate variance-covariance matrix for the logistic effectiveness model

X'_h= the vector of values of length, log(density), conductivity, mean depth, and three interaction terms for each length bin, *h*, in the sample plot

After iteratively estimating the initial plot density, the simulation model generates a random normal probability of capture for each length bin, of mean $X_h\beta$(where $\beta$is the vector of logistic model parameter estimates) and variance *var(EF)*. The inverse of these probabilities of capture are summed to estimate the plot densities incorporating variable sampling efficiency, and these densities are used in the ESTR simulation model to estimate mean density throughout the river.

Proportion of Type 1 Larval Density Attributable to Type 2 Habitat

Backpack electrofisher sampling is conducted in an average of 90 streams annually. To ensure that all streams are sampled, larval lampreys are sampled exclusively from Type 1 habitat. The sampling protocol specifies that lamprey larvae be sampled from Type 2 habitat only when there is not enough preferred Type 1 habitat available for electrofishing. The occurrence of insufficient Type 1 habitat for sampling is rare in Great Lakes tributaries; consequently, the streams selected for the simulation do not have sampling information for lamprey densities in Type 2 habitat. The control agents currently assign the density of larval lampreys in Type 2 habitat as 0.275 of the larval lamprey density in Type 1 habitat.

Data are available from a research study in which both Type 1 and Type 2 habitats were sampled to assess larval lamprey abundance (M. Jones, Michigan State University, unpublished data). There were 26 streams sampled in the study, with some streams sampled in multiple years, providing 46 stream-year combinations with comparative Type 1 and Type 2 larval densities.

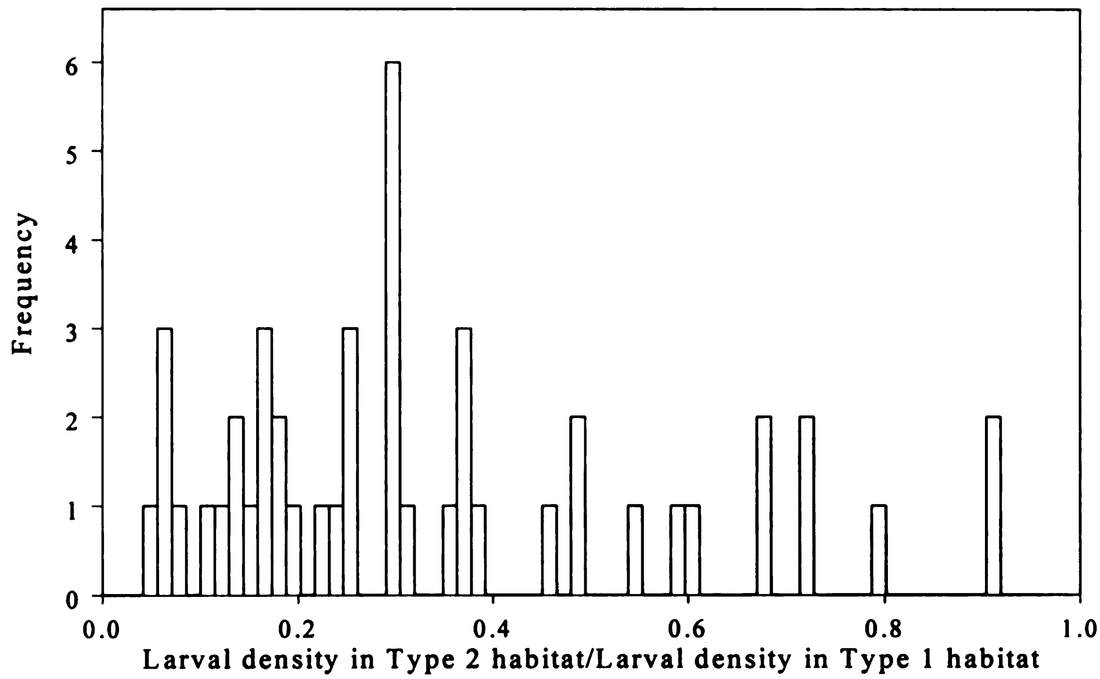


Figure 10. Distribution of the T2/T1 ratios in the multi-year lamprey study.

The distribution of the density ratio data is not easily described parametrically (Figure 10). I assumed that the comparative density data represented a random sample from the population of density ratios that occur throughout Great Lakes tributaries. In each iteration of the model, an observation from the data set was randomly sampled and this estimate of the Type 1 density to be attributed to Type 2 habitat was used as R in equation A.5.

Growth Rate

The control agents use the length of larval lampreys at the end of the season of collection as an indicator of metamorphic potential (Appendix A). However, larvae are collected from April through October each year, requiring the control agents to estimate the length the collections of larvae will be at the end of the growing season. The procedure for estimating end-of-season larval length uses a stream-specific daily growth rate, calculated for each sea lamprey producing tributary in the Great Lakes. Among- and within-stream variability in the average daily growth rate is expected, however the current growth rates have been estimated once per stream and do not provide a measure of this uncertainty.

As growth varies with temperature (Potter 1980), I assumed that the growth rates would be similar for streams in the same geographic location. The average daily growth rates for all streams within a region were pooled. The resulting distributions were approximately normal in distribution, and an overall mean and variance in growth rate were calculated for the region. For each iteration of the model, average daily growth rate is determined by randomly sampling from a normal distribution with region-specific mean and variance.

Probability of Metamorphosis

Data from samples of larval and metamorphosed sea lampreys collected during 106 separate TFM treatments were used to develop length-dependent logistic models of the probability of metamorphosis for 11 geographic regions around the Great Lakes. The collections for streams within each region were pooled, and an individual logistic model fit to the data. The models use the estimated length at the end of the growing season to predict the probability of metamorphosis for each larvae collected.

The regional probability of metamorphosis models estimated from the pooled data do not encompass the within- and among-stream variability that is present when each of the individual stream models of metamorphosis are estimated (Figure 11). To reflect this underlying variability, I assumed that each stream-specific logistic model represented a possible model of metamorphosis for the streams in a region. For each iteration of the simulation model one pair of the stream and year-specific parameter estimates was selected from the individual logistic models for that region and used to calculate the length-dependent probability of metamorphosis.

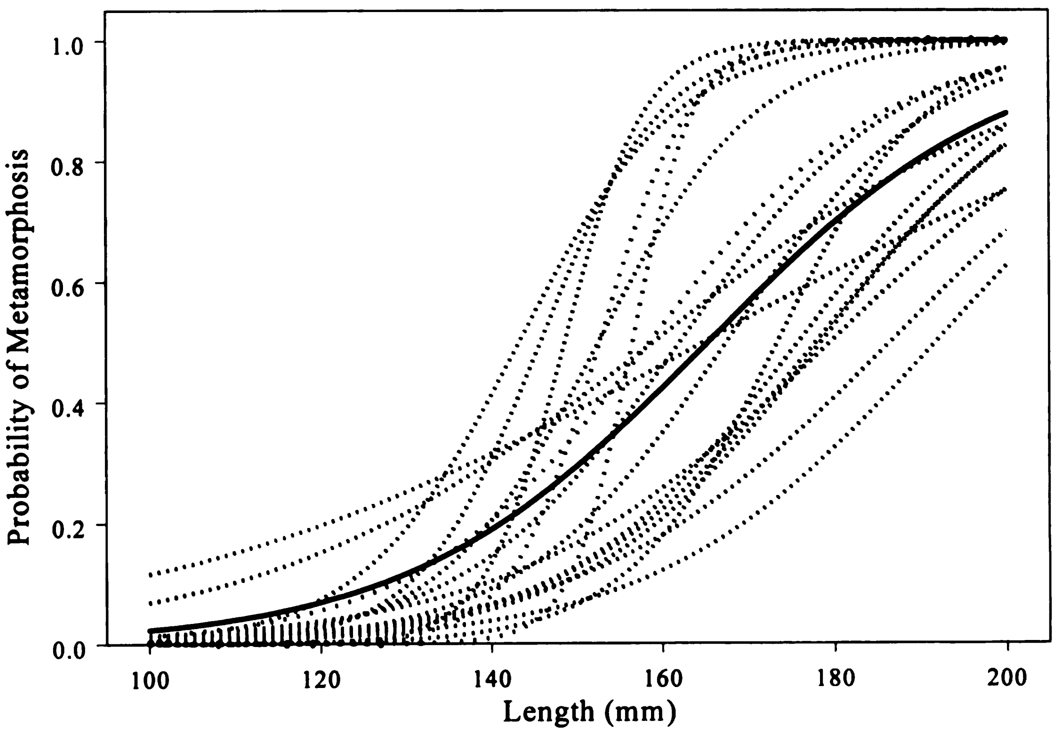


Figure 11. Regional logistic model to predict probability of metamorphosis (solid line) versus the logistic models for the individual stream data within the region (dashed lines).

Evaluation of uncertainties in variables and predictions

Since some of the parameterizations for the simulation model differ from those in the current ESTR model, the simulation model outputs may not equal those of the initial ESTR model. For example, the estimates of density using the logistic model of electrofisher efficiency are expected to differ from those obtained using the fixed estimate of 0.48, resulting in different estimates of lamprey abundance. The simulation model outputs will be compared with the mark-recapture estimates to determine if these changes in parameterization provide more accurate abundance estimates.

The number of simulations to use was determined by using the simulation model to sample one of the data sets 10000 times and observing when the coefficient of variation of the estimates of metamorphosed lampreys became relatively stable (Figure 12). This occurred after approximately 5000 simulations. Given that 5000 simulations require approximately one hour of computing time and there were 81 scenarios to simulate, the added expense of additional simulations did not substantially improve the coefficient of variation. The simulation model was used to provide 5000 estimates of larval and metamorphosed lampreys for each stream in the data set. The 2.5 and 97.5 percentiles were used to bound the uncertainty in the estimates of larval lamprey abundance and in the predictions of metamorphosed lamprey production.

The models that predict larval and parasitic lamprey production (Appendix A) cannot be easily linearized. To evaluate the influence of variability in the input variables on the uncertainty in the model prediction I used a nonparametric approach (McKay 1995). The

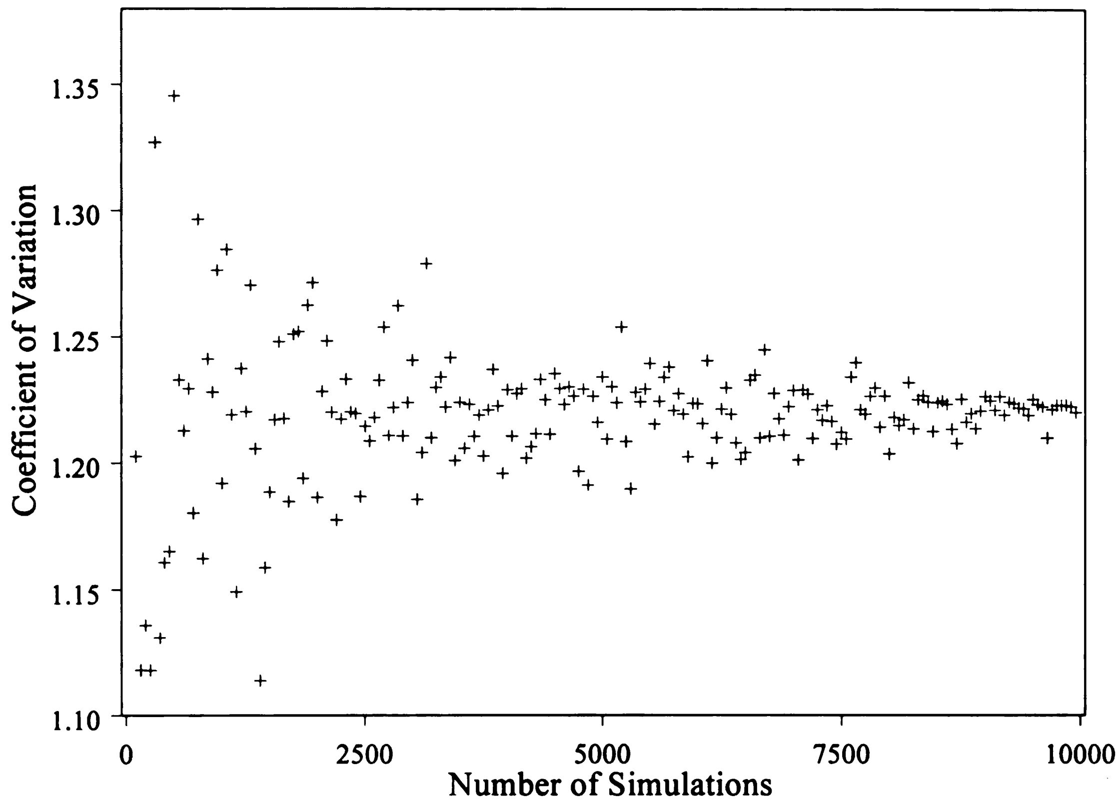


Figure 12. The number of simulations required to stabilize the coefficient of variation of the simulation model outputs.

importance of uncertainty in each of the 9 variables on the ammocoete abundance and parasitic production estimates of the ESTR model was assessed as the difference in the coefficient of variation of M_y – the CV of the ESTR model prediction when all inputs y vary – and the conditional CV's of $M_{y|s}$ – the CV of the ESTR model prediction when each variable s is fixed at its nominal value (McKay 1995).

I assigned nominal values to the model parameters of catchability, growth, lamprey density in Type 2 habitat, and probability of metamorphosis as the mean values of the data used for resampling. I assigned nominal values to the hierarchy of access point, habitat, total catch, and length data by recoding the model to sample the data without replacement when the simulation model was conditioned for the respective variable. Sampling without replacement forced the simulation model to select the same data combination and subsequently calculate a consistent value for each conditioned variable during each iteration of the simulation model. This removed the contribution to output uncertainty for the conditioned variable.

The simulation model was reiterated 5000 times for each of the 8 variables fixed at their nominal values (Table 8). The estimates of mean and variance of the abundance estimates for both larval and metamorphosed lampreys are not independent (Figure 13). For this reason, I chose to use the coefficient of variation (CV) to compare the difference in variability between the fully randomized simulation model outputs and outputs of each conditioned model.

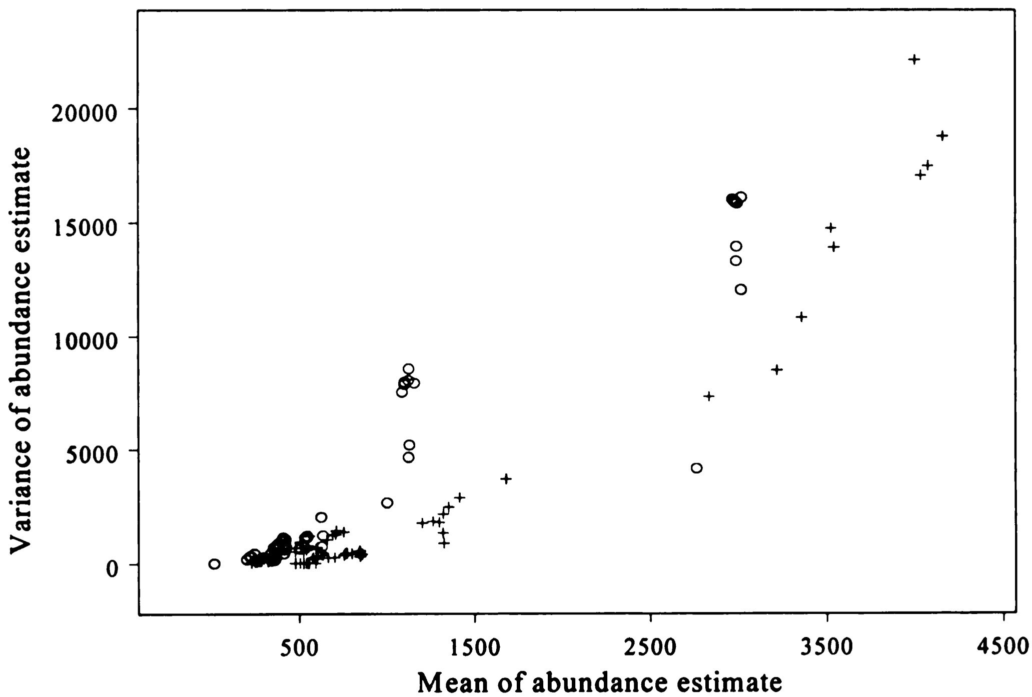


Figure 13. Scatterplot of variance versus mean for the simulation model abundance estimates of larval (open circles) and metamorphosed (crosses) lampreys. The values of mean larval abundance and metamorphosed lamprey variance are scaled by 10^{-3}, larval variance by 10^{-6} to fit common axes.

Table 8. Nominal values for variables in the ESTR simulation model.

Stream	Access	Catch		Habitat			q^A	Growth	Metamorphosis		TII/TI
	Sites	Plots	# of Larvae	Transects	TI Area (m^2)	TII Area (m^2)		(mm/day)	β0	β1	Ratio
Batchawana R	6	20	254	72	10760	128321	---	0.148	-15.59	0.118	0.296
Club Cr.	6	12	327	72	7302	15315	---	0.171	-24.82	0.163	0.296
Crystal Cr.	3	11	311	16	1711	22452	---	0.156	-30.60	0.218	0.296
Gargantua R.	4	12	279	17	5359	17142	---	0.148	-16.59	0.118	0.296
Meyer's Cr.	6	12	96	72	957	4298	---	0.171	-24.82	0.163	0.296
Proctor's Cr.	3	12	242	36	2147	7088	---	0.215	-33.92	0.267	0.296
Salem Cr.	3	12	152	36	2106	3535	---	0.215	-37.92	0.267	0.296
Watson's Cr.	3	12	166	36	1756	6262	---	0.156	-30.60	0.218	0.296
Wilson Cr.	10	45	1945	113	5592	17126	---	0.170	-34.48	0.239	0.296

[A] Nominal catchability was estimated using the logistic equation without the variance-covariance matrix

To determine which conditioned variables produced a significant reduction in output variability, I used a bootstrap procedure to determine the 2.5 and 97.5 percentiles of the CV for the fully randomized model outputs. For each stream, I resampled the 5000 estimates of larval and metamorphosed lampreys from the fully randomized model 1000 times, with replacement, and calculated the CV for each resample. From the 1000 bootstrap CV's I calculated the 2.5 and 97.5 percentiles of the CV for the fully randomized model. A CV for the conditional model that fell outside of this 95 percentile range was considered a significant deviation.

RESULTS

Mark-recapture population estimates

The mark-recapture estimates of larval and metamorphosed lamprey abundance are presented in Table 9. The initial ESTR model forecasts, used to determine the target number of larvae to mark and release, do not accurately predict larval or metamorphosed lamprey abundance in the majority of the streams. For larval abundance forecasts, the initial ESTR model estimates do not fall within the 95% confidence intervals of mark-recapture larval abundance estimates for any stream. The initial ESTR model forecasts of metamorphosed lampreys lie within the 95% confidence intervals of the mark-recapture estimates for 2 of the 9 streams; Batchawana River and Meyer's Creek.

Since the parameterization of the simulation model for the Monte Carlo approach to quantifying model uncertainties differs from the original ESTR model specification, I also compared the relative accuracy of the simulation model forecasts with the mark-recapture estimates of abundance (Figures 14 and15). The comparisons where the both the vertical and horizontal error bars encompass the replacement line represent those

Table 9. Mark-recapture estimates of larval and metamorphosed (or juvenile) lamprey abundance for the 9 study streams. The upper panel contains the estimate of lamprey abundance for all species and life stages in each study stream. The middle and bottom panels contain estimates of larval and juvenile sea lamprey abundance, respectively. The initial larval and juvenile abundance estimates are the one-year ESTR forecasts from the survey data, used to set target levels of larvae to mark and recapture.

Stream Name	Treatment Date	M	R	C	N*	95% C.I.* Lower	95% C.I.* Upper
Batchawana R.	Oct 14-16, 1998	2618	41	5102	318209	223489	412928
Club Cr.	Sept 6, 1999	1386	187	3500	25829	22247	29411
Crystal Cr.	Sept 20-22, 1999	1608	144	5023	55749	46837	64661
Gargantua R.	Aug 3-4, 1999	692	214	1573	5073	4445	5702
Meyer's Cr.	Oct 5, 1999	393	28	382	5204	3413	6994
Proctor's Cr.	Aug 19-21, 1998	1068	112	2398	22695	18628	26762
Salem Cr.	Aug 19-20,1998	1309	43	3770	112273	79661	144885
Watson's Cr.	Sept 30, 1998	1339	154	3350	28970	24530	33410
Wilson Cr.	July 26-28, 1999	3276	135	11547	278256	231936	324576

* Population estimate includes all species and life stages of lampreys

Stream Name	Proportion of N as larval sea lampreys	Estimate of Larval Abundance	95% C.I. Lower	95% C.I. Upper	Initial Larval Abundance Estimate
Batchawana R.	0.289	92120	64392	118974	29344
Club Cr.	0.990	25572	22025	29118	33432
Crystal Cr.	0.975	54336	45650	63022	26906
Gargantua R.	0.999	5067	4439	5695	26403
Meyer's Cr.	0.657	3419	1992	4084	1533
Proctor's Cr.	0.997	22629	18574	26684	13622
Salem Cr.	0.999	112154	79577	144731	13384
Watson's Cr.	0.939	27189	23021	31356	8417
Wilson Cr.	0.999	277894	231635	324154	142339

Stream Name	Proportion of N as juvenile sea lampreys	Estimate of Juvenile Abundance	95% C.I. Lower	95% C.I. Upper	Initial Juvenile Abundance Estimate
Batchawana R.	0.00137	437	88	785	164
Club Cr.	0.00997	258	165	350	92
Crystal Cr.	0.02534	1413	1082	1744	164
Gargantua R.	0.00127	6	0	15	327
Meyer's Cr.	0.0733	381	192	570	427
Proctor's Cr.	0.00292	66	16	117	496
Salem Cr.	0.00106	119	0	241	453
Watson's Cr.	0	0	-	-	298
Wilson Cr.	0.0013	361	169	554	1862

streams where the mean simulation model estimate of lamprey abundance falls within the 95% CI of the mark-recapture estimate. Two of the estimates of larval abundance fall near the replacement line (Figure 14); the Batchawana River and Wilson Creek. Similar to the ESTR model estimates, two of the simulation model estimates of metamorphosed lamprey abundance lie within the 95% CI of the mark-recapture estimates and fall near the replacement line (Figure 15); the Batchawana River and Meyer's Creek. In all comparisons, the Monte Carlo simulation model estimates are more variable than the mark-recapture estimates, demonstrated by the greater range between the 2.5 and 97.5 percentiles of the simulation forecasts than the 95% confidence intervals of the mark-recapture estimates. Conversely, in 16 of 18 comparisons, the mark-recapture estimate falls within the 95-percentile range of the simulation model estimates. There is no evidence of systematic differences between the simulation and mark-recapture estimates of lamprey abundance.

Monte Carlo Simulation model outputs

The larval and metamorphosed lamprey abundance estimates from the 5000 simulations for all models are presented for each stream in Figures 16 through 24. In all cases the median values of abundance are approximately equal, indicating that the model consistently estimates the same central measure of lamprey abundance whether the model is fully randomized or a conditioned on a nominal value for each variable. The coefficients of variation for estimates of metamorphosed lamprey abundance are higher than the coefficients of variation for estimates of larval abundance within the same stream (Table 10). This may be due to the contribution of the added variability from growth rates and probability of metamorphosis in the metamorphosed lamprey abundance estimates that does not affect the estimates of larval lamprey abundance.

Table 10. Means and bootstrap percentiles for the coefficients of variation for the larval and metamorphosed (juvenile) lamprey abundance estimates from the fully randomized simulation model.

	Larval Estimates			**Juvenile Estimates**		
		Percentiles			**Percentiles**	
Stream	**Mean**	**2.5**	**97.5**	**Mean**	**2.5**	**97.5**
Batchawana R.	0.798	0.776	0.817	1.917	1.747	2.152
Club Cr.	0.532	0.520	0.544	1.832	1.778	1.886
Crystal Cr.	0.766	0.748	0.786	1.777	1.690	1.864
Gargantua R.	0.771	0.746	0.793	1.613	1.557	1.705
Meyer's Cr.	0.621	0.607	0.635	1.252	1.221	1.284
Proctor's Cr.	0.626	0.612	0.639	1.053	1.018	1.088
Salem Cr.	0.717	0.699	0.733	1.199	1.162	1.236
Watson's Cr.	0.775	0.760	0.791	0.880	0.853	0.909
Wilson Cr.	0.423	0.415	0.430	0.967	0.942	0.993

Three variables, the access points sampled, observed catch, and the ratio of Type 1 larval density assigned to Type 2 habitat, reduced the coefficient of variation in most streams below the 2.5 percentile of the fully randomized model estimates of larval lamprey abundance (Table 11). The CV of larval lamprey estimates was significantly different in 5 of 9 streams when the variability in the amount of habitat was removed from the model. In Club Creek, the model conditioned on length also had a significantly lower CV than the CV for the fully randomized model.

Seven of the 8 conditioned simulation models changed the coefficient of variation for estimates of metamorphosed lamprey abundance in at least 6 of the 9 streams in this study (Table 12). Conditioning on the Type 1:Type 2 ratio again reduced the CV for metamorphosed lamprey estimates in all 9 streams, followed by the models conditioned on access point and observed catch for 8 of the 9 streams. Notably, fixed capture effectiveness significantly changes the CV for metamorphosed lamprey abundance

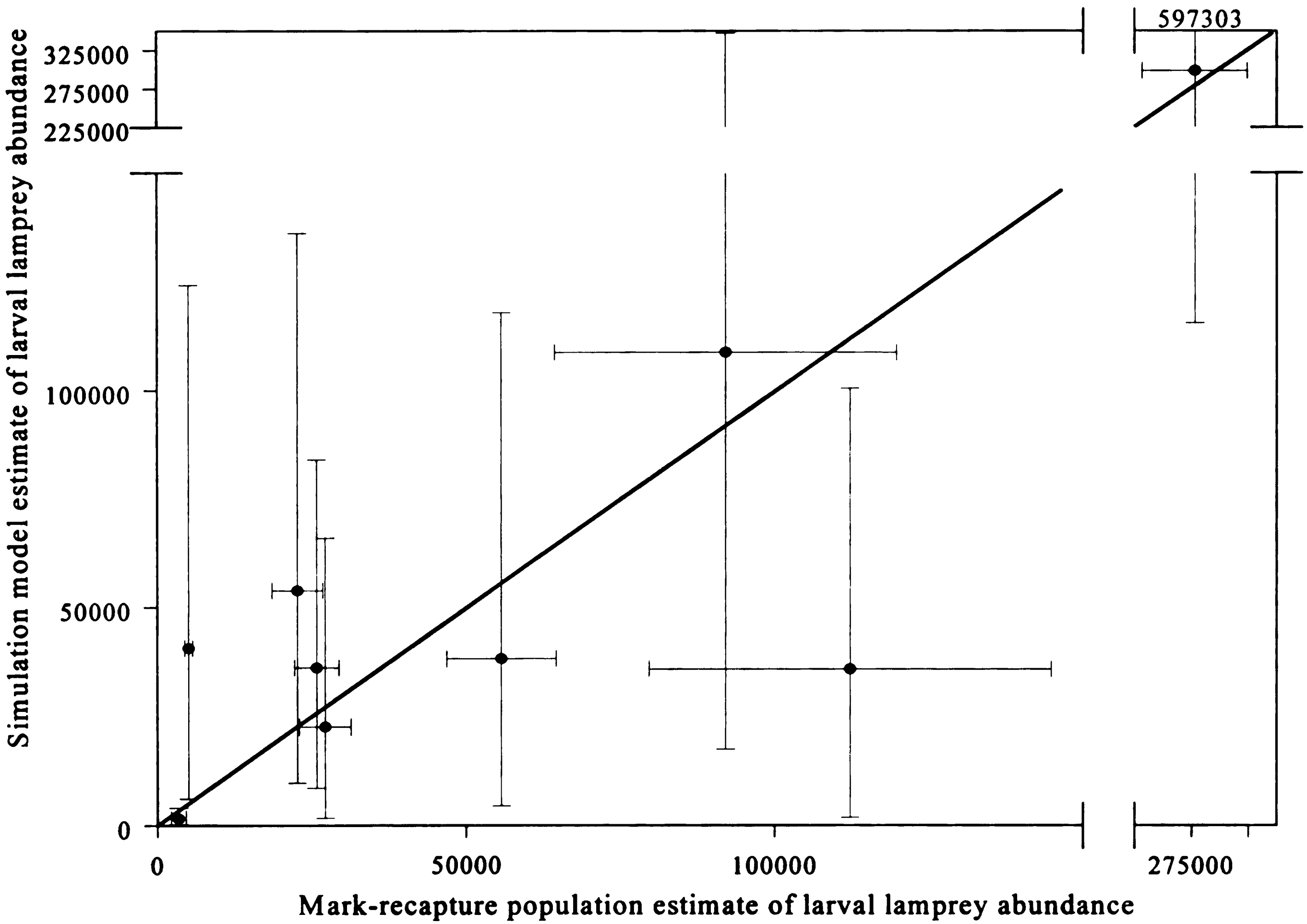


Figure 14. Comparison of the mark-recapture and mean Monte Carlo simulation model estimates of larval lamprey abundance. The error bars represent the 95% confidence interval (horizontal) and the 2.5 and 97.5 percentiles (vertical), for mark-recapture and Monte Carlo estimates, respectively. The bold line indicates the 1:1 line.

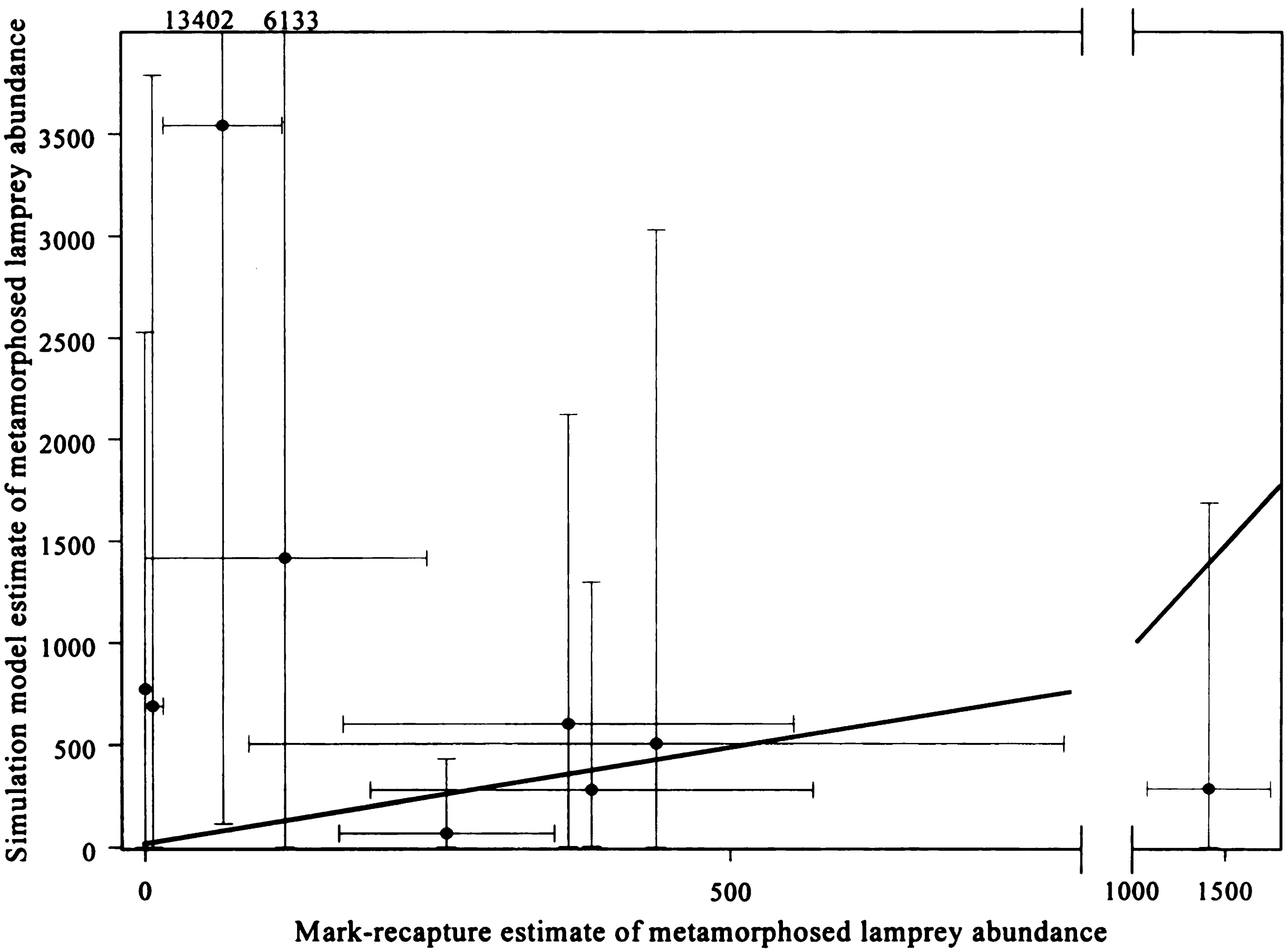


Figure 15. Comparison of the mark-recapture and mean Monte Carlo simulation model estimates of metamorphosed lamprey abundance. The error bars represent the 95% confidence interval (horizontal) and the 2.5 and 97.5 percentiles (vertical), for mark-recapture and Monte Carlo estimates, respectively. The bold line indicates the 1:1 line.

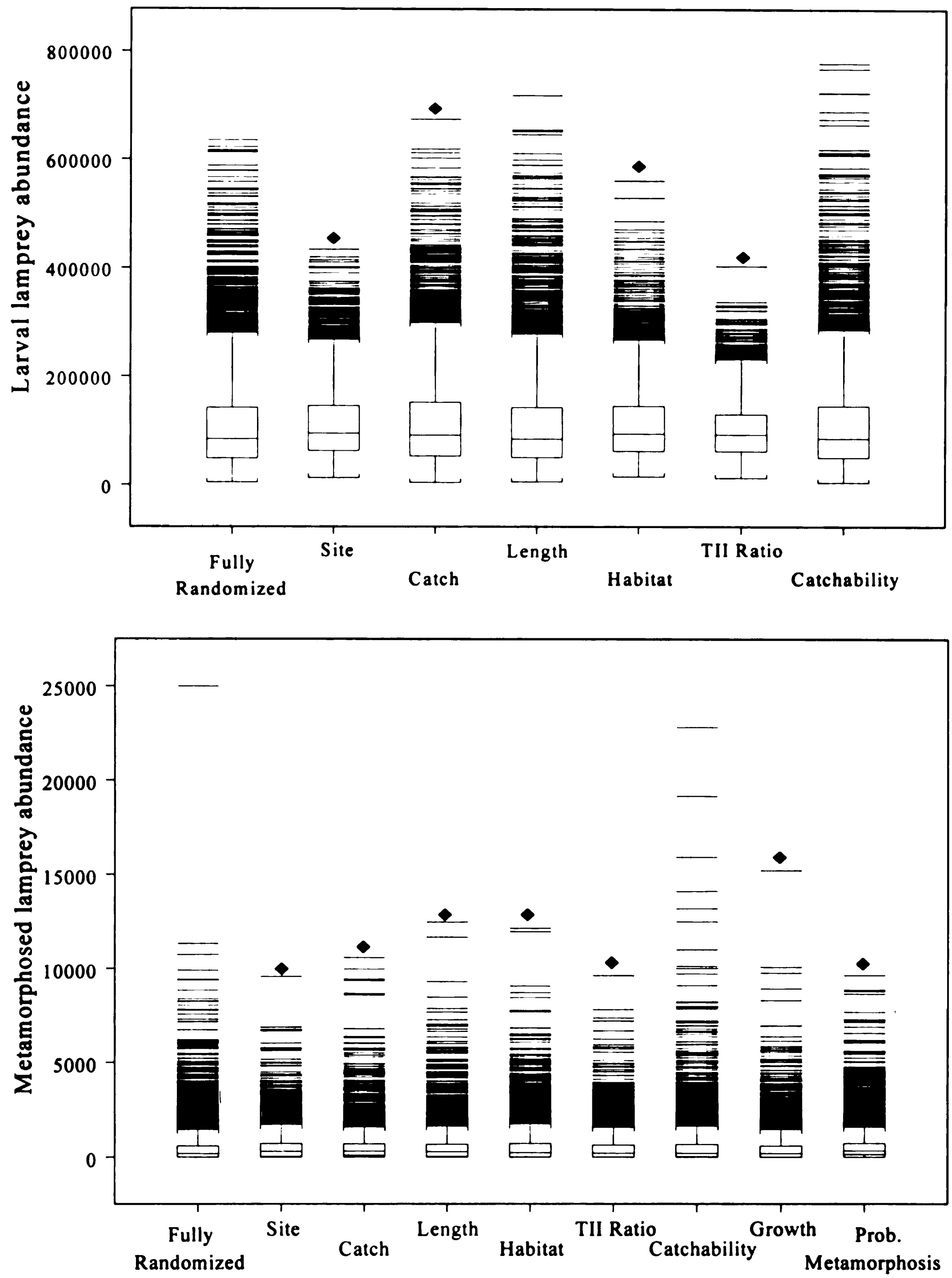
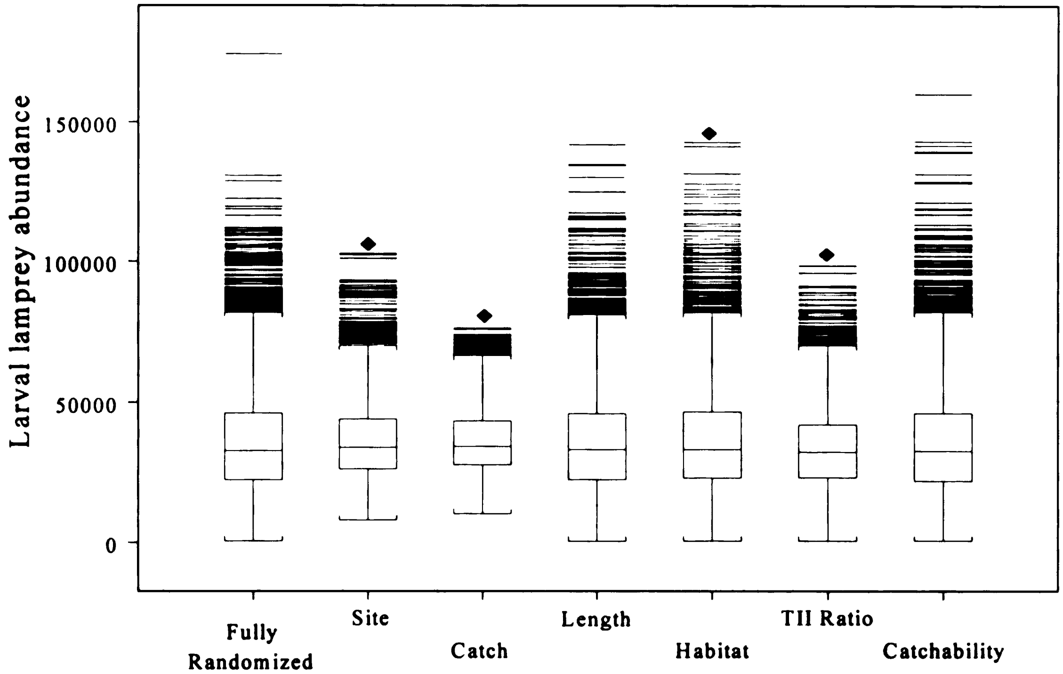


Figure 16. Boxplots for the fully randomized and conditioned variable simulation model estimates of larval and metamorphosed sea lampreys in the Batchawana River. The open boxes represent the 25th and 75th quartiles, the lines within the boxes represent the median estimates for each set of simulations, and the whiskers are 1.5 times the interquartile distance. The lines above the uppermost whisker represent observations greater than 1.5 times the interquartile distance from the median. The diamonds represent conditional models with CV's outside of the 95 percentile range of the CV for the fully randomized model.



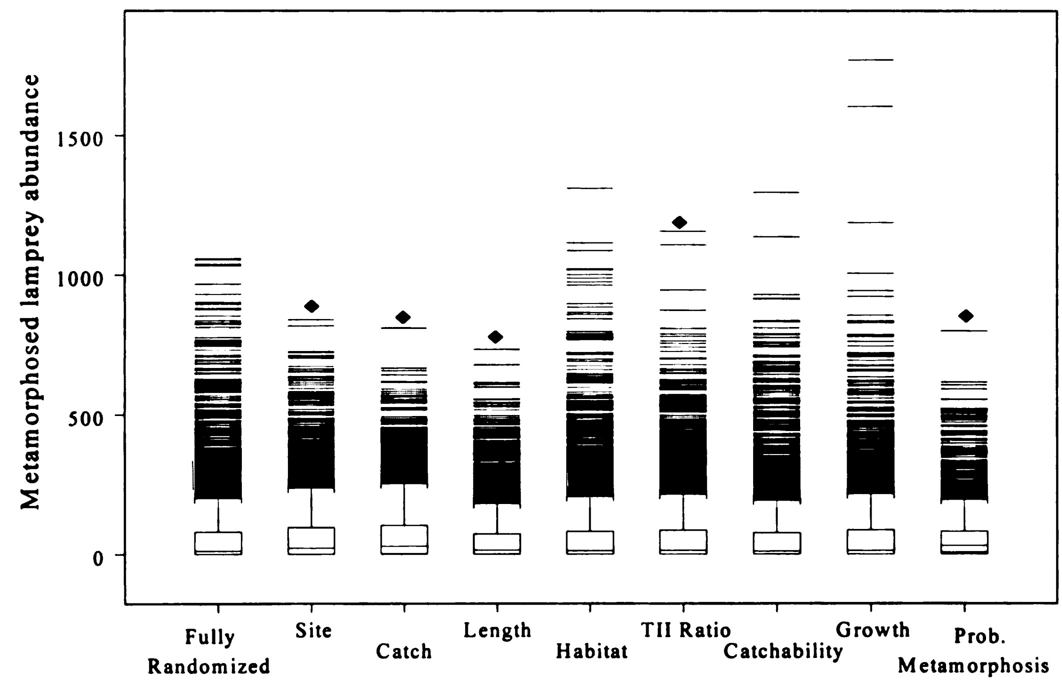


Figure 17. Boxplots for the fully randomized and conditioned variable simulation model estimates of larval and metamorphosed sea lampreys in the Club Creek. The open boxes represent the 25th and 75th quartiles, the lines within the boxes represent the median estimates for each set of simulations, and the whiskers are 1.5 times the interquartile distance. The lines above the uppermost whisker represent observations greater than 1.5 times the interquartile distance from the median. The diamonds represent conditional models with CV's outside of the 95 percentile range of the CV for the fully randomized model.

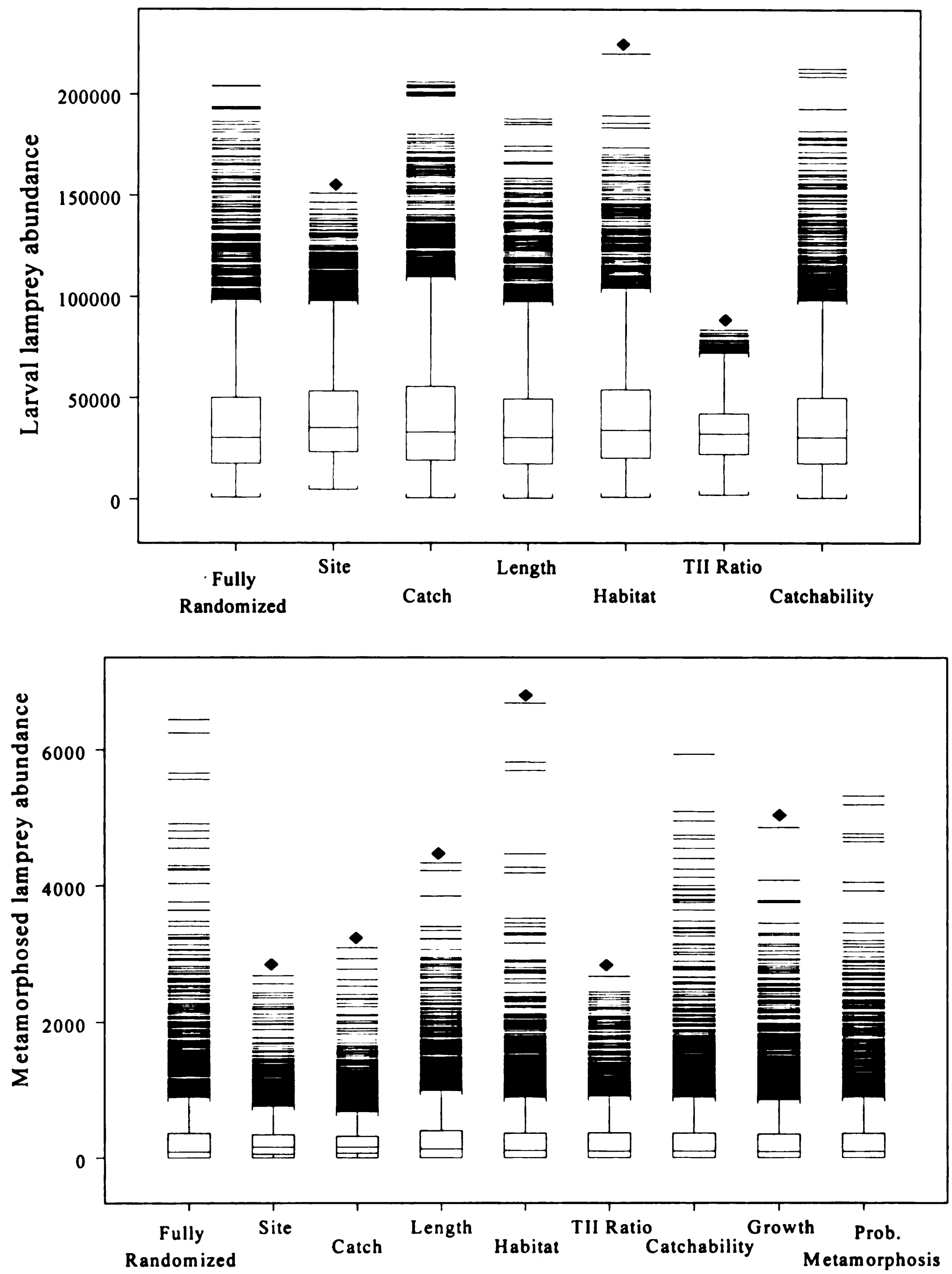
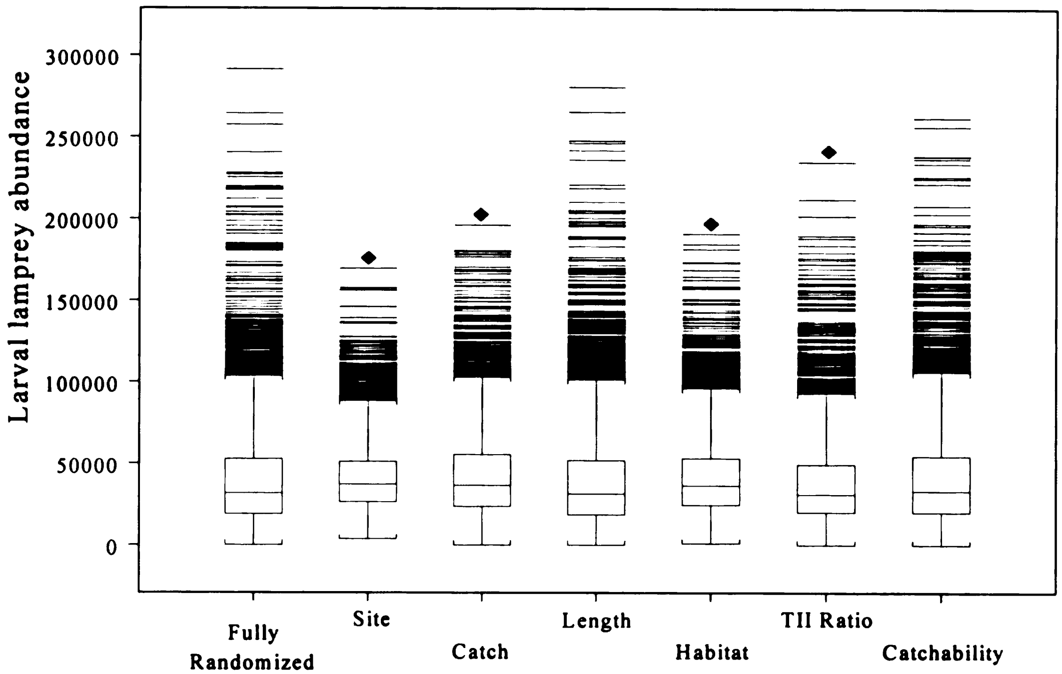


Figure 18. Boxplots for the fully randomized and conditioned variable simulation model estimates of larval and metamorphosed sea lampreys in the Crystal Creek. The open boxes represent the 25th and 75th quartiles, the lines within the boxes represent the median estimates for each set of simulations, and the whiskers are 1.5 times the interquartile distance. The lines above the uppermost whisker represent observations greater than 1.5 times the interquartile distance from the median. The diamonds represent conditional models with CV's outside of the 95 percentile range of the CV for the fully randomized model.



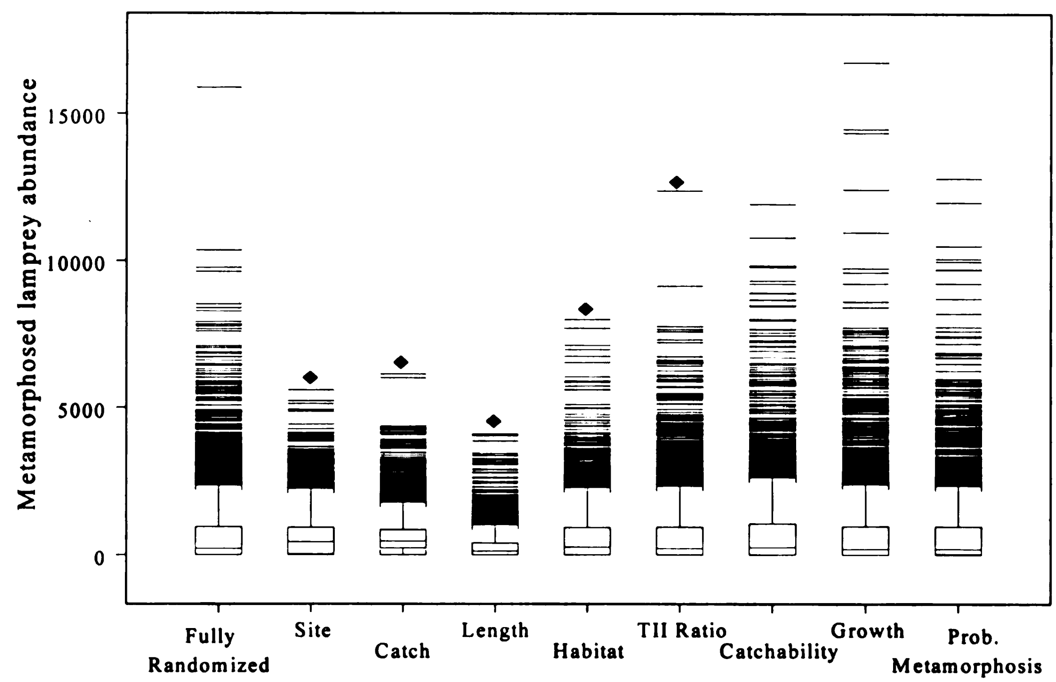


Figure 19. Boxplots for the fully randomized and conditioned variable simulation model estimates of larval and metamorphosed sea lampreys in the Gargantua River. The open boxes represent the 25th and 75th quartiles, the lines within the boxes represent the median estimates for each set of simulations, and the whiskers are 1.5 times the interquartile distance. The lines above the uppermost whisker represent observations greater than 1.5 times the interquartile distance from the median. The diamonds represent conditional models with CV's outside of the 95 percentile range of the CV for the fully randomized model.

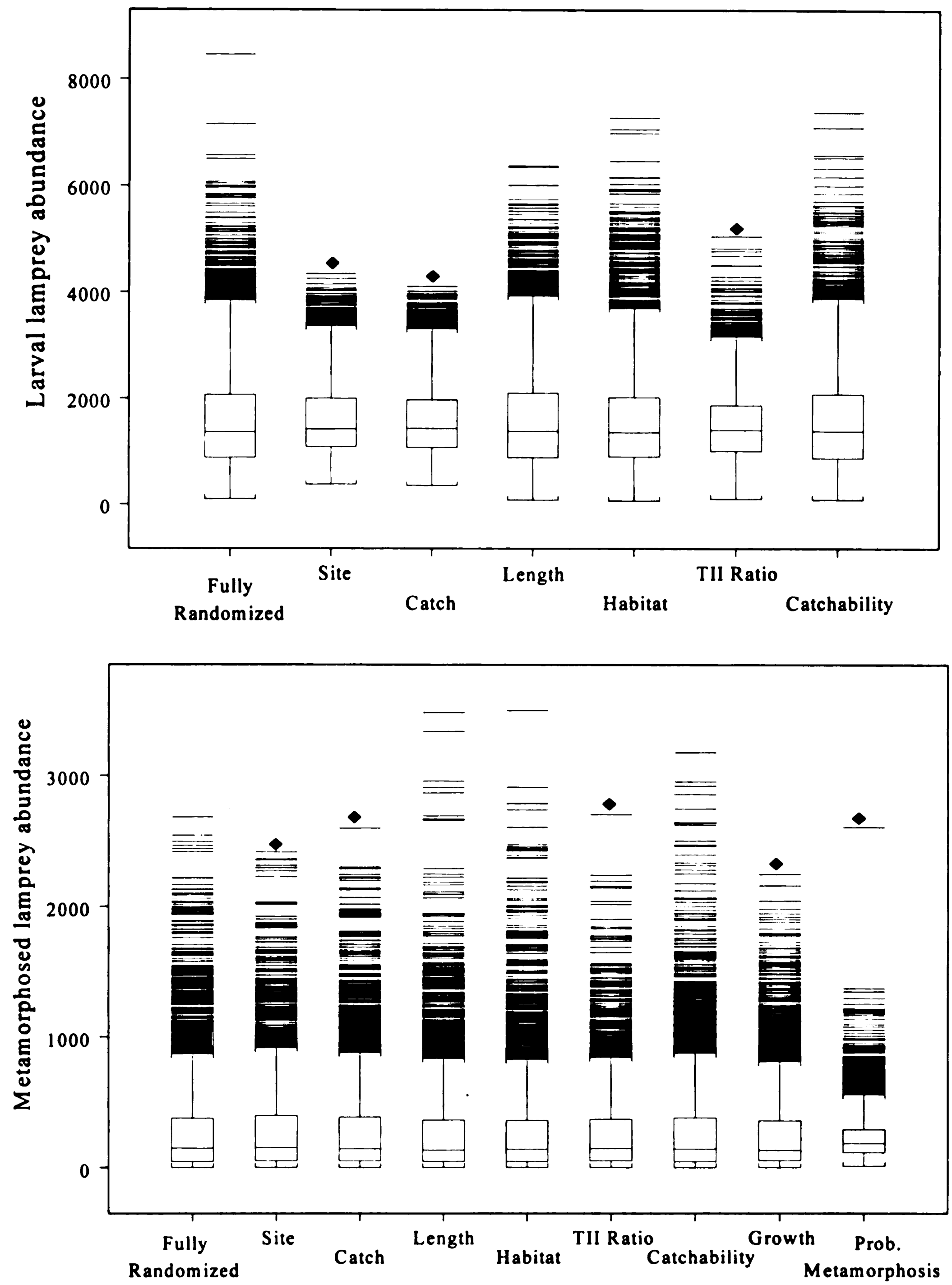


Figure 20. Boxplots for the fully randomized and conditioned variable simulation model estimates of larval and metamorphosed sea lampreys in the Meyer's Creek. The open boxes represent the 25th and 75th quartiles, the lines within the boxes represent the median estimates for each set of simulations, and the whiskers are 1.5 times the interquartile distance. The lines above the uppermost whisker represent observations greater than 1.5 times the interquartile distance from the median. The diamonds represent conditional models with CV's outside of the 95 percentile range of the CV for the fully randomized model.

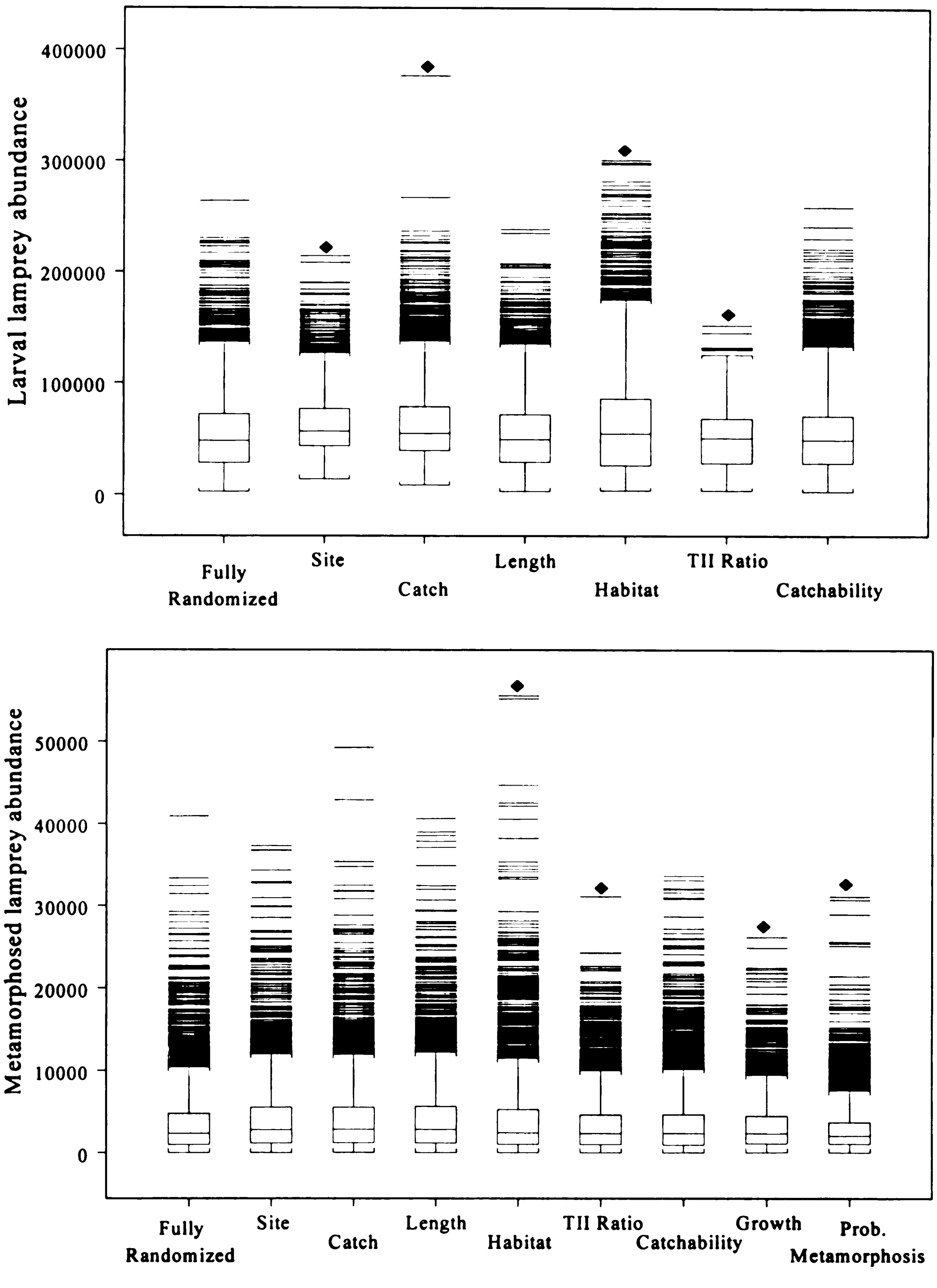
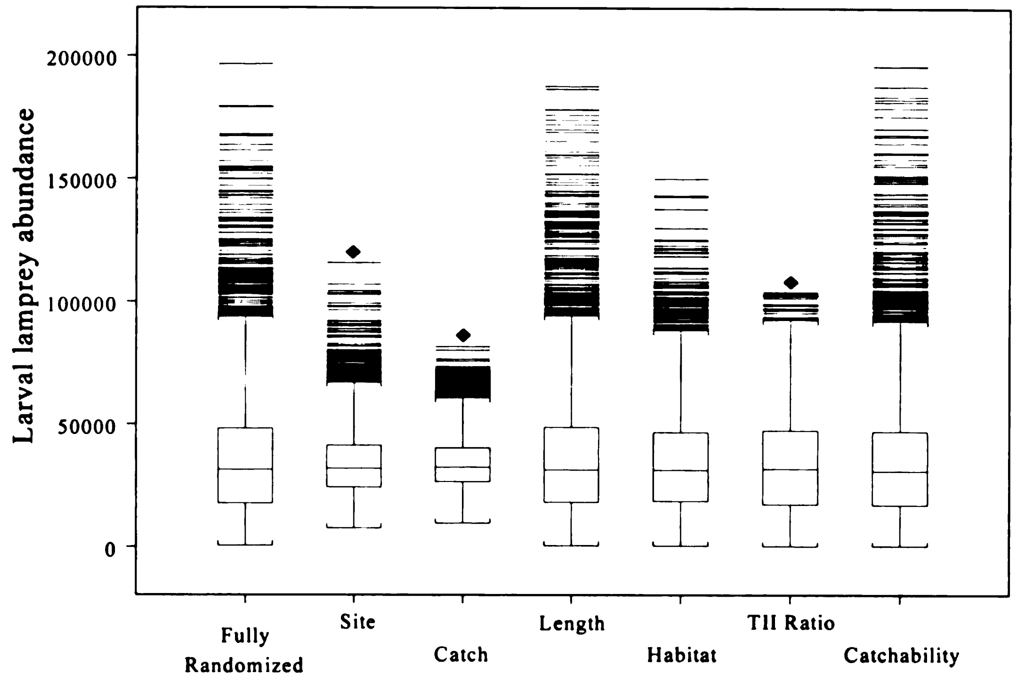


Figure 21. Boxplots for the fully randomized and conditioned variable simulation model estimates of larval and metamorphosed sea lampreys in the Proctor's Creek. The open boxes represent the 25th and 75th quartiles, the lines within the boxes represent the median estimates for each set of simulations, and the whiskers are 1.5 times the interquartile distance. The lines above the uppermost whisker represent observations greater than 1.5 times the interquartile distance from the median. The diamonds represent conditional models with CV's outside of the 95 percentile range of the CV for the fully randomized model.



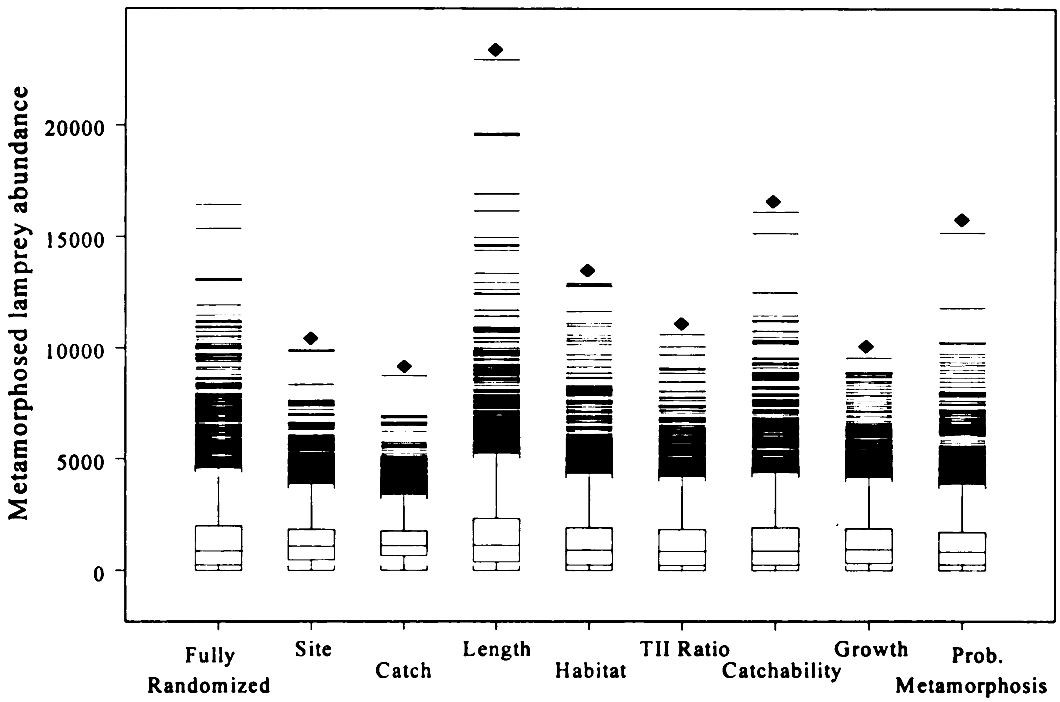


Figure 22. Boxplots for the fully randomized and conditioned variable simulation model estimates of larval and metamorphosed sea lampreys in the Salem Creek. The open boxes represent the 25th and 75th quartiles, the lines within the boxes represent the median estimates for each set of simulations, and the whiskers are 1.5 times the interquartile distance. The lines above the uppermost whisker represent observations greater than 1.5 times the interquartile distance from the median. The diamonds represent conditional models with CV's outside of the 95 percentile range of the CV for the fully randomized model.

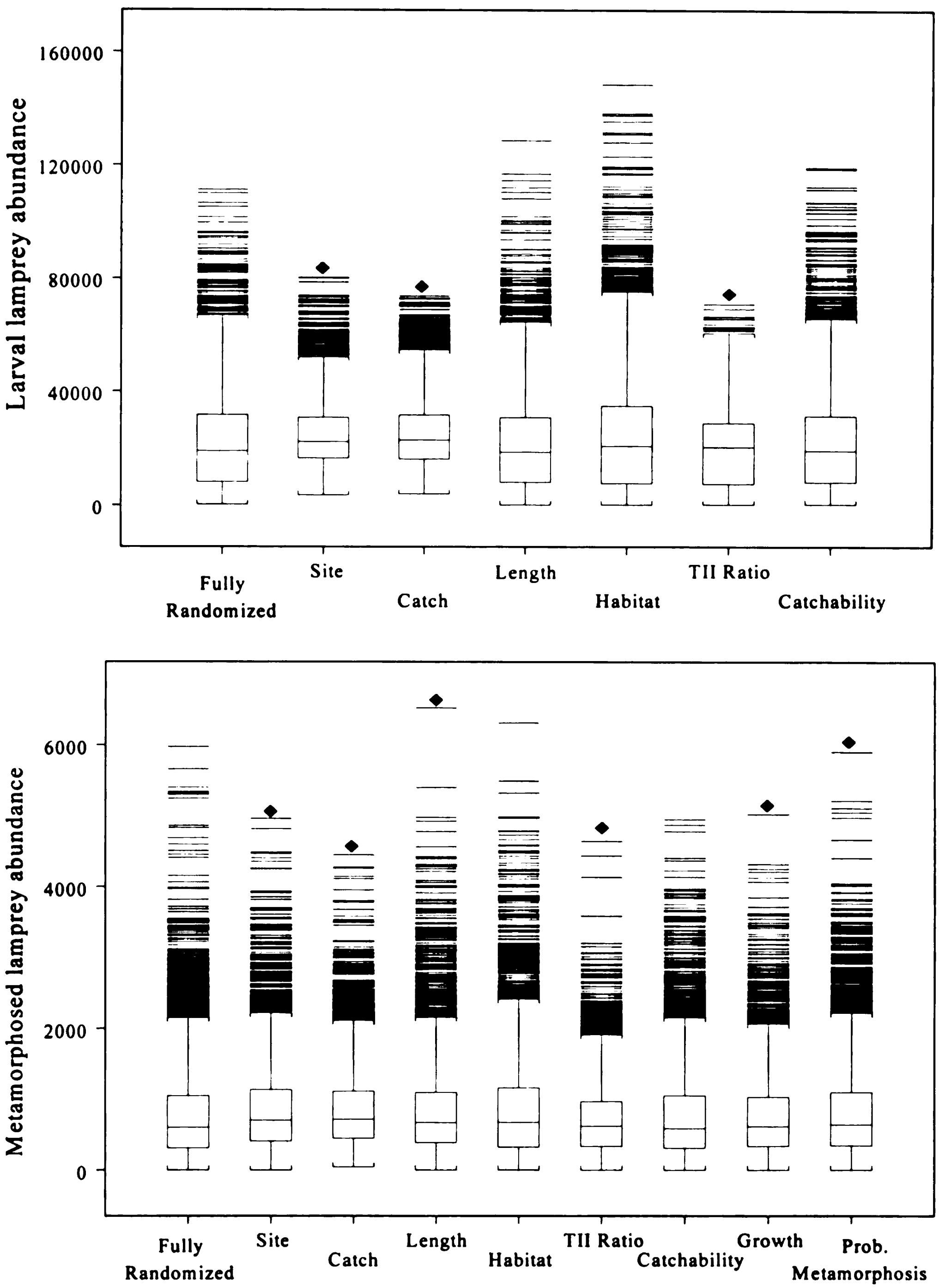
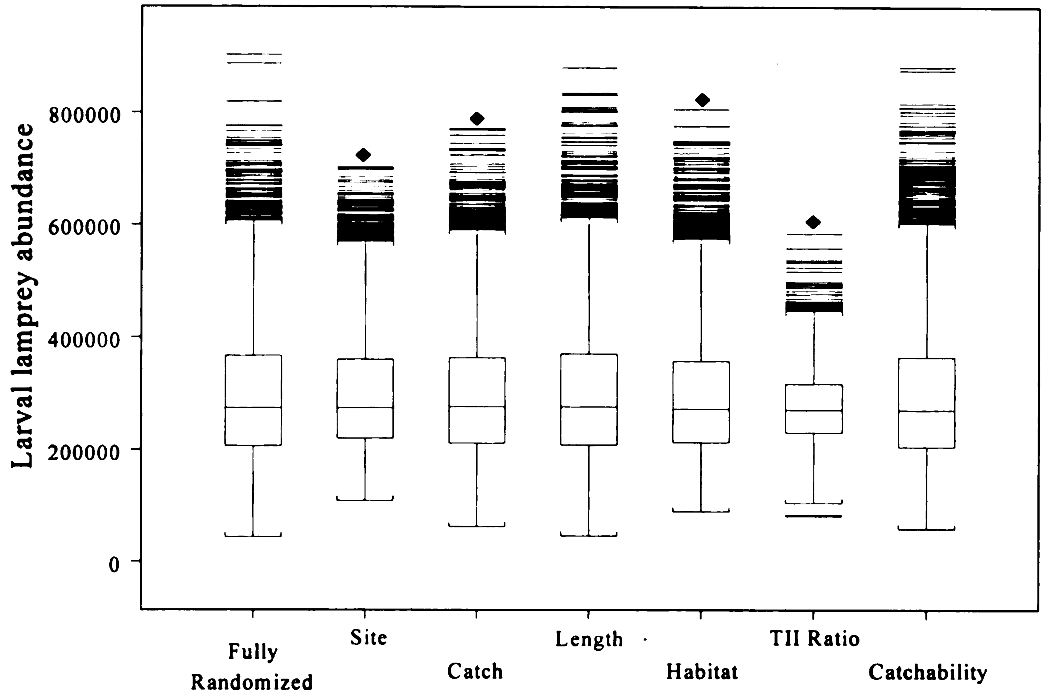


Figure 23. Boxplots for the fully randomized and conditioned variable simulation model estimates of larval and metamorphosed sea lampreys in the Watson's Creek. The open boxes represent the 25th and 75th quartiles, the lines within the boxes represent the median estimates for each set of simulations, and the whiskers are 1.5 times the interquartile distance. The lines above the uppermost whisker represent observations greater than 1.5 times the interquartile distance from the median. The diamonds represent conditional models with CV's outside of the 95 percentile range of the CV for the fully randomized model.



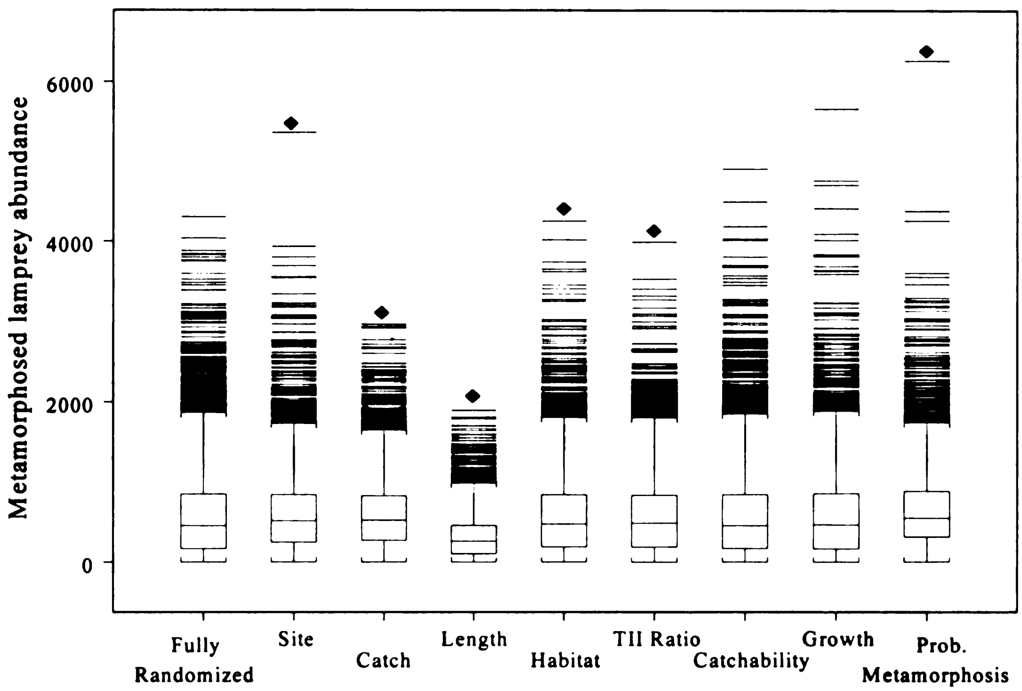


Figure 24. Boxplots for the fully randomized and conditioned variable simulation model estimates of larval and metamorphosed sea lampreys in the Wilson Creek. The open boxes represent the 25th and 75th quartiles, the lines within the boxes represent the median estimates for each set of simulations, and the whiskers are 1.5 times the interquartile distance. The lines above the uppermost whisker represent observations greater than 1.5 times the interquartile distance from the median. The diamonds represent conditional models with CV's outside of the 95 percentile range of the CV for the fully randomized model.

Table 11. Coefficient of variation of simulation model estimates of larval lamprey abundance. Bold entries are conditional model CV's outside of the 95 percentile range of the CV for the fully randomized simulation model.

	Batchawana R.	Club Cr.	Crystal Cr.	Gargantua R.	Meyer's Cr.	Proctor's Cr.	Salem Cr.	Watson's Cr.	Wilson Cr.
Fully Randomized	0.798	0.532	0.766	0.771	0.621	0.626	0.717	0.775	0.423
Site	**0.606**	**0.401**	**0.599**	**0.504**	**0.432**	**0.431**	**0.409**	**0.470**	**0.364**
Catch	**0.769**	**0.326**	0.766	**0.627**	**0.434**	**0.549**	**0.313**	**0.471**	**0.395**
Length	0.806	**0.515**	0.753	0.780	0.610	0.617	0.720	0.779	0.420
Habitat	**0.638**	0.525	**0.701**	**0.589**	0.618	**0.720**	**0.631**	0.832	0.386
Type 1:Type 2 Ratio	**0.514**	**0.440**	**0.458**	**0.687**	**0.450**	**0.498**	**0.624**	**0.643**	**0.233**
Catchability	0.822	0.537	0.763	0.765	0.618	0.629	0.733	0.785	0.426

Table 12. Coefficient of variation of simulation model estimates of metamorphosed lamprey abundance. Bold entries are conditional model CV's outside of the 95 percentile range of the CV for the fully randomized simulation model.

	Batchawana R.	Club Cr.	Crystal Cr.	Gargantua R.	Meyer's Cr.	Proctor's Cr.	Salem Cr.	Watson's Cr.	Wilson Cr.
Fully Randomized	1.917	1.832	1.777	1.613	1.252	1.053	1.199	0.880	0.967
Site	**1.355**	**1.540**	**1.161**	**1.117**	**1.180**	1.024	**0.873**	**0.747**	**0.814**
Catch	**1.419**	**1.395**	**1.172**	**0.950**	**1.214**	1.026	**0.708**	**0.656**	**0.750**
Length	**1.545**	**1.596**	**1.512**	**1.480**	1.270	1.042	**1.146**	**0.817**	**0.874**
Habitat	**1.605**	1.817	**1.627**	**1.387**	1.285	**1.176**	**1.114**	0.879	**0.890**
Type 1:Type 2 Ratio	**1.525**	**1.713**	**1.452**	**1.546**	**1.146**	**0.979**	**1.076**	**0.739**	**0.853**
Catchability	1.971	1.826	1.746	1.560	1.276	1.089	**1.160**	0.868	0.961
Growth	**1.713**	1.780	**1.668**	1.689	**1.189**	**0.905**	**1.032**	**0.808**	0.947
Metamorphosis	**1.339**	**1.314**	1.698	1.588	**0.736**	**0.955**	**1.106**	**0.827**	**0.753**

estimates in Salem Creek and does not reduce the CV for larval lamprey estimates in any stream.

In the case of Proctor's Creek, fixing the amount of habitat at nominal values resulted in an increase in the CV for estimates of larval and metamorphosed lamprey abundance. When the simulation model is conditioned on habitat area, Type 1 and 2 habitat areas are assigned as constant values, while the remaining access point variables (site, catch, and length) are sampled with replacement. If larval lamprey length or abundance is correlated with the amount of habitat available at an access point, this sampling approach removes any correlation between habitat area and the remaining access point variables. In turn, this may artificially increase the variability in the sampling data, where, for example, larval lamprey catches may be assigned to areas where the actual stream data do not reflect this relationship. This is an indication of the importance of maintaining the structure when resampling the survey data, where removing correlation within the data by relaxing the sampling scheme can result in more variable model outputs.

DISCUSSION

Uncertainty in prediction models is derived from three general sources (Sargent 1998, Rykiel 1996, Draper 1995, McKay 1995, Power 1993, Grant 1986). The first is uncertainty in the model parameters, and how this parameter uncertainty is propagated through the model to the model output. The second is uncertainty in the structural assumptions of the model that defines the relationships between the model components. The third is uncertainty in the accuracy of the model forecasts, and may be influenced by the uncertainty from the first two sources.

Validation, calibration, and verification of prediction models is an ongoing process that reduces these uncertainties, where model components and relationships are updated as new information refines or reshapes the understanding of model users (Kleijnen 1996, Rykiel 1996, McKay 1995, Grant 1986). Validation consists of determining if the model predictions reflect the behaviour of the system, sometimes defined as the accuracy of the model. Calibration ensures that the parameters and constants within the model are appropriately specified to provide agreement between model output and the system being modeled, improving model accuracy. Calibrating the model can also reduce the propagation of uncertainty in the model parameters through the model to the outputs, improving the ability to prioritize streams for TFM treatment based on the model forecasts. Verification consists of examining the model for structural and logical integrity, ensuring that the model formalism is correct. I will discuss how the results of the mark-recapture study and the simulation model analyses may be used to validate, calibrate, and verify the ESTR model, improving the utility of the model forecasts for treatment prioritization purposes.

Assuming that the mark-recapture estimates are unbiased estimators of lamprey abundance at the time of treatment, the current ESTR model (Appendix A) estimates of lamprey abundance are comparable in 2 of 18 cases. The simulation model, which contains slightly different parameters than the ESTR model, does not fare much better, providing comparable estimates of lamprey abundance in 4 of 18 comparisons. The lack of systematic differences between the mark-recapture and the ESTR or simulation model estimates indicates that there is no consistent source of error that may be reduced to increase the accuracy of the predictions (Power 1993). For example, the ESTR model does not account for mortality between the time of sampling and the time of treatment. If the mark-recapture estimates were consistently lower than the model predictions, incorporating a mortality term into the model could provide some improvement in prediction accuracy. Comparing the mark-recapture estimates with the ESTR model outputs to validate the model indicates that the current model does not reproduce the behaviour of the system (Sargent 1998, Rykiel 1996, Power 1993). Consequently, the current ESTR model is invalid for the purpose of providing reliable forecasts of lamprey abundance as a component of the cost-benefit ranking of streams for TFM treatment.

Several sources may contribute to the inaccuracy in the ESTR model predictions. Invalid data provided by the sampling protocol, improper values assigned to the driving variables within the model, or an improper model structure used to predict lamprey abundance would result in inaccurate model outputs (Sargent 1998, McKay 1996, Draper 1995). With respect to model structure, the specification of the ESTR model is one of many plausible alternative models that could be used to predict parasitic sea lamprey production. Alternative models may include additional parameters, such as the aforementioned mortality parameter, or may specify different relationships among the input variables (Morgan and Henrion 1990).

The importance of model structure is illustrated by an examination of how the sampling data are used to estimate larval lamprey abundance. The habitat and density data are currently collected from discrete sites within a stream, and may be many hundreds of metres apart. The ESTR model pools the sampling data for all sites to calculate stream-wide estimates of habitat area and mean larval lamprey density. By pooling the data there is an implicit assumption that there is no correlation between the habitat and larval density found at a specific access point. I will use the sampling information from Club Creek to illustrate a potential for error in this assumption.

Table 13 contains a summary of the catch and habitat information for Club Creek. The ESTR model estimate of larval lamprey abundance is calculated following the formula (Appendix A):

(Mean density x Type 1 habitat area) + (Mean density x Type 2 habitat area x 0.1)

and results in an estimated 33,432 lamprey larvae. An alternative method for estimating larval lamprey abundance is to treat each sample site as an individual section of the stream, estimate the abundance for each section using the above formula, and sum across sections to estimate the overall stream abundance of larval lampreys. I have done this for each of the 6 sites in Club Creek. For illustrative purposes I have assumed that the sites were evenly spaced along the length of the stream, giving equal weight to the population estimate for each stream section. The incremental estimate of 27,911 lampreys now falls within the 95% confidence interval of the mark-recapture estimate for the Club Creek population (22025,29118; Table 9). However, an improved estimate of larval abundance is not always the case when using the incremental approach to estimating abundance for every stream in the study. The same technique applied to the data for Salem Creek results in an abundance estimate of 11,758 larval lampreys, which is further from the mark-recapture abundance estimate. As well, the improved estimate of larval abundance does not necessarily result in an improved estimate of metamorphosed lamprey abundance. Since the same catch information is used to estimate the proportion of larvae that will metamorphose in the two approaches, I expect that 92/33,432 or 0.00275 of the incremental larval population estimate, approximately 77 larvae, would metamorphose in

Club Creek. As with the Salem Creek larval abundance estimates, this is further from the mark-recapture estimate of metamorphosed lamprey abundance for Club Creek. This illustration is not intended to prescribe a method that results in improved accuracy in the ESTR model predictions. Rather, it is intended to demonstrate the effect that verifying the structural assumptions of the model can have on the accuracy of model predictions.

Table 13. Summary of the sampling data for Club Creek, illustrating an alternative approach to estimating larval lamprey abundance.

Incremental Method

		Density	**Habitat Areas (m^2)**			**Population**
Site	**Catch**	**($\# \cdot m^{-2}$)**	**Type 1**	**Type 2**	**Type 3**	**Estimate**
1	1	0.069	646.1	3100.3	507.3	66
2	46	3.194	381.6	2636.4	238.5	2061
3	88	6.111	841.2	2445.6	0.0	6635
4	114	7.917	524.7	2541.0	60.7	6165
5	76	5.278	2129.0	2575.7	43.4	12596
6	2	0.139	2597.3	1933.9	99.7	388
				Incremental Total		27911
ESTR model estimates						
1-6	327	3.785	7302.0	15315.1	711.1	33432

As well as being inaccurate, the model outputs have a high degree of uncertainty (Figures 16-24). The range of values between the 2.5 and 97.5 percentiles for the simulation model outputs are from 1.5 to 90 times greater than the mark-recapture confidence intervals in the estimates of larval abundance, and from 2 to more than 200 times greater in the metamorphosed lamprey estimates. The quantification of the uncertainty around the model outputs illustrates the potential risk of not treating streams that may have a high abundance of metamorphosing sea lampreys (Morgan and Henrion 1990).

The control agents review the ESTR model forecasts of metamorphosed lamprey abundance, and base their treatment decisions on an evaluation of whether they believe the ESTR model estimates are accurate. The control agents reject the estimates and place a lower priority on streams that they believe the ESTR model has overestimated the abundance of metamorphosed lampreys. This most often occurs in the larger streams where the 12 plots electrofished for lamprey larvae represents a very small proportion of the available lamprey habitat. In these larger streams, lamprey density is typically low, and few (e.g. less than 50) lampreys are obtained from the sample plots. This relatively small sample of lamprey larvae would contain a low number of larvae that are greater than 100 mm in length and have the potential to metamorphose the following year. Extrapolating these few large larvae in the sample over a large amount of habitat results in a large estimate of lampreys with the potential to metamorphose. Intuitively, the uncertainty in this estimate is also large, since the addition (or removal) of one potentially metamorphic larva would have large effects on the forecast of metamorphosed lampreys.

As mentioned, this most often occurs in large streams, which are also expensive to treat with TFM. The control agents' approach to stream prioritization attempts to minimize the chance of the worst possible outcome (Morgan and Henrion 1990), which they view as the treatment of a stream when the forecast of metamorphosed lamprey abundance overestimates the true population. In these situations, the control agents subjectively balance the cost of treating a stream where few metamorphic lampreys exist against the risk of not treating the stream when the lampreys are truly there. This method of stream prioritization using a qualitative estimate of uncertainty in the model forecasts clearly indicates the need to acquire better information on which to base treatment decisions (Morgan and Henrion 1990).

One solution to these problems may be to collect more samples from the streams that contain the most uncertainty, thereby reducing the variability in the model forecasts as well as potentially increasing the accuracy of the estimate. However, with up to 100 streams requiring a quantitative estimate of lamprey abundance each year, increasing the number of samples is an expensive proposition.

Additional sampling of the streams with the highest uncertainty may be accomplished through the development of a more optimal allocation of sampling effort. The control agents know which streams will be quantitatively sampled prior to the sampling year. This list of streams usually contains streams that consistently produce high numbers of sea lampreys and are cost-effective to treat, as well as streams that have historically had uncertain abundance estimates and may require additional sampling each year. Developing a methodology to assess the productive streams more rapidly, such as a rapid, single-pass index of abundance on fewer sites per stream (Jones and Stockwell 1995, Lobon-Cervia and Utrilla 1993), would reduce the amount of time and effort required to determine the relative abundance of lampreys in the streams known to be cost-effective for treatment. The effort could then be used in streams that are expected to have a high degree of uncertainty in the estimates of lamprey abundance. This method of allocating sampling resources is only worthwhile if the additional sampling effort on streams with high output uncertainty improves the accuracy and precision of the estimates of larval and metamorphosed lamprey abundance.

The final analysis examines which of the input variables contributes most to output uncertainty and would be the most beneficial to calibrate within the model. An examination of the contribution of parameter uncertainty to output uncertainty can be misleading when there is uncertainty about the structure of the model and the accuracy of the outputs (Morgan and Henrion 1990). However, modeling is an iterative process (Pace 2001, Rykiel 1996), and calibrating those parameters that most affect output uncertainty could lead to more accurate and more precise model outputs.

Input uncertainty in the simulation model can be divided into two categories: uncertainty in the sampling data and uncertainty in the parameters within the model. I will first consider how these two categories affect the estimate of larval lamprey abundance. The explanations for the observed effect that reducing uncertainty in the model components has on the uncertainty in larval lamprey estimates are valid for the forecasts of metamorphosed lamprey abundance. Calibrating the model components that significantly influence the estimate of the larval lamprey population may be a significant step towards more accurate and precise estimates of potentially metamorphic lampreys.

Forcing the simulation model to select the same combination of sites for each iteration consistently reduced the variability in the estimates of larval and metamorphosed lampreys (Table 11, Table 12). This is likely due to correlation between the amount of habitat and the number of lampreys found at discrete access points within the stream. During the development of the backpack electrofishing protocol, this potential for longitudinal correlation was investigated using archival sampling data for U.S. streams (M. Fodale, U.S. Fish and Wildlife Service, Marquette, Michigan, personal communication). There was no evidence of longitudinal correlation of habitat, catch, or length of lampreys and the sampling location within a stream, which lead to the protocol assumption that random selection of access points would yield similar forecasts of metamorphosed lamprey production regardless of the location of the access points. The results of the simulation model conditioned on the site data indicate that there is a considerable amount of among-site variability in the sampling data, and the selection of access sites can influence the model outputs.

The influence of the site-specific data on the uncertainty in the estimates of abundance can be explained when one of three situations occurs within the data. Habitat is the most influential of the site-specific variables when there is a disparity between the relative abundance of Type 1 and Type 2 habitat among the sites. This occurs, for example, when the random selection of access sites selects a point that is associated with the estuary of a stream. Stream estuaries tend to have greater stream width, lower water velocities, and a higher proportion of Type 1 habitat than do the rest of the stream. The option of including (or not including) an estuarine site when resampling the data using the fully randomized model creates variability in the estimated amount of available larval habitat and the associated estimate of abundance.

Similar arguments exist for the influence of the catch and length information on model outputs. In those streams where the reducing the variability in the catch information reduces variability in the model outputs, there is at least one sample site where the number of lampreys collected differs considerably from the other sample sites. Similarly, in those streams where reducing variability in the length information reduces uncertainty in the forecasts of metamorphosed lamprey abundance, at least one electrofished plot contains a higher abundance of large lamprey larvae than do other electrofished plots in the data set. The influence of uncertainty in length data is discussed in more detail along with catchability later in this discussion.

If there were no within-site correlation among data at an access site, the nested resampling scheme would not be necessary. Length, plot, and habitat data could be randomly resampled without contributing additional variability to the estimates of lamprey abundance. In this case, the ESTR model approach of pooling the data to obtain estimates of mean habitat area and lamprey abundance would not affect the model outputs. However, as both the example using Club Creek data as well as the output of the model conditioned on the site variables shows, the selection of the access site and the catch and habitat data that accompany it are important to the model outputs. This relationship is further illustrated with an examination of the data for Proctor's Creek (Table 14), where conditioning the simulation model on the estimated amount of habitat results in an increased coefficient of variation of the estimates of larval and metamorphosed lampreys.

Table 14. Summary of the catch and habitat information for Proctor's Creek. Note that a higher proportion of the total catch is captured from Site 2, which contains a lower proportion of the available habitat. This results in higher estimates of larval lamprey density.

Site	Number of Plots	Total Catch	Proportion of Total Catch	Proportion of of Type 1 Area	Proportion of of Type 2 Area	Estimated Type 1 Density (#·m^{-2})
1	4	38	0.157	0.359	0.243	1.9
2	4	175	0.723	0.214	0.060	8.75
3	4	29	0.120	0.427	0.697	1.45

In the Proctor's Creek data, the catch from sample site 2 contained over 70% of the lampreys collected, while the habitat data for the site represents less than 20% of the estimated available habitat. The model conditioned on habitat ignores this correlation between habitat and catch at each site. Consequently, as many as 3 samples of catch data from site 2 can be incorporated into the density estimates without the correlated value for habitat area. This results in the highest density of lampreys being applied to areas of high habitat abundance within the model, when the association does not exist in the data. The range of estimates for larval and metamorphosed lampreys is greater in Proctor's Creek for the model conditioned on the habitat variable, resulting in increased variability in the model outputs and a higher coefficient of variation.

The examination of the driving variables in the simulation model shows that the variability in the estimates of larval and metamorphosed lamprey abundance is significantly reduced when the variability of the density of lampreys in Type 2 habitat is removed (Table 11, Table 12). This is not unexpected, as most tributaries to the Great Lakes, including the ones used in this study, have higher abundance of Type 2 habitat. Consequently, the proportion of lampreys in Type 1 habitat assigned to Type 2 habitat will significantly impact the estimates of lamprey abundance. The effect varies as the proportion of Type 2 habitat increases. In the Batchawana River and Crystal Creek, where the ratio of Type 2:Type 1 habitat area is 11.9 and 13.7 respectively, reducing the variability in the proportion of lampreys assigned to Type 2 habitat causes the largest reduction in variability in the estimates of larval lamprey abundance.

Notably, the reduction in variability in either catchability or length is not propagated through the model to the uncertainty around larval lamprey estimates. With respect to catchability, this is most likely due to the specification of the model, where the reduction in the variance of catchability is achieved by removing the influence of the variance-covariance matrix in the logistic model of electrofisher effectiveness. Since there is little variability around the logistic model it makes sense that removing this small source of uncertainty does not significantly reduce the uncertainty in the estimate of larval lampreys.

The effect of reducing the variability associated with randomly resampling the length data is also associated with the logistic model of sampling efficiency. Although the length of the lampreys captured will influence the iterative procedure in the logistic model, with smaller lampreys equating to a greater estimate of density, resampling the length information results in a relatively consistent length distribution. Resampling the length distribution within each sample plot does not contribute enough variability to propagate through the logistic model of electrofisher effectiveness and significantly influence uncertainty in estimates of larval lamprey abundance. The estimates of larval lamprey abundance are primarily influenced by the absolute abundance of the lampreys collected, not the size structure in the catch.

Conversely, the uncertainty in the forecasts of metamorphosed lampreys is sensitive to the parameters that affect the number of larvae of potentially metamorphic size. This includes the catch and habitat parameters that affect the estimate of larval abundance, and also includes length, growth and probability of metamorphosis parameters, that affect the estimated proportion of the catch that will metamorphose. For example, in the Batchawana River and Club and Crystal creeks, larvae greater than 100mm make up a small proportion of the total collection, and are contained within one or two electrofishing samples. The effect of resampling these data by first selecting the plot data and then resampling the length data can geometrically increase the number of large larvae in the simulation. When the variability in the simulation model is reduced by conditioning on length, the number of large larvae in the collection is significantly less variable, and results in more precise estimates of metamorphosed lampreys. Similarly, variation in the average daily growth rate will affect the number of larvae that are expected to be over 100mm at the end of the growing season. The specific model selected to estimate probability of metamorphosis will, in turn, affect the forecast of number of these larvae expected to metamorphose.

The analysis of the propagation of parameter uncertainty demonstrates that the contribution of one parameter to uncertainty in the model output may depend upon the value assigned to another parameter, or may be affected by the structure of the sampling data used as model inputs. This has been demonstrated for the hierarchy within the access point data used in this model. Although not done in this study, the effects of the co-dependency of additional parameters, such as between growth rate and probability of metamorphosis, can be explicitly modeled and examined, and may warrant further investigation in the reduction of uncertainty in ESTR model estimates (Warren-Hicks and Moore 1998, McKay 1995, Morgan and Henrion 1990).

The inclusion of a stream on the TFM treatment schedule is a decision process that balances the risks of treating a subset of streams to remove the parasitic lamprey population at the cost of not treating the remaining streams that will also produce parasitic lampreys. The ESTR model currently used by the control agents of the sea lamprey control program does not accurately forecast the abundance of either larval or metamorphosed sea lampreys, and is not adequate for the task of providing sound quantitative estimates as the basis for treatment decisions. To improve the accuracy of the ESTR forecasts the control agents must continue to develop their understanding of the processes that affect lamprey production, and use this improved understanding to refine the ESTR model parameters and underlying model structure. To do this, I recommend that the control agents begin by refining the sampling protocol and ESTR model structure to estimate larval lamprey abundance with a predetermined level of accuracy. This should be accompanied by methodologies that quantify the amount of uncertainty in the estimates, so that the potential consequences of treatment decisions can be assessed. Once a reliable model of larval lamprey abundance has been developed, the parameters to forecast the expected number of metamorphosed lampreys can be evaluated. By quantifying the uncertainty in the predictions as well as improving the accuracy of the ESTR model, uncertainty in stream treatment decisions can be better assessed and balanced against the ecological, social, and economic needs of Great Lakes fisheries management.

APPENDIX A

Specifications of the ESTR model used by the sea lamprey management program to predict metamorphosed sea lamprey abundance in Great Lakes tributaries.

1. Sample Allocation

The objective of the ESTR model is to use habitat and larval density data to forecast the number of larval and metamorphosed lampreys in Great Lakes tributaries the year after sampling. To meet this objective, a larval assessment sampling protocol has been established to formalize how the stream-specific habitat and larval density data are collected. The sampling protocol for backpack electrofishing specifies that information describing 12 habitat transects and 2 electrofishing plots be collected at 6 access points, such as road or trail crossings, in each stream. The 6 access points are selected randomly from a list of all available access points. When fewer than 6 access points are available, the number of habitat transects measured in the stream is reduced to 12 transects at each access point (e.g. 4 access points x 12 transects = 48 habitat transects). To ensure that an adequate number of larval lampreys are collected to describe the year-class structure of the larval population, the minimum number of electrofishing plots remains at 12. In the case where fewer than 6 access points are sampled, two electrofishing plots are assigned to each available access point, and the remaining plots are evenly distributed among the reduced number of access points. In the case of 5 access points, where the 12 electrofishing plots cannot be evenly divided among access points, the 2 remaining plots are randomly assigned to 2 of the 5 access points.

2. Habitat Estimates

Stream substrate is subjectively classified as one of three habitat types available to larval lampreys along 12 transects at each access point. Preferred larval habitat (Type 1) is found in depositional areas of the stream, where slower water velocity allows fine silt, sediments, and detritus to accumulate. Secondary larval habitat (Type 2) is composed of coarse sand and fine gravel, and is typically associated with higher water velocities. Type 3 habitat is composed of hardpan clay or bedrock, substrates that larval lampreys cannot burrow into.

Transects are located perpendicular to stream flow, and an observer measures the amount of each habitat type encountered along each transect. The transects are spaced at three mean stream widths if the stream is less than 5m wide, and at two mean stream widths if the stream is greater than 5m wide. The transects are used to calculate the area of each habitat type as:

$$H_i = \frac{\sum_{i=1}^{M} \sum_{j=1}^{2} T_{i,j}}{M} \cdot S_L \qquad \textbf{(A.1)}$$

where: H_i = area of stream that is habitat type j, j = 1 or 2;

$T_{i,j}$ = length of transect i that is habitat type j, in metres;

M = number of transects measured in stream; and

S_L = the measured length of the stream that contains sea lamprey larvae, in metres

3. Larval Lamprey Density Estimates

Larval lampreys are electrofished from 12 measured plots located in Type 1 habitat. The observed catch is adjusted by the estimated sampling efficiency for backpack electrofishing gear, and the number of lampreys in each plot is calculated as:

$$C_A = \frac{C}{q} \qquad \textbf{(A.2)}$$

where: C_A = observed catch adjusted for sampling effectiveness;

C = the number of lampreys collected from plot *k*;

q = 0.48, the estimate of sampling effectiveness calculated from the 1996-97 data from the initial electrofisher efficiency studies (unpublished data)

The mean density of sea lamprey larvae in the stream is calculated as the mean of the plot densities using the adjusted catch, as:

$$D_{\bar{x}} = \frac{\sum_{k=1}^{P}\left[\frac{C_k}{q \cdot a_k}\right]}{P} \qquad \textbf{(A.3)}$$

where: $D_{\bar{x}}$ = mean density;

C_k = the number of lampreys collected from plot k;

a_k = area of plot *k*;

P = the number of plots electrofished

4. The proportion of larval lamprey density in Type 1 habitat that is attributed to Type 2 habitat.

As mentioned in section A3, larval lampreys are sampled in Type 1 habitat. The density of larval lampreys in Type 2 habitat is estimated as a proportion of the gear-adjusted mean density estimated in Type 1 habitat, as:

$$R = 0.275 \qquad \textbf{(A.4)}$$

where: R = the proportion of larval lampreys in Type 1 habitat that is attributed to Type 2

The proportion, R, is the mean proportion of Type2/Type 1 lamprey densities from an independent study that examined larval lamprey density in both habitat types.

5. Estimate of larval lamprey population.

Habitat area, larval lamprey density, and the estimated proportion of lampreys in Type 2 habitat are used to estimate the larval sea lamprey population in each stream.

$$\hat{N}_i = \frac{\sum_{i=1}^{M} T_{i,1}}{M} \cdot \frac{\sum_{k=1}^{P} \left[\frac{C_k}{q \cdot a_k} \right]}{P} \cdot S_L + \frac{\sum_{i=1}^{M} T_{i,2}}{M} \cdot \frac{\sum_{k=1}^{P} \left[\frac{C_k}{q \cdot a_k} \right]}{P} \cdot S_L \cdot R \qquad \textbf{(A.5)}$$

where: $\hat{N}_l$ = the estimate of larval sea lamprey abundance, and other variables are as previously defined

6. Length of observed catch at end of growing season.

Lamprey larvae have been shown not to increase in length in the year of metamorphosis (Youson 1988, Potter 1980) and the total length of an ammocoete after growth has ceased is an indicator of metamorphic potential the following year. However, lamprey larvae used to forecast parasitic production are captured between April and October each year, while there is still time remaining in the season for larvae to grow. Since virtually all of the growth of larval lampreys occurs in the warmer months (Potter 1980), the control agents are required to estimate the length the larvae will be at the end of the growing season, typically late October to mid-November. For each stream, an average daily growth rate in $mm \cdot day^{-1}$ has been calculated from data for the first larval cohort re-established in the stream after TFM treatment. The approximate end of the larval lamprey growing season was estimated from climatic data, as the date when average daily air temperature drops below 5°C. To calculate the larval length at the end of the growing season, the product of the stream-specific average daily growth rate and the number of days from capture to the projected end of the larval growing season is added to the measured length at the time of capture. This 'final' length is used in the logistic equation to calculate probability of metamorphosis.

$$L_F = L_C + (D_F - D_C) \cdot G_D \tag{A.6}$$

where: L_F = length of lamprey larvae at the end of the growing season;

L_C = length of lamprey larvae at the time of capture;

D_F = date of the end of the growing season;

D_C = the date of sampling;

G_D = the average daily growth rate, in $mm \cdot day^{-1}$

7. Probability of metamorphosis.

Probability of metamorphosis is estimated from lamprey length and life-stage data collected from 106 TFM treatments between 1969 and 1996. Using this data, length-dependent logistic regression models were developed for 11 separate geographic regions around the Great Lakes (Table A1). Probability of metamorphosis is estimated for each individual larva as:

$$\Pr\{Met\} = \frac{1}{\left[1 + \exp^{-\left(\beta_o + \beta_1 \cdot L_F\right)}\right]} \tag{A.7}$$

where: Pr{Met} = the length-dependent probability of metamorphosis for a larva;

β0,β1 = parameter estimates for the regional logistic model

Table A1. Parameter estimates for length-dependent logistic models developed for 11 regions around the Great Lakes.

Geographic Region	β0	β1
Lake Ontario South Shore	0.201	-25.821
Lake Ontario/Lake Erie North Shore	0.267	-33.917
Lake Erie South Shore	0.299	-39.875
Lake Huron Main Basin & Georgian Bay (Can)	0.155	-23.636
Lake Huron North Channel (Can)	0.218	-30.596
Lake Michigan/Lake Huron North (U.S.)	0.163	-24.821
Lake Michigan/Lake Huron South (U.S.)	0.204	-29.075
Superior East (Can)	0.118	-16.591
Superior Central & West (Can)	0.122	-18.842
Lake Superior East (U.S.)	0.239	-34.484
Lake Superior West (U.S.)	0.233	-32.458

8. Proportion of catch that is expected to metamorphose.

The proportion of the electrofishing catch that is expected to metamorphose is used to infer the proportion of the estimated larval population that will metamorphose. The proportion of the catch that will metamorphose is equal to the sum of the probability of metamorphosis for each larva in the whole-stream collection divided by the total catch for the stream, and is estimated as:

$$C_M = \frac{\sum_{a=1}^{C_T}\left[\frac{(L_F)_a}{q_a} \cdot \Pr\{Met\}_a\right]}{C_T} \qquad \textbf{(A.8)}$$

where: C_M = the proportion of the observed catch expected to metamorphose;

$(L_F)_a$ = the final length of ammocoete a;

q_a = the plot-specific catchability of ammocoete a;

$\Pr\{Met\}_a$ = the length-dependent probability of metamorphosis of ammocoete a

C_T = the total number of lampreys collected from the stream

9. Expected number of metamorphosed lampreys one-year post-sampling.

The larval lamprey population estimate and the proportion of catch expected to metamorphose are used to forecast the expected number of metamorphosed lampreys the year after sampling, as:

$$\hat{N}_T = \hat{N}_i \cdot C_M \qquad \textbf{(A.9)}$$

$$= \left[\frac{\sum_{i=1}^{M} T_{i,1}}{M} \cdot \frac{\sum_{k=1}^{P} \left[\frac{C_k}{q \cdot a_k} \right]}{P} \cdot S_L + \frac{\sum_{i=1}^{M} T_{i,2}}{M} \cdot \frac{\sum_{k=1}^{P} \left[\frac{C_k}{q \cdot a_k} \right]}{P} \cdot S_L \cdot R \right] \cdot \frac{\sum_{a=1}^{C} \left[\frac{(L_F)_a}{q_a} \cdot \frac{1}{\left[1 + \exp^{-\left(\beta_o + \beta_1 \cdot L_F\right)} \right]} \right]}{C}$$

APPENDIX B

Derivation of the variance of the capture proportion in the backpack electrofishing effectiveness study.

Capture proportion p for each length increment i is estimated as:

$$\hat{p}_i = \frac{M_i}{\hat{N}_i} \qquad \textbf{(B.1)}$$

where: M_i = the electrofishing catch in increment i

$\hat{N}_i$ = estimated abundance of larvae in increment i

Lockwood et al. (1999, p15) derive the variance of a proportion as:

$$\text{var}\left(\frac{a}{b}\right) = \left(\frac{a}{b}\right)^2 \cdot \left[\frac{\text{var}(a)}{a^2} + \frac{\text{var}(b)}{b^2}\right] \text{ where a,b are independent} \qquad \textbf{(B.2)}$$

$$\therefore \text{var}(\hat{p}_i) = \left(\frac{M_i}{\hat{N}_i}\right)^2 \cdot \left[\frac{\text{var}(M_i)}{M_i^2} + \frac{\text{var}(\hat{N}_i)}{\hat{N}_i^2}\right] = \left(\frac{M_i}{\hat{N}_i}\right)^2 \cdot \left[\frac{\text{var}(\hat{N}_i)}{\hat{N}_i^2}\right] \qquad \textbf{(B.3)}$$

where: $\text{var}(\hat{N}_i) = \text{var}\left[\frac{(M_i+1)(C_i+1)}{R_i+1}\right]$, with M_i and C_i known, and R_i is Poisson

distributed for low values of R (Krebs 1999), so that:

$$\text{var}(\hat{N}_i) = [(M_i+1)(C_i+1)]^2 \cdot \text{var}\left(\frac{1}{(R_i+1)}\right) \qquad \textbf{(B.4)}$$

From B.2, $\operatorname{var}\left(\dfrac{1}{(R_i+1)}\right)=\left(\dfrac{1}{R_i+1}\right)^2\cdot\left[\dfrac{\operatorname{var}(1)}{(1)^2}+\dfrac{\operatorname{var}(R)}{(R_i+1)^2}\right]$ **(B.5),**

which simplifies to: $\operatorname{var}\left(\dfrac{1}{(R_i+1)}\right)=\dfrac{R}{(R_i+1)^4}$ **(B.6)**

$$\therefore \operatorname{var}(\hat{N}_i)=\left[(M_i+1)(C_i+1)\right]^2\cdot\frac{R}{(R_i+4)^4}=\hat{N}_i^2\cdot\frac{R}{(R_i+1)^2}$$

and $\operatorname{var}(\hat{p}_i)=\left(\dfrac{M_i}{\hat{N}_i}\right)^2\cdot\dfrac{(\hat{N}_i)^2\cdot\dfrac{R}{(R_i+1)^2}}{(\hat{N}_i)^2}$

$$=\frac{M_i^2\cdot\dfrac{R}{(R_i+1)^2}}{(\hat{N}_i)^2} \quad \textbf{(B.7)}$$

Appendix C. Plot data for the six study streams sampled to examine the sampling effectiveness of backpack electrofishing gear.

Site	Stream	Date	Electrofishing Catch (M)	Dredge Catch (C)	Recaptures (R)	Plot Area (m^2)	Conductivity (μmhos)	Temperature (°C)	Mean Depth (m)
1	Watson's	29-05-98	56	83	22	5	130	17.5	0.2
2	Watson's	02-06-98	13	42	12	5	75	10	0.3
3	Watson's	02-06-98	2	4	1	5	75	10	0.15
4	Watson's	04-06-98	91	126	64	5	70	10	0.15
5	Watson's	05-06-98	78	113	58	5	80	10	0.25
6	Watson's	05-06-98	50	74	31	5	80	10	0.6
7	Sturgeon	10-06-98	3	3	3	5	275	12	0.1
8	Sturgeon	11-06-98	4	3	3	5	280	14	0.3
9	Sturgeon	11-06-98	2	2	2	5	280	14	0.3
10	Sturgeon	12-06-98	4	4	4	5	280	15	0.2
11	Sturgeon	12-06-98	1	1	1	5	280	15	0.5
12	Sturgeon	13-06-98	1	1	1	5	290	15	0.4
13	Sturgeon	13-06-98	15	12	11	5	290	15	0.4
14	Sturgeon	13-06-98	10	11	9	5	290	15	0.2
15	Sturgeon	14-06-98	11	18	9	5	295	15	0.4
16	Sturgeon	14-06-98	16	17	11	5	295	15	0.3
17	Sturgeon	14-06-98	10	18	8	5	295	15	0.7
18	Sturgeon	15-06-98	13	13	11	5	300	15	0.3
19	Sturgeon	15-06-98	14	19	14	5	300	15	0.3
20	Sturgeon	15-06-98	17	15	10	5	300	15	0.3
21	Lynde	17-06-98	3	5	2	5	500	20	0.25
22	Lynde	17-06-98	1	2	1	5	500	20	0.1

Appendix C (continued)

Site	Stream		Electrofishing Catch (M)	Dredge Catch (C)	Recaptures (R)	Plot Area (m^2)	Conductivity (μmhos)	Temperature (°C)	Mean Depth (m)
23	Lynde	17-06-98	5	6	4	5	500	20	0.2
24	Lynde	18-06-98	2	2	1	5	495	19	0.4
25	Lynde	18-06-98	11	6	5	5	495	19	0.2
26	Lynde	19-06-98	7	7	3	5	500	20	0.2
27	Lynde	19-06-98	10	11	8	5	500	20	0.4
28	Lynde	21-06-98	3	5	2	5	550	21	0.35
29	Lynde	21-06-98	3	3	3	5	550	21	0.2
30	Lynde	22-06-98	7	8	7	5	550	21	0.25
31	Lynde	22-06-98	9	7	7	5	550	21	0.2
32	Lynde	23-06-98	9	13	7	4.9	550	21	0.25
33	Lynde	23-06-98	3	6	3	4.7	550	21	0.35
34	Lynde	23-06-98	2	4	2	5.1	550	21	0.35
35	Batchawana	02-07-98	30	30	14	5	50	19	0.6
36	Batchawana	02-07-98	50	79	41	5	50	19	0.2
37	Batchawana	03-07-98	55	45	37	5.1	50	19	0.4
38	Batchawana	03-07-98	27	25	21	5.1	50	19	0.35
39	Batchawana	06-07-98	46	48	32	5	50	19	0.4
40	Batchawana	06-07-98	36	66	32	5	50	19	0.2
41	Batchawana	07-07-98	29	45	20	5	50	18	0.6
42	Batchawana	07-07-98	16	27	13	5	50	18	0.7
43	Batchawana	08-07-98	41	65	32	5.1	49	20	0.75
44	Batchawana	08-07-98	26	57	14	5	49	20	0.8
45	Batchawana	09-07-98	26	43	18	5	50	20	0.6

Appendix C (continued)

Site	Stream		Electrofishing Catch (M)	Dredge Catch (C)	Recaptures (R)	Plot Area (m^2)	Conductivity (μmhos)	Temperature (°C)	Mean Depth (m)
46	Batchawana	09-07-98	38	54	26	5	50	20	0.4
47	Batchawana	14-07-98	47	70	39	5	56	21	0.55
48	Batchawana	14-07-98	48	66	39	4.95	56	21	0.4
49	Batchawana	15-07-98	56	55	43	4.5	55	22	0.25
50	Batchawana	15-07-98	91	92	58	5	55	22	0.45
51	Batchawana	16-07-98	28	25	16	4.95	55	21	0.45
52	Batchawana	17-07-98	77	101	60	4.95	52	20	0.6
53	Batchawana	17-07-98	70	90	49	5	52	20	0.5
54	Salem	06-08-98	56	251	41	4.9	440	19	0.15
55	Salem	06-08-98	12	29	11	4.5	440	19	0.15
56	Salem	06-08-98	33	61	31	5	440	19	0.1
57	Salem	07-08-98	29	114	26	5	440	18	0.3
58	Salem	07-08-98	35	48	27	5	440	18	0.25
59	Salem	09-08-98	43	82	31	5	455	19	0.2
60	Salem	07-08-98	18	44	14	5	440	18	0.45
61	Salem	08-08-98	43	109	33	4.96	440	18	0.3
62	Salem	08-08-98	31	84	27	5	440	18	0.3
63	Salem	08-08-98	31	59	27	4.8	440	18	0.4
64	Salem	08-08-98	16	24	13	5	440	18	0.25
65	Salem	09-08-98	6	49	3	4.95	455	19	0.4
66	Salem	09-08-98	14	36	12	4.95	455	19	0.5
67	Salem	10-08-98	5	12	5	4.5	462	20	0.25
68	Salem	10-08-98	13	32	11	4.88	462	20	0.25

Appendix C (continued)

Site	Stream		Electrofishing Catch (M)	Dredge Catch (C)	Recaptures (R)	Plot Area (m^2)	Conductivity (μmhos)	Temperature (°C)	Mean Depth (m)
69	Salem	10-08-98	32	74	29	4.88	462	20	0.25
70	Salem	10-08-98	23	22	16	4.88	462	20	0.15
71	Proctor's	11-08-98	3	5	3	5	470	20	0.35
72	Proctor's	11-08-98	7	8	6	5	470	20	0.25
73	Proctor's	11-08-98	2	3	2	5	470	20	0.4
74	Proctor's	12-08-98	3	5	2	5	460	17	0.25
75	Proctor's	12-08-98	1	2	1	5	460	17	0.4
76	Proctor's	12-08-98	4	9	4	5	460	17	0.2
77	Proctor's	12-08-98	4	8	3	5	455	17	0.3
78	Proctor's	13-08-98	16	27	14	5	455	17	0.4
79	Proctor's	13-08-98	13	12	9	5	455	17	0.2
80	Proctor's	13-08-98	15	12	7	5	455	17	0.15
81	Proctor's	13-08-98	18	18	13	5	442	16	0.2
82	Proctor's	14-08-98	18	26	17	5	442	16	0.2
83	Proctor's	14-08-98	6	12	5	5	442	16	0.35
84	Proctor's	14-08-98	29	24	19	5.1	442	16	0.2

Appendix D. Length and catch data for the six study streams sampled to examine the sampling effectiveness of backpack electrofishing gear.

Site	Stream	Length Increment	Electrofishing Catch (M)	Dredge Catch (C)	Recaptures (R)	Mean Length (mm)
1	Watson's	80	50	80	20	53.62
		100	6	3	2	86.17
2	Watson's	80	11	39	10	57.64
		100	1	1	1	93.00
		120	1	2	1	105.00
3	Watson's	80	2	4	1	70.00
4	Watson's	80	86	119	59	52.27
		100	3	4	3	92.67
		120	2	3	2	107.00
5	Watson's	80	76	110	56	52.46
		100	2	3	2	86.00
6	Watson's	80	47	70	28	55.79
		100	3	4	3	88.33
7	Sturgeon	80	1	1	1	73.00
		100	1	1	1	94.00
		140	1	1	1	135.00
8	Sturgeon	100	1	1	1	88.00
		120	3	2	2	110.33
9	Sturgeon	80	1	1	1	79.00
		120	1	1	1	101.00
10	Sturgeon	100	2	2	2	99.00
		120	2	2	2	111.50
11	Sturgeon	100	1	1	1	91.00
12	Sturgeon	120	1	1	1	101.00
13	Sturgeon	80	3	2	2	52.67
		100	9	6	6	92.11
		120	3	4	3	104.67
14	Sturgeon	100	7	7	6	96.86
		120	3	4	3	107.33
15	Sturgeon	80	1	2	1	42.00
		100	5	7	4	97.20
		120	3	7	2	110.33
		140	2	2	2	126.00
16	Sturgeon	100	16	17	11	93.81

Appendix D (continued)

Site	Stream	Length Increment	Electrofishing Catch (M)	Dredge Catch (C)	Recaptures (R)	Mean Length (mm)
17	Sturgeon	80	2	2	1	63.00
		100	6	14	6	92.83
		120	2	2	1	105.00
18	Sturgeon	80	1	2	1	63.00
		100	5	6	5	93.40
		120	7	5	5	108.14
19	Sturgeon	80	4	8	4	60.50
		100	4	4	4	89.00
		120	5	6	5	110.20
		140	1	1	1	122.00
20	Sturgeon	80	4	5	2	62.25
		100	6	6	5	89.83
		120	7	4	3	105.57
21	Lynde	80	3	5	2	63.00
22	Lynde	80	1	2	1	56.00
23	Lynde	80	3	4	2	60.67
		120	2	2	2	104.00
24	Lynde	80	2	2	1	68.50
25	Lynde	80	9	3	3	63.11
		140	2	3	2	134.50
26	Lynde	80	6	5	2	63.17
		120	1	2	1	104.00
27	Lynde	80	5	4	3	66.60
		100	1	1	1	90.00
		120	1	2	1	120.00
		140	2	2	2	133.50
		200	1	2	1	143.00
28	Lynde	80	3	5	2	66.67
29	Lynde	80	2	2	2	70.50
		140	1	1	1	127.00
30	Lynde	80	3	4	3	59.67
		100	2	2	2	87.50
		140	1	1	1	125.00
		200	1	1	1	141.00
31	Lynde	80	6	4	4	66.83
		140	3	3	3	131.00

Appendix D (continued)

Site	Stream	Length Increment	Electrofishing Catch (M)	Dredge Catch (C)	Recaptures (R)	Mean Length (mm)
32	Lynde	80	6	10	5	64.17
		100	1	2	1	95.00
		120	2	1	1	110.50
33	Lynde	80	2	5	2	68.50
		100	1	1	1	85.00
34	Lynde	80	1	3	1	63.00
		120	1	1	1	119.00
35	Batchawana	80	16	18	4	51.75
		100	9	7	6	89.44
		120	3	3	2	106.67
		140	2	2	2	123.50
36	Batchawana	80	24	54	18	64.71
		100	15	13	13	92.00
		120	4	6	4	111.25
		140	5	4	4	129.80
		200	2	2	2	158.50
37	Batchawana	80	25	18	14	50.12
		100	12	10	8	95.42
		120	10	8	7	106.10
		140	5	6	5	131.60
		200	3	3	3	154.33
38	Batchawana	80	19	19	15	60.95
		100	7	5	5	89.71
		140	1	1	1	132.00
39	Batchawana	80	35	35	21	46.80
		100	4	6	4	88.75
		120	4	4	4	107.00
		140	2	2	2	129.50
		200	1	1	1	157.00
40	Batchawana	80	22	52	20	59.36
		100	5	5	4	86.00
		120	4	5	4	111.75
		140	2	1	1	124.50
		200	1	1	1	166.00
		200	2	2	2	152.00

Appendix D (continued)

Site	Stream	Length Increment	Electrofishing Catch (M)	Dredge Catch (C)	Recaptures (R)	Mean Length (mm)
41	Batchawana	80	15	31	10	49.47
		100	8	10	7	91.00
		120	2	1	1	114.50
		140	2	2	1	130.00
		200	2	1	1	150.50
42	Batchawana	80	13	23	10	50.69
		100	3	4	3	85.67
43	Batchawana	80	24	45	17	46.00
		100	6	9	5	88.00
		120	3	3	3	110.00
		140	6	7	6	132.50
		200	2	1	1	147.50
44	Batchawana	80	15	46	6	52.27
		100	4	5	3	90.25
		120	1	1	1	107.00
		140	2	2	1	128.00
		200	4	3	3	160.75
45	Batchawana	80	18	34	11	45.00
		100	1	2	1	82.00
		120	2	3	2	116.00
		140	2	2	2	130.50
		200	3	2	2	165.33
46	Batchawana	80	24	41	16	52.38
		100	6	5	4	91.00
		120	4	2	2	111.50
		140	2	2	2	126.50
		200	2	4	2	160.50
47	Batchawana	80	27	47	23	61.19
		100	8	11	6	89.38
		120	3	4	3	110.67
		140	5	5	4	130.20
		200	4	3	3	149.00
48	Batchawana	80	37	51	29	62.24
		100	5	8	5	91.40
		120	3	4	3	108.33
		140	3	3	2	127.33

Appendix D (continued)

Site	Stream	Length Increment	Electrofishing Catch (M)	Dredge Catch (C)	Recaptures (R)	Mean Length (mm)
49	Batchawana	80	38	37	28	52.76
		100	7	8	7	89.00
		120	6	5	4	106.50
		140	5	5	4	128.40
50	Batchawana	80	64	75	45	57.00
		100	17	11	9	87.41
		120	3	2	1	106.00
		140	4	2	2	132.00
		200	3	2	1	148.67
51	Batchawana	80	14	16	8	56.86
		100	9	7	6	89.78
		120	5	2	2	114.60
52	Batchawana	80	41	61	32	55.10
		100	16	22	15	89.69
		120	12	12	8	111.83
		140	3	1	1	130.67
		200	5	5	4	156.00
53	Batchawana	80	45	63	30	59.84
		100	13	16	11	88.00
		120	6	7	4	111.50
		140	2	1	1	130.00
		200	4	3	3	146.00
54	Salem	80	40	221	27	53.13
		100	10	21	8	89.70
		120	2	4	2	112.00
		140	4	5	4	128.50
55	Salem	80	8	24	7	50.63
		100	2	3	2	92.50
		120	1	1	1	112.00
		140	1	1	1	135.00
56	Salem	80	32	59	30	48.38
		100	1	2	1	83.00
57	Salem	80	18	92	15	51.50
		100	6	14	6	91.83
		120	2	2	2	103.00
		140	1	3	1	138.00
		200	2	3	2	142.50

Appendix D (continued)

Site	Stream	Length Increment	Electrofishing Catch (M)	Dredge Catch (C)	Recaptures (R)	Mean Length (mm)
58	Salem	80	29	39	21	50.79
		100	2	4	2	98.00
		120	3	3	3	112.33
		140	1	2	1	137.00
59	Salem	80	29	52	17	48.00
		100	5	12	5	89.20
		120	4	7	4	107.25
		140	2	6	2	135.00
		200	3	5	3	148.67
60	Salem	80	6	29	3	55.83
		100	8	11	7	88.88
		120	4	4	4	106.25
61	Salem	80	22	78	16	52.27
		100	16	23	13	90.44
		120	3	5	2	101.67
		140	2	3	2	133.50
62	Salem	80	23	65	19	50.26
		100	4	11	4	91.25
		120	3	5	3	103.33
		140	1	3	1	127.00
63	Salem	80	21	49	21	48.71
		100	4	6	3	91.00
		120	4	2	2	104.50
		200	2	2	1	150.50
64	Salem	80	12	19	9	48.75
		100	1	2	1	94.00
		140	2	2	2	135.50
		200	1	1	1	162.00
65	Salem	80	6	49	3	46.17
66	Salem	80	8	25	6	55.25
		100	3	6	3	87.67
		120	2	3	2	113.50
		140	1	2	1	132.00
67	Salem	80	5	12	5	62.00

Appendix D (continued)

Site	Stream	Length Increment	Electrofishing Catch (M)	Dredge Catch (C)	Recaptures (R)	Mean Length (mm)
68	Salem	80	5	13	3	63.40
		100	2	7	2	97.50
		120	4	10	4	107.00
		140	2	2	2	126.50
69	Salem	80	21	43	19	65.05
		100	6	18	6	88.17
		120	4	11	3	110.75
		140	1	2	1	137.00
70	Salem	80	14	12	8	63.50
		100	6	6	5	91.50
		120	3	4	3	116.33
71	Proctor's	80	3	5	3	69.67
72	Proctor's	80	2	1	1	59.00
		100	3	3	3	86.00
		120	2	4	2	104.50
73	Proctor's	100	2	3	2	98.00
74	Proctor's	80	2	2	1	67.00
		100	1	3	1	96.00
75	Proctor's	100	1	2	1	96.00
76	Proctor's	80	1	5	1	70.00
		120	2	3	2	108.50
		140	1	1	1	128.00
77	Proctor's	100	4	8	3	89.75
78	Proctor's	80	5	9	3	63.60
		100	8	14	8	92.00
		120	1	1	1	111.00
		140	1	2	1	121.00
		200	1	1	1	149.00
79	Proctor's	80	6	4	3	58.50
		100	7	8	6	89.71
80	Proctor's	80	10	6	4	59.40
		100	4	5	2	94.00
		140	1	1	1	135.00
81	Proctor's	80	8	8	4	59.88
		100	7	7	6	93.86
		120	3	3	3	107.67

Appendix D (continued)

Site	Stream	Length Increment	Electrofishing Catch (M)	Dredge Catch (C)	Recaptures (R)	Mean Length (mm)
82	Proctor's	80	13	19	12	56.00
		100	2	3	2	85.50
		120	1	2	1	111.00
		140	2	2	2	134.00
83	Proctor's	80	1	4	1	54.00
		100	1	2	1	98.00
		140	3	5	2	135.67
		200	1	1	1	141.00
84	Proctor's	80	18	12	10	57.11
		100	4	5	4	92.25
		120	6	6	4	107.17
		200	1	1	1	149.00

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