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Development and Evaluation of a New Predictive Model for Metamorphosis of Great Lakes Larval Sea Lamprey (*Petromyzon marinus*) Populations

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ABSTRACT. *Accurate forecasts of the number of larval sea lamprey* (Petromyzon marinus) *within a stream that will enter into metamorphosis are critical to currently used methods for allocating lampricide treatments among streams in the Great Lakes basin. To improve our ability to predict metamorphosis we used a mark-recapture technique, involving the marking of individual larval lamprey with sequentially coded wire tags, to combine information regarding individual and stream level parameters collected in year t, with direct observations of metamorphic outcome of lamprey recaptured in year t+1. We used these data to fit predictive models of metamorphosis. The best model demonstrated excellent predictive capabilities and highlighted the importance of weight, age, larval density, stream temperature and geographic location in determining when individual lamprey are likely to transform. While this model was informative, it required data whose measures are not practical to obtain routinely during the larval sea lamprey assessment program. A second model, limited to data inputs that can be easily obtained, was developed and included length of larvae the fall prior to metamorphosis, stream latitude and longitude, drainage area, average larval density in type-2 habitat, and stream lamprey production category (a measure of the regularity with which treatments are required). This model accurately predicted metamorphosis 20% more often than current models of metamorphosis; however, we recommend further validation on an independent set of streams before adoption by the Great Lakes Fishery Commission for ranking streams.*

INDEX WORDS: *Sea lamprey control,* Petromyzon marinus, *metamorphosis, predictive model.*

INTRODUCTION

The invasion of the Great Lakes by the parasitic sea lamprey (*Petromyzon marinus*) and the subsequent impacts on both fish populations and the ecosystem as a whole have been well documented (Smith and Tibbles 1980, Pearce *et al.* 1980, Christie and Goddard 2003). Since 1958, the lampricide 3-trifluoromethyl-4-nitrophenol (TFM) has been used by the Great Lakes Fishery Commission (GLFC) to reduce the abundance of sea lampreys in Great Lakes streams, resulting in a significant reduction in overall sea lamprey abundance in the Great Lakes (Smith and Tibbles 1980). Owing to the fact that the larval stage lasts several years (Manion and Smith 1978), it is neither necessary nor cost-effective to treat all sea lamprey producing streams with TFM every year. Effective lampricide control, therefore, requires choices to be made about which streams to treat each year. The logistics of the sea lamprey management program dictate that information for these choices be gathered 1 year prior to the anticipated year of stream treatment. Specifically, it is important to know what the sea lamprey production is in a given stream and what proportion of the sea lamprey population pre-

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sent is likely to undergo metamorphosis and enter the Great Lakes as parasitic-phase sea lampreys the following year. In this paper we develop an empirical model of metamorphosis and discuss why it might provide a preferred alternative to the current methods for predicting metamorphosis.

Methods used to select streams for treatment have changed considerably since the beginning of the lampricide program. Initially, subjective decisions about the treatment of streams were made based on the observed presence or absence of substantial numbers of large larvae during stream sampling. In 1982, the GLFC initiated a program of integrated sea lamprey management (IMSL), which among other things called for a more objective approach to balancing the benefits and costs of control alternatives (Sawyer 1980). Adoption of this approach led to the need for a more rigorous quantitative method to determine the sea lamprey population in streams and thus the potential benefit of stream-level control decisions. In 1995 the GLFC adopted a quantitative assessment survey (QAS) and stream ranking methodology, which combines survey data on larval density and habitat with predictive models of growth and metamorphosis to forecast the number of parasitic-stage lampreys that will leave a stream the following year. Streams are selected for lampricide treatment based on this estimate of parasitic escapement relative to the cost of stream treatment.

Metamorphosis in larval sea lampreys comprises a change in both physical form and behavior; from blind, burrowing, filter-feeding ammocoetes to eyed, free-swimming juveniles that are predators on teleost fish (Youson 2003). The models that are currently used to forecast when metamorphosis is likely to occur were developed by collecting and measuring lengths of larvae and recently metamorphosed juveniles (transformers) during lampricide treatments. Estimates of stream-specific average daily growth were used to predict the length of sea lamprey larvae from the year of collection to their estimated length at the end of the previous year, while for transformers it was assumed that no growth in length would have occurred. This latter assumption was justified by research suggesting that larval sea lamprey enter a period of arrested somatic growth prior to entering into metamorphosis, instead directing energy intake to build up lipid reserves (Potter 1980, Holmes and Youson 1997). Logistic regression was then used to fit models to these data to forecast the length-dependent probability of metamorphosis in the following year. At present, two regional models are used to predict metamorphosis in the Great Lakes (Hansen *et al.* 2003); one for the upper lakes (Lakes Huron, Michigan, and Superior) and one for the lower lakes (Lakes Ontario and Erie). Although these models were developed from the best data available at the time, the assumptions that growth is constant throughout the larval phase, that animals enter into an arrested growth phase prior to metamorphosis, and that length is the only critical factor in determining the onset of metamorphosis, contribute substantial uncertainty to our ability to select the most appropriate streams for treatment (Steeves 2002).

An independent review of the assessment and stream ranking process (Hansen *et al.* 2002) identified length-based probability of metamorphosis models as a major source of uncertainty that currently limits confidence in the selection of streams for treatment. Collections made at the time of lampricide treatment, as well as numerous field and laboratory studies, have documented that length at metamorphosis can be highly variable both among and within streams from year to year (Manion and Stauffer 1970, Purvis 1980, Morkert *et al.* 1998). Previous research has suggested that individual- and population-level variables such as sex, age, and larval density, along with stream-level environmental parameters such as temperature, stream location, and water chemistry characteristics may affect growth and/or metabolism in such a way as to introduce variability over both space and time in rates of metamorphosis (Morman 1987, Murdoch *et al.* 1992, Rodriguez-Munoz *et al.* 2003). Near the end of the larval phase, somatic growth tends to decrease as metabolism shifts to the accumulation of lipids (Lowe *et al*. 1973, Youson *et al*. 1979). Potter (1980) documented an increase in lipid content of larval sea lampreys from approximately 4%, up to 14% prior to the onset of metamorphosis. This phase of reduced growth complicates the use of length as the sole predictor of metamorphosis, because two groups of lampreys in different stages of development may exist in a single length-class: those that recently attained that size, and those that attained their size earlier, and have shifted from somatic growth to the accumulation of lipids (for review, see Youson 2003).

Accurate measures of lipid content in fishes have until recently required lethal sampling, which eliminates the ability to observe the individual's metamorphic fate and thereby empirically establish the link between lipids and the onset of metamorphosis. Other models of metamorphosis have attempted to account for this stage of lipid accumulation by using various measures of condition (e.g., Fulton's condition factor = weight/length^3 × 10^6) (Holmes *et al.* 1994, Henson *et al.* 2003). Unfortunately, there is often an inverse relationship between lipids and water content in fishes, and thus increases in lipid content are not necessarily reflected in proportional increases in mass or condition (Youson *et al.* 1993, Holmes and Youson 1994, Jonas *et al.* 1996). While hormonal and metabolic studies have illustrated the utility of condition factor in predicting metamorphosis in close proximity to the event (Youson 2003), these models have not performed well at predicting metamorphosis many months in advance, as is required to rank streams for lampricide treatment (Treble 2006).

The objective of this study was to develop a predictive model of metamorphosis in larval sea lampreys based on direct measurements of individual lamprey and stream-specific characteristics. Because previous research has emphasized the importance of lipid accumulation in preparing larvae for metamorphosis, this study incorporated direct, non-invasive estimates of lipid content in addition to other biotic and abiotic variables. By combining individual mark-recapture data with stream- and year-specific measures of temperature and water chemistry parameters, our goal is to explain some of the variation associated with metamorphosis in Great Lakes sea lamprey populations. Our overall objective was to improve our ability to predict metamorphosis and thus more accurately rank streams for lampricide treatment.

METHODS

Our approach, following methods established by Hollett (1998), was to collect and individually mark large sea lamprey larvae from several Great Lakes streams where lampricide treatment was anticipated for the following year. Suitable streams were selected through consultation with both United States Fish and Wildlife Service (USFWS) and Department of Fisheries and Oceans Canada (DFO) sea lamprey biologists, who identified streams with abundant populations of large sea lamprey larvae (length > 100 mm) that would be suitable candidates for a fall lampricide treatment the following year. Eight streams were selected from across the Great Lakes basin (Fig. 1) that fit these criteria, as well as providing contrast in geographic location, water chemistry, and larval densities.

In late summer of 2003, larval sea lampreys measuring > 100 mm were collected from Bowmanville Creek, Little Sandy Creek, and Pancake River, using ABP-2 DC backpack electrofishing gear (University of Wisconsin Engineering Technical Services, Madison, WI). Animals were anaesthetized using clove oil, measured for length (± 1 mm), weight (± 0.01 g), and scanned for total body electrical conductivity (TOBEC) using an EM-Scan Model SA-3000 Small Animal Body Composition Analyzer (EM-Scan Inc., Springfield, IL, 62704-5026). TOBEC provides a non-invasive index of lipid content based on the electrical impedance created when an individual is placed within a low-frequency electrical field (Piasecki *et al.* 1995, Scott *et al.* 2001, Treble 2006). Following the methodology described by Bergstedt *et al.* (1993), larval lampreys were injected with an individually identifiable coded wire tag (CWT, Northwest Marine Technology, Shaw Island, WA, USA) and released back into their natal stream. The same procedure was used in 2004 on larvae from Ceville Creek, Juniata Creek (tributary to Cass & Saginaw Rivers), Silver Creek, Root River, and Crystal Creek. In both years, following the release of tagged larvae, temperature loggers (HOBO Water Temp Pro, Onset Computer Corporation, Pocasset, MA, USA) were installed within the release area and set to record water temperature every 4 hours.

The year following marking, streams were visited in late August to mid October during a scheduled lampricide treatment. Using long handled scap nets, crews collected dead and dying larval and metamorphosing sea lamprey throughout the study section of stream, from the uppermost point where marked animals were released, to the downstream limit of wadable water. Drift nets were also placed at suitable points throughout the study area to collect dead and dying animals as they drifted downstream with the lampricide block. After the treatment was completed, collections of lampreys were scanned for the presence of CWTs, using a Northwest Marine Coded Wire Tag V-Detector, and lampreys containing a CWT were measured for length and weight, and then frozen individually for transport back to the lab. A complete summary of marked and recaptured lamprey from the eight study streams is provided in Table 1.

Averages of alkalinity, pH, and conductivity measurements were calculated from water chemistry records of both current and prior lampricide treatments. Temperature loggers were retrieved following treatments and the data downloaded. In two instances, loggers were lost, so temperature data

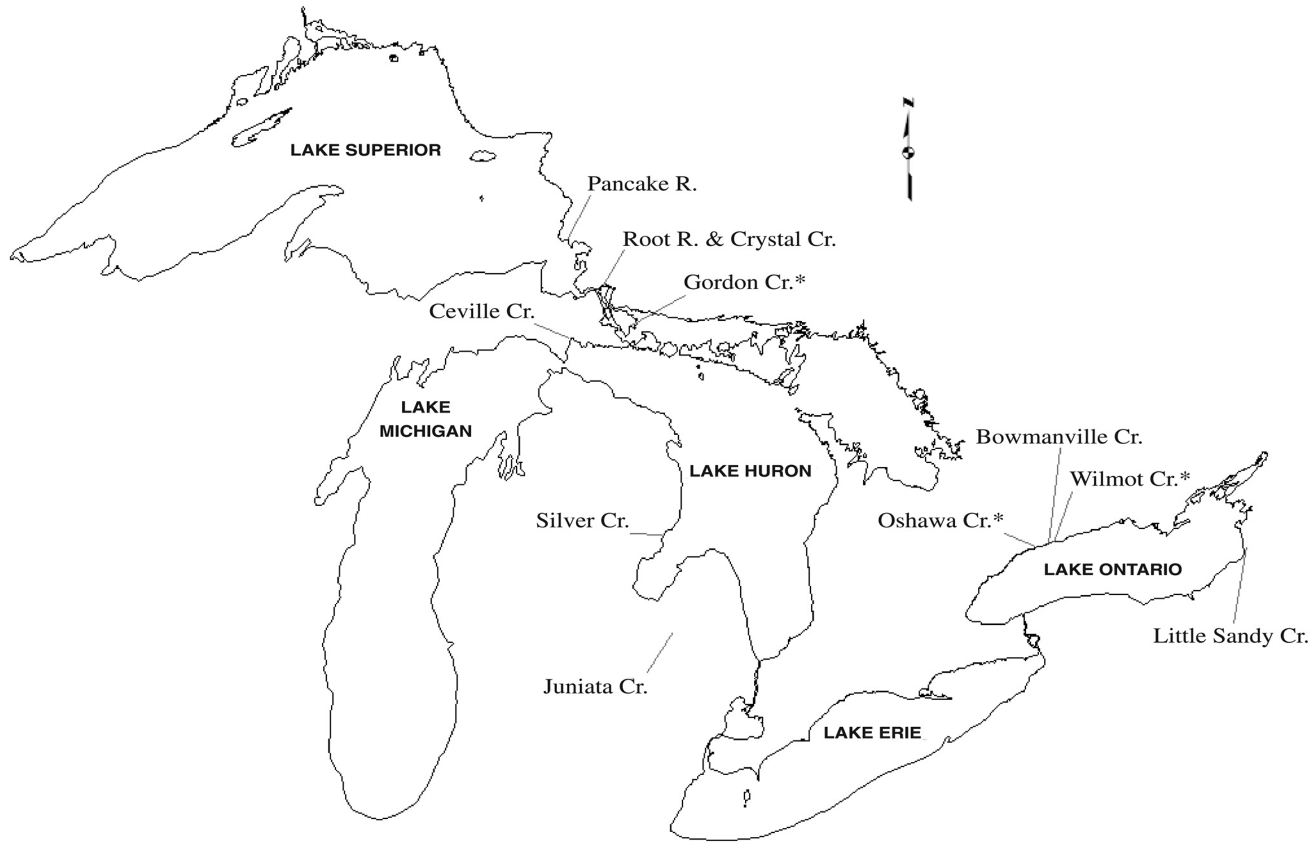

FIG. 1. Location of the eight study streams selected for this study within the Great Lakes basin. * indicates the locations of streams added to the management model dataset from Hollett (1998).

TABLE 1. Number of marked and recaptured sea lamprey larvae by stream, including the year of marking and total numbers.

Stream	Lake	Total Marked	Number Recaptured	Larvae	Transformers	Recapture Rate
Pancake River[1]	Superior	144	10	4	6	6.9%
Bowmanville Cr.[1]	Ontario	344	50	12	38	14.5%
Little Sandy Cr.[1]	Ontario	121	22	11	11	18.2%
Root River[2]	Huron	254	11	6	5	4.3%
Crystal Creek[2]	Huron	170	15	13	2	9.4%
Silver Creek[2]	Huron	182	40	37	3	22.0%
Juniata Creek[2]	Huron	168	37	34	3	22.0%
Ceville Creek[2]	Michigan	142	27	25	2	19.0%
Totals		1,525	212	143	70	13.9%

[1] denotes streams with larvae marked in 2003 and recaptured during lampricide treatments in 2004.
[2] denotes streams with larvae marked in 2004 and recaptured during lampricide treatments in 2005.

from nearby streams were used as surrogates. On the Root River, temperature data from a logger installed in a tributary, Crystal Creek, was used, and on Little Sandy Creek, data were obtained from two nearby streams and the average of the two daily temperature values was used (Fisheries and Oceans Canada, Sea Lamprey Control Centre, unpublished data).

Based on larval assessment and treatment data from the lamprey control program, estimates of the average larval density in type-1 (optimal) and type-2 (satisfactory) habitat (Dustin *et al.* 1989, Slade *et al.* 2003), along with the number of years since each stream was last treated, were added to the list of the variables examined. Streams were also categorized based on the regularity with which they are treated, and this was added as a categorical variable. Category one streams tend to have regular treatment intervals and consistent recruitment after treatment, whereas category three streams exhibit irregular treatment and lamprey production cycles; category two streams are intermediate between these two extremes (Anderson 2007). The geographic location of each stream mouth (latitude/longitude (decimal degrees)) and the size of its drainage area (ha) were obtained from the Sea Lamprey Control Centre's GIS database. A complete list of stream-level characteristics for each stream used in this study is presented in Table 2.

Laboratory Methods

Tags were retrieved from recaptured lamprey by scanning each larva with a V-notch detector and continuously sectioning each tagged lamprey until the tag was found. Tags were cleaned, mounted between two magnetic brass pencils, and read using a stereoscopic dissecting microscope. Tag numbers, age, gender, and developmental stage of each recaptured animal were matched with measurements taken on the same individual when they were marked and released the previous year.

The age of recaptured lampreys was determined by extracting the statoliths following procedures described in Hollett (1998). Extracted statoliths were stored in a multiwell plate containing immersion oil for a period of 10–15 days, to improve the transparency and clarity of the annuli before being mounted to numerically coded slides using a small amount of Crystal Bond™ adhesive. Statoliths were aged by three people, using a compound microscope, without prior knowledge of the life stage, source stream, or previous age assignments. The interpreted ages were then compared; for 33 lampreys there was no agreement among readers, so these individuals were removed from further analysis.

The sex of recaptured lampreys was determined following procedures described by Docker and Beamish (1994). Portions of recaptured lampreys were cross-sectioned while frozen and microscopically examined for the presence of ovaries. The remaining portion of the lamprey was fixed in a 10% formalin solution for later independent verification. Where the state of the specimen precluded the determination of sex (n = 11), the animal was removed from the dataset. Estimates of pre-metamorphic lipid weight and percent body lipids were generated using empirical models developed specifically for larval sea lamprey (Treble 2006), that combine larval condition factor and TOBEC measurements (taken at the time of marking) to provide an estimate of lipid weight.

Data collected from temperature loggers were used to generate several possible explanatory temperature variables. For each stream, the number of days within a suitable temperature range for metamorphosis (9–25°C) (Holmes and Youson 1998), the number of days within 2°C of the optimal temperature for metamorphosis (21°C) (Holmes and Youson 1998), the average temperatures for each of the 3 months leading up to the onset of metamorphosis (April, May, June), and the overall mean annual temperature were calculated. A measure of the spring warming rate was also included, calculated as the average daily increase in water temperature, starting when streams reached the lower thermal limit of 9°C, and ending when the stream was within 2°C of the suggested optimal temperature for metamorphosis (as some streams did not reach 21°C) (Holmes and Youson 1998).

Statistical Methods

We used a best-subsets multiple logistic regression technique (Statistica Version 7, StatSoft Inc., Tulsa, OK, USA), with the developmental fate of individual sea lamprey (larvae versus transformer) as the dependent variable, to compare among models with different sets of independent variables. Corrected Akaike's Information Criterion (AIC_C) values were used to compare models, as sample size relative to the number of possible parameters was low (Burnham and Anderson 2004). Because AIC_C values could only distinguish between models differing by more than a value of two, variance inflation factor (VIF) was used to remove models that

TABLE 2. Summary of stream-specific characteristics used in the development of the biological and management-based models.

	Pancake River	Root River	Crystal Creek	Silver Creek	Juniata Creek	Ceville Creek	Bowmanville Creek	Little Sandy Creek	Gordon Creek*	Oshawa Creek*	Wilmot Creek*
Lake Basin:	Superior	Huron	Huron	Huron	Huron	Michigan	Ontario	Ontario	Huron	Ontario	Ontario
Stream Characteristics											
Drainage Area (ha)	11,219	13,132	1,508	3,097	2,389	383	15,964	4,184	1,500	12,800	10,800
Latitude (dd.dd°)	46.96	46.54	46.56	44.35	43.41	46.00	43.89	43.64	46.15	43.87	43.90
Longitude (dd.dd°)	84.66	84.21	84.24	83.49	83.49	84.36	78.66	76.17	83.89	78.82	78.60
Alkalinity†	15.3	21.6	22.3	140.1	203.3	197.6	202.4	50.6	41.6	230.1	216.3
Conductivity†	30	98	40	280	466	250	370	110	95	487	95
pH†	7.1	7.2	7.3	8.3	8.2	7.9	8.3	7.7	7.5	8.4	8.3
Stream-level Lamprey Characteristics											
Average Type-1 Density (#/m^2)†	2.66	1.36	2.60	23.59	0.22	6.63	6.98	6.27	0.28	3.15	2.83
Average Type-2 Density (#/m^2)†	0.76	1.24	5.33	12.92	0.08	1.67	2.43	5.20	0.02	2.35	0.37
Lamprey Production Category†	1	1	1	1	2	3	1	1	3	1	1
Last TFM Treatment (Years)†	6	6	2	5	7	5	3	3	4	3	3

† Unpublished data, Sea Lamprey Control Centre, 1 Canal Drive, Sault Ste. Marie, ON
* Streams added from Hollett (1998) for management model development

TABLE 3. Results of Analysis of Variance (ANOVA) for differences in (A) length at the time of marking and (B) weight at the time of marking, between larval and metamorphosed sea lamprey from eight different streams.

(A) ANOVA Table (Dependent variable = Length)

Source	Effect	SS	DF	MS	F	Pr > F
Intercept	Fixed	1095034	1	1095034	3078.253	< 0.0001
Stream	Random	4338	7	620	6.475	< 0.0001
Larvae/Transformer	Fixed	6052	1	6052	63.230	< 0.0001
Sex	Fixed	92	1	92	0.962	0.3282
Error		15123	158	96		

(B) ANOVA Table (Dependent variable = Weight)

Source	Effect	SS	DF	MS	F	Pr > F
Intercept	Fixed	551.522	1	551.522	549.791	< 0.0001
Stream	Random	11.462	7	1.637	4.326	0.0002
Larvae/Transformer	Fixed	27.624	1	27.624	72.982	< 0.0001
Sex	Fixed	0.518	1	0.518	1.368	0.2440
Error		59.804	158	0.379		

contained highly correlated variables from the list of possible models. Model averaging was also used to develop a model that was a hybrid of the top models (Burnham and Anderson 2004). Given the large number of potential variables involved (n = 21), a Principal Components Analysis (PCA) was also performed to see if a less redundant, more parsimonious model would have improved predictive capabilities over the other models. The Kappa statistic (κ) (Cohen 1960) was used to select the final model, based on a confusion matrix (Manel *et al.* 2001). Parameters for the final model were then estimated using a mixed-effects generalized linear model with stream as a random effect.

Once the top model was selected, its ability to predict metamorphosis in larval sea lampreys was compared with that of two metamorphic models in common use, also using the Kappa statistic. These two models were: (1) the two-region length-based probability of metamorphosis model currently used by the GLFC in the empirical stream treatment ranking (ESTR) software (Christie *et al.* 2003); and (2) a minimum criteria (MC) model, which sets minimum thresholds for length, weight, and condition factor before metamorphosis is predicted to occur (Holmes and Youson 1994, Holmes *et al.* 1994, Hollett 1998, Henson *et al.* 2003). The number of correct transformer predictions, the number of correct predictions overall (of both larvae and tranformers) and the Kappa statistic were all used to compare the performance of each model relative to the other two.

Because one purpose of this study was to develop a model that could be used within the framework of the Great Lakes Fishery Commission's stream ranking process, a second model analysis was performed to develop a management-oriented model, following the same procedures as described above. In this analysis, the suite of variables used was limited to those that could be readily collected by field staff over the course of the field season. Additional stream-specific data were obtained from a similar mark-recapture study that was performed in 1995/1996 (Hollett 1998), allowing for the combination of these two data sets and providing an increase in both the number of streams and the overall number of observations with which to develop the management model.

RESULTS

General Findings

Recaptured lampreys that entered into metamorphosis were significantly longer and heavier in the fall (at the time of marking) than those that did not (Table 3), with significant differences in the average size of both larvae and transformers from different streams. There was not a significant difference in size (either length or weight) between male and female larvae or transformers (Table 3). There was a significant trend for the growth of larvae to be greater in southern and eastern streams of the basin ($r = -0.26$, $p < 0.0001$, $N = 212$ for both latitude and longitude) and in streams with higher pH values ($r = 0.22$, $p < 0.01$, $N = 212$). Of the eight temperature

TABLE 4. Model selection results for the biological model.

Model variables	df	AICc	Percent Overall Correct	Percent Larvae Correct	Percent Transformers Correct	Kappa Statistic
W / A / OT / Lat / Lon / T2	5	68.98	92.86%	96.75%	82.22%	0.8126
W / A / OT / pH / Lon / T2	5	68.30	92.26%	95.93%	82.22%	0.7984
W / A / OT / Con / Lon / T2	5	68.72	92.26%	95.93%	82.22%	0.7984
W / A / OT / pH / Lon / T1	6	68.78	92.26%	95.93%	82.22%	0.7984
W / A / Con / DA / Lon	5	68.96	92.26%	95.93%	82.22%	0.7984
W / A / MT / DA / Lon	6	68.37	92.26%	96.75%	80.00%	0.7955
W / A / Con / DA / LT	6	69.00	92.26%	96.75%	80.00%	0.7955
W / A / Lat / T2 / Cat	5	68.42	91.67%	95.12%	82.22%	0.7845
W / A / MT / DA / Lon / T1	7	68.67	91.67%	95.12%	82.22%	0.7845
W / A / DA / Lon / LT	6	68.52	91.67%	95.93%	80.00%	0.7814
W / A / OT / Con / Lon / T2 / Sx	5	68.54	91.67%	95.93%	80.00%	0.7814
W / A / Apr / May / DA / LT	6	68.76	91.67%	95.93%	80.00%	0.7814
W / A / Jun / DA / LT	6	68.87	91.67%	95.93%	80.00%	0.7814
W / A / OT / Alk / Lon / T1	5	68.92	91.67%	95.93%	80.00%	0.7814
W / A / SWT / DA / LT	5	68.96	91.67%	95.93%	80.00%	0.7814
W / A / DA / LT	4	67.07	91.67%	96.75%	77.78%	0.7782
W / A / Con / DA / Lon / LT	7	68.60	91.07%	95.12%	80.00%	0.7674
W / A / OT / Lat / Lon / T2 / Sx	6	68.61	91.07%	95.12%	80.00%	0.7674
W / A / ST / Lon / T1	6	68.67	91.07%	95.12%	80.00%	0.7674
W / A / DA / LT / ADG	6	69.04	91.07%	95.12%	80.00%	0.7674
W / A / OT / DA / LT	5	69.05	91.07%	95.12%	80.00%	0.7674
W / A / May / DA / LT	5	69.07	91.07%	95.12%	80.00%	0.7674
W / PLP / A / DA / LT	5	69.04	91.07%	95.93%	77.78%	0.7640
W / A / ST / Lon / T1 / Sx	6	68.52	90.48%	94.31%	80.00%	0.7537
W / A / MT / Lon / T1	6	68.94	90.48%	94.31%	80.00%	0.7537
W / A / OT / Lon / T1	5	68.11	90.48%	95.12%	77.78%	0.7501
W / A / DA / LT / Sx	5	69.05	90.48%	95.12%	77.78%	0.7501
PLW / A / DA / LT	5	69.01	89.29%	94.31%	75.56%	0.7189
W / A / pH / DA / Lon / LT	4	69.03	89.29%	94.31%	75.56%	0.7189

Where:
W = Weight (g)
A = Age (years)
Sx = Sex of lamprey
PLW = Predicted Lipid Weight (g)
PLP = Predicted Lipid (Percent of wet body weight)
Lat = Latitude (decimal degrees)
Lon = Longitude (decimal degrees)
DA = Stream drainage area (km^2)
Con = Conductivity (S/cm)
Alk = Alkalinity($CaCo_3$/mg)
pH = pH of stream (measure of acidity)
LT = years since last treatment
Cat = Stream Lamprey Production category
T1 = Average larval density in Type-1 habitat
T2 = Average larval density in Type-2 habitat
ADG = Avererage Daily Growth (mm)
ST = Suitable Temperature (between 9 and 25°C)
OT = Optimal Temperature (between 19 and 23°C)
MT = Mean Annual Temperature (°C)
Apr = Average stream temperature in April (°C)
May = Average stream temperature in May (°C)
Jun = Average stream temperature in June (°C)
SWT = Spring Warming Trend (slope of the line showing increase in temperature over time)

parameters explored in this analysis, only the average temperatures during May and June were significantly related to growth on the set of streams in this study (May: $r = 0.19$, $p < 0.05$; June: $r = –17$, $p < 0.05$). Growth rates of category one and two streams, while not significantly different from one another, were significantly higher than growth rates from category three streams (one-way ANOVA, $F_{2, 209} = 6.035$, $p = 0.003$).

Biological Model Analysis

The number of lampreys available for the development of the biological model analysis was reduced from the original 212 recaptures to 168,

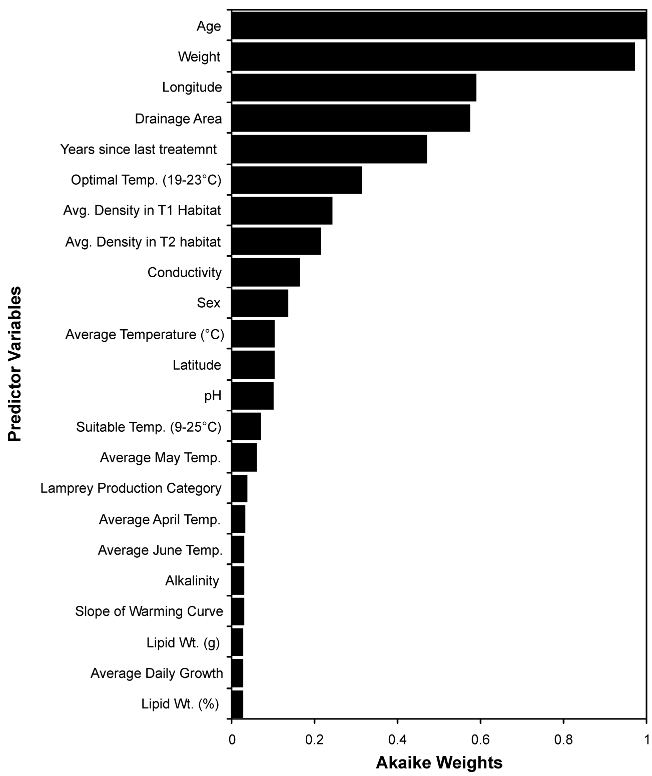

FIG. 2. Relative importance, based on Akaike weights, of predictor variables from the list of 26 top biological models for the prediction of metamorphosis. Age, with a weight of one, was the only predictor variable to be found in each one of the top models.

because reliable estimates of age or sex could not be determined for 44 larvae. The best-subsets model selection procedure, using the full suite of variables, produced a list of 29 potential models, all with AIC_C values differing by less than two (Burnham and Anderson 2004). The use of principal components to identify independent variables did not improve model fit.

Since AIC_C values alone were not able to identify a single best model, the ability to correctly predict the occurrence of metamorphosis in individual lamprey and the kappa statistic were added to the selection criteria, resulting in the selection of a model that contained a measure of lamprey weight and age, as well as the stream-level effects of stream latitude, longitude, average larval density in type-2 habitat, and the number of days where the water temperature was between 19 and 23°C. This model correctly predicted the fate of 92.9% of the recaptured animals, and 82.2% of those that underwent metamorphosis (Table 4). The kappa statistic value for this model was 0.8126, which indicates nearly perfect agreement (Landis and Koch 1977).

Model averaging was utilized to develop a hybrid model from the list of potential models, but the resulting composite model exhibited poor kappa values and could not consistently differentiate from streams with different rates of metamorphosis. The resulting Akaike weights, however, were useful in illustrating variables important to metamorphosis, in particular highlighting the importance of weight, age, stream longitude, and drainage area measurements in the prediction of metamorphosis (Fig. 2).

The variance estimate for the random effect of river was close to zero, and models that excluded river as a random effect had lower AIC_C values, leading us to conclude that the explicit inclusion of stream-level variables was able to account for the observed variability in metamorphic rates among streams (Table 5). As a result, the final model does not contain river as a random effect and should be applicable to streams outside of those used in model development.

Management Oriented Model

The final biological model included variables (age, sex, time-integrated temperature) that are impractical to collect given the number of streams and lampreys that are sampled by the control agents each year. We conducted a second analysis, limiting the explanatory variables to those that could readily be obtained by management agencies. Since age or sex was not included in this analysis, the full dataset of 212 recaptured lampreys was used. Supplementary water chemistry data from the lamprey control program allowed for the addition of mark-recapture data from Hollett (1998), which increased the number of streams in this analysis to 11 and brought the overall size of the dataset to 315 lampreys (214 larvae, 101 transformers).

The results of the model selection procedure on the combined dataset produced four similar top models, only differing in their inclusion or omission of condition factor and stream conductivity (Table 6). While a model consisting of length, condition factor, and stream latitude, longitude, drainage area, and lamprey production category possessed the highest kappa value, the parameter estimate for condition factor was not significant, so a similar model without condition factor (the model ranked second based on kappa) was selected as the top model. This model was able to correctly predict the

TABLE 5. Parameter estimates, standard errors, and p-values from a mixed model analysis for the biological model of metamorphosis selected as best (with the highest kappa statistic value and predictive accuracy), based on mark-recapture data (n = 168) from eight streams.

Effect	Parameter Estimate	Standard Error	p-value
Fixed Effects:			
Intercept	39.49	17.67	0.025
Weight	4.76	1.03	< 0.001
Age	3.05	0.96	0.002
# Days between 19 and 23°C	–0.16	0.06	0.008
Stream Latitude	1.27	0.49	0.010
Stream Longitude	–1.40	0.30	< 0.001
Estimated Mean Larval Density in Type-2 Habitat	–0.39	0.16	0.013
	Variance Estimate	**Standard Error**	**p-value**
Random Effects:			
Stream	< 0.0001	—	—

fate of individual larvae 87.6% of the time. Model averaging was not employed during the management model development, because only four very similar models were in consideration. Again, principal components did not improve model fit. As was the case with the biological model, the random effect of stream was not significant, showing that the inclusion of the stream-specific parameters accounted for inter-stream variability in metamorphic rate (Table 7).

Comparison with Other Predictive Models of Metamorphosis

The two models developed in this study were much better at predicting which larvae would enter metamorphosis than the other two existing models (Table 8). A direct comparison of the management model with the biological model was not performed, as the datasets used to derive the two models differed in both the number of variables and their sample size. Kappa values for the biological model indicated almost perfect agreement (Table 8A) while the management model exhibited substantial agreement (Table 8B) (Landis and Koch 1977). In contrast, the kappa values for the MC and ESTR models ranged only from slight to fair agreement when applied to either the biological or management model datasets. A stream-specific analysis of model output indicated that the management model provided equal or more accurate predictions of metamorphosis relative to the ESTR and MC models, on 8 of 11 streams.

TABLE 6. Model selection results for the management-based model.

Model Variables	df	AICc	Percent Overall Correct	Percent Larvae Correct	Percent Transformers Correct	Kappa Statistic
L / CF / Lat / Lon / DA / T2 / Cat	8	182.44	87.94%	92.99%	77.23%	0.717
L / Lat / Lon / DA / T2 / Cat	7	182.66	87.62%	92.52%	77.23%	0.711
L / CF / Lat / Lon / DA / Con / T2 / Cat	9	184.12	87.30%	92.99%	75.25%	0.701
L / Lat / Lon / DA / Con / T2 / Cat	8	184.31	86.98%	92.06%	76.24%	0.696

Where:
L = Length (mm)
CF = Condition Factor
Lat = Latitude (decimal degrees)
Lon = Longitude (decimal degrees)
DA = Stream drainage area (km^2)
Con = Conductivity (S/cm)
Cat = Stream Lamprey Production category
T2 = Average larval density in Type-2 habitat

TABLE 7. Parameter estimates, standard errors, and p-values from a mixed model analysis for the management model selected as best (with the highest kappa statistic value and predictive accuracy), based on combined mark-recapture data (n = 315) from this study and Hollett (1998).

Effect	Parameter Estimate	Standard Error	p-value
Fixed Effects:			
Intercept	–62.9748	16.3993	0.0001
Length	0.2125	0.0311	< 0.0001
Latitude	3.8683	0.9445	< 0.0001
Longitude	–1.7307	0.3771	< 0.0001
Drainage Area	0.0004	0.0001	0.0001
Estimated Mean Larval Density in Type-2 Habitat	0.6541	0.2078	0.0016
Categorical Effects:			
Stream Production Category			
(Category 1)	4.0551	1.6122	0.0119
(Category 2)	–6.8757	1.9908	0.0006
(Category 3)	1.0000	0.0000	—
	Variance Estimate	Standard Error	p-value
Random Effects:			
Stream	< 0.0001	—	—

DISCUSSION

Our results suggest that including additional variables within predictive models of metamorphosis can account for much of the variability observed in metamorphic rates of sea lamprey across the Great Lakes and greatly improve our ability to forecast parasitic sea lamprey production. The predictive accuracy of both the biological and management models was far superior to the length-based and condition-based models currently in use, for the streams used to develop our models. We recognize that this is not an ideal comparison because the data used to fit our models were also used to evaluate their accuracy. For this reason and others outlined below, we

TABLE 8. Comparison of model predictions from the two models developed in this study with the two other common models of sea lamprey metamorphosis. Table A is based on the data collected in the mark-recapture study, minus animals where an accurate estimate of age was not obtained. Table B is based on a combination of these mark-recapture data, plus those of Hollett (1998), but where the variables included in the model analysis were limited to those easily collected within the scope of the sea lamprey management program.

Model	Correct Larval Predictions	Correct Transformer Predictions	Correct Transformer Predictions (%)	Incorrect Predictions	Kappa Statistic
(A Full dataset (123 larvae / 45 transformers):					
Biological Model	119	37	82.2%	12	0.813
ESTR	119	18	40.0%	31	0.439
Minimum Criteria	122	4	8.9%	42	0.112
(B Expanded dataset (214 larvae / 101 transformers):					
Management Model	198	78	77.2%	48	0.711
ESTR	201	57	56.4%	57	0.548
Minimum Criteria	208	16	15.8%	91	0.164

strongly recommend further efforts to test the accuracy of the new models relative to existing tools.

The biological model may not be practical for use within the existing sea lamprey control program, but it does point to factors that appear to influence the probability of metamorphosis in sea lamprey populations. Sea lamprey age was included in all of the top biological models, indicating that older larvae, independent of their length and weight, are more likely to enter metamorphosis. Weight was included in all but one of the top models, with estimated lipid weight replacing total weight in the one exceptional case. This result is consistent with the hypothesis that larvae must reach a certain mass and possess sufficient energy reserves prior to entering into metamorphosis (Holmes and Youson 1994). In contrast, our non-invasive estimates of larval lipid content only entered into two of the top biological models. Previous research has indicated that lipid accumulation is important to metamorphosis in sea lampreys, a phenomenon unique to sea lampreys (Holmes *et al.* 1999, for review, see Youson 2003). Our results suggest that either our non-invasive methods were not sufficiently accurate to discriminate important differences in actual lipid levels, or that this indicator is not evident in larvae sampled during the growing season prior to metamorphosis. To discriminate among these explanations, we recommend further investigation into non-invasive methods for determining lipid content of larval sea lampreys (Cox and Hartman 2005, Crossin and Hinch 2005).

Both the biological and management models included several stream-level variables that account for variation in the probability of metamorphosis among individual sea lampreys with similar lengths, weights, and ages but from different streams. These included a stream temperature variable (biological model only), latitude and longitude, larval density in Type 2 habitat, drainage area (management model only), and stream category (management model only). Each of these factors represent environmental variables that could plausibly affect metamorphosis (temperature, regional edaphic factors, stream productivity, etc.), but in general the direction of the observed effects was inconsistent either among models (e.g., larval density) or with *a priori* hypotheses. For example we observed a negative relationship between a stream temperature variable and probability of metamorphosis in the biological model, in contrast with previous studies (Holmes *et al.* 1994, Holmes and Youson 1997) which concluded that it is the rise in temperature in the spring that is the important cue, not the magnitude of the temperature increase. Because our analysis is limited to nine (biological) or eleven (management) streams, and because the mechanisms underlying these environmental effects are not clear, it may be inappropriate to extrapolate our models that contain these variables to other streams without further validation and exploration of mechanisms.

We recommend that both existing and future models of metamorphosis be evaluated using individual-specific mark-recapture studies in the field before being affirmed as a basis for making lampricide treatment decisions. Recently, emphasis has been placed on evaluating larval assessment accuracy by conducting mark-recapture studies during lampricide treatments to estimate abundance (Hansen *et al.* 2003). In these evaluations, sea lamprey larvae are mass-marked by removing a piece of non-vascular tissue from the distal end of the caudal fin; consequently the physiological fate of individuals cannot be followed. Valuable additional information on metamorphosis could be obtained by modifying some of these mark-recapture studies to include measurements of individual lampreys and coded wire tag implantation at the time of marking, following the methods used for this study. In particular, selecting streams where the discrepancy in transformer estimates between different metamorphic models is the greatest may lead to a rapid improvement in our ability to develop models that more accurately predict metamorphosis.

Finally, the methods currently used by the GLFC to rank streams for lampricide treatment suffer from the fact that the models of metamorphosis being used, along with their underlying assumptions, have not been evaluated to assess how errors in their predictions might affect the stream ranking process. The uncertainty associated with both existing and new models should be integrated into a stream selection simulation analysis to compare the performance of alternative stream ranking protocols. We have conducted a preliminary analysis of this type which indicated that although stream ranking methods based on predictions of metamorphosis are optimal when the models are precise and accurate, other ranking methods may be more robust to the high degree of uncertainty that actually exists in these models (Steeves 2002, Treble 2006). Our results also suggest that a new metamorphic model that decreases uncertainty surrounding transformer forecasts could lead to a substantial improvement in our ability to control lamprey populations in the Great Lakes.

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REFERENCES

Anderson, G. 2007. Improving larval sea lamprey assessment in the Great Lakes using adaptive management and historical records. M.Sc. thesis. Michigan State University. East Lansing, Michigan.

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

Burnham, K.P., and Anderson, D.R. 2004. Multimodel inference. Understanding AIC and BIC in model selection. *Sociol. Method. Res.* 33:261–304.

Christie, G.C., and Goddard, C.I. 2003. Sea Lamprey International Symposium (SLIS II): Advances in the integrated management of sea lamprey in the Great Lakes. *J. Great Lakes Res.* 29 (Suppl. 1):1–14.

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

Cohen, J. 1960. A coefficient of agreement for nominal scales. *Education and Psychological Measurement* 20:37–46.

Cox, M.K., and Hartman, K.J. 2005. Non-lethal estimation of proximate composition in fish. *Can. J. Fish. Aquat. Sci.* 62(2):269–275.

Crossin, G.T., and Hinch, S.G. 2005. A nonlethal, rapid method for assessing the somatic energy content of migrating adult Pacific salmon. *Trans. Am. Fish. Soc.* 134:184–191.

Docker, M.F., and Beamish, F.W.H. 1994. Age, growth, and sex ratio among populations of least brook lamprey, *Lampetra aepyptera*, larvae: An argument for environmental sex determination. *Environ. Biol. Fish.* 41:191–205.

Dustin, S.M., Schleen, L.P., Popowski, J., and Klar, G.T. 1989. *Sea lamprey management in the Great Lakes.* Great Lakes Fish. Comm. Annual Report. Ann Arbor, Michigan.

Hansen, M.J., Ebener, M.P., Lester, N.P., Somers, K., and Sullivan, P.J. 2002. *Larval sea lamprey assessment program: review panel comments and recommendations*. Great Lakes Fish. Comm. Ann Arbor, Michigan.

_____, Adams, J.V., Cuddy, D.W., Richards, J.M., Fodale, M.F., Larson, G.L., Ollila, D.J., Slade, J.W., Steeves, T.B., Young, R.J., and Zerrenner, A. 2003. Optimizing larval assessment to support sea lamprey control in the Great Lakes. *J. Great Lakes Res.* 29 (Suppl. 1):766–782.

Henson, M.P., Bergstedt, R.A., and Adams, J.V. 2003. Comparison of spring measures of length, weight, and condition factor for predicting metamorphosis in two populations of sea lamprey (*Petromyzon marinus*) larvae. *J. Great Lakes Res.* 29 (Suppl. 1):204–213.

Hollett, A.K. 1998. Condition factor and statolith aging in assessment of metamorphosis in sea lampreys (*Petromyzon marinus*), in the Great Lakes. M.Sc. thesis. University of Toronto. Toronto, Ontario.

Holmes, J.A., and Youson, J.H. 1994. Fall condition factor and temperature influence the on incidence of metamorphosis in sea lampreys, *Petromyzon marinus*. *Can. J. Zoolog.* 72:1134–1140.

_____, and Youson, J.H. 1997. Laboratory study of the effects of spring warming and larval density on the metamorphosis of sea lampreys. *Trans. Am. Fish. Soc.* 126:647–657.

_____, and Youson, J.H. 1998. Extreme and optimal temperatures for metamorphosis in sea lampreys. *Trans. Am. Fish. Soc.* 127:206–211.

_____, Beamish, F.W.H., Seelye, J.G., Sower, S.A., and Youson, J.H. 1994. Long-term influence of water temperature, photoperiod, and food deprivation on metamorphosis of sea lamprey, *Petromyzon marinus*. *Can. J. Fish. Aquat. Sci.* 51: 2045–2051.

_____, Chu, H., Khanam, S., Manzon, R., and Youson, J.H. 1999. Spontaneous and induced metamorphosis in the American brook lamprey, *Lampetra appendix* . *Can. J. Zoolog* 77(6): 959–971.

Jonas, J.L., Kraft, C.E., and Margenau, T.L. 1996. Assessment of seasonal changes in energy density and condition in age-0 and age-1 muskellunge. *Trans. Am. Fish. Soc.* 125:203–210.

Landis, R.J., and Koch, G.G. 1977. The Measurement of observer agreement for categorical data. *Biometrics* 33:159–174.

Lowe, D.R., Beamish, F.W.H., and Potter, I.C. 1973. Changes in the proximate body composition of the landlocked sea lamprey, *Petromyzon marinus* (L.)

during larval life and metamorphosis. *J. Fish. Biol.* 5:673–682.

Manel, S., Williams, H.C., and Ormerod, S.J. 2001. Evaluating presence-absence models in ecology: the need to account for prevalence. *J. Appl. Ecol.* 38:921–931.

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

_____, and Smith, B.R. 1978. *Biology of larval and metamorphosing sea lampreys, Petromyzon marinus, of the 1960 year class in the Big Garlic River, Michigan. Part II, 1966–1972.* Great Lakes Fish. Comm. Tech. Rep. 30.

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

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

Murdoch, S.P., Docker, M.F., and Beamish, F.W.H. 1992. Effect of density and individual variation on growth of sea lamprey (*Petromyzon marinus*) larvae in the laboratory. *Can. J. Zoolog.* 70:184–188.

Pearce, W.A., Braem, R.A., Dustin, S.M., and Tibbles, J.J. 1980. Sea lamprey (*Petromyzon marinus*) in the lower Great Lakes. *Can. J. Fish. Aquat. Sci.* 37:1802–1810.

Piasecki, W., Kotega, P., Weiner, J., and Froncisz, W. 1995. New way of body composition analysis using total body electrical conductivity method. *Rev. Sci. Instrum.* 66(4):3037–3041.

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

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

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

Sawyer, A.J. 1980. Prospects for integrated pest management of the sea lamprey (*Petromyzon marinus*). *Can. J. Fish. Aquat. Sci.* 37:2081–2092.

Scott, I., Selman, C., Mitchell, P. I., and Evans, P. E. 2001. The use of total body electrical conductivity (TOBEC) to determine body composition in vertebrates. In *Body Composition Analysis: A handbook of non-destructive methods,* J.R. Speakman, ed., pp. 127–160. Cambridge, UK: Cambridge University Press.

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

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

Steeves, T.B. 2002. Uncertainty in estimating sea lamprey (*Petromyzon marinus*) abundance in Great Lakes tributaries. M.Sc. thesis. Michigan State University. East Lansing, Michigan.

Treble, A.J. 2006. Choosing streams for sea lamprey control: using alternative models of metamorphosis to optimize the stream selection process. M.Sc. thesis. Michigan State University. East Lansing, Michigan.

Youson, J.H. 2003. The biology of metamorphosis in sea lampreys: endocrine, environmental and physiological cues and events: application to lamprey control. *J. Great Lakes Res. 29* (Suppl. 1):26–49.

_____, Lee, J., and Potter, I.C. 1979. The distribution of fat in larval, metamorphosing, and your adult anadromous sea lampreys, *Petromyzon marinus* L. *Can. J. Zoolog.* 57:237–246.

_____, Holmes, J.A., Guchardi, J.A., Seelye, J.G., Beaver, R.E., Gersmehl, J.E., Sower, S.A., and Beamish, F.W.H. 1993. Importance of condition factor and the influence of water temperature and photoperiod on metamorphosis of sea lamprey, *Petromyzon marinus*. *Can. J. Fish. Aquat. Sci.* 50:2448–2456.

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