



Stage Based Population Viability Model for Sea Lamprey (*Petromyzon marinus*)

Prepared by
Howe, Eric A., E. Marsden and T. M. Donovan, UVM School of Natural Resources and R.H. Lamberson, Humboldt University
Department of Mathematics

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(*Petromyzon marinus*)**

Project Completion Report, Lake Champlain Sea Lamprey Alternatives Workgroup

by

Eric A. Howe, J. Ellen Marsden, and Therese M. Donovan

School of Natural Resources

University of Vermont, Burlington, VT 05405

and

Roland H. Lamberson

Department of Mathematics

Humboldt University, Arcata, CA 95521

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Executive Summary

A sea lamprey control program in Lake Champlain was developed in 1985 with the goals of reducing the lamprey population to a level where it would have minimal impact on the fishery, and developing an effective sea lamprey management program in the Lake Champlain basin that would encompass all possible avenues of control, with environmental consciousness. The Lake Champlain Sea Lamprey Alternatives Working Group was formed in 2002 to review and explore experimental projects aimed at non-chemical control for sea lamprey. The first project that the workgroup recommended was the development of a population viability model for the sea lamprey population in Lake Champlain. This report describes the development of the first stage of this model, i.e., a deterministic version, and presents preliminary results of the model. The objectives of the model are to: 1) determine which life stages of sea lamprey are most sensitive to control; 2) examine optimal combinations of control methods; and 3) identify optimal control methods for individual streams in the Champlain basin. The model closely follows the life cycle of the sea lamprey, and identifies the vulnerable points in the cycle where the population can be controlled with the least amount of effort. The model also highlights information gaps in the life-cycle, especially for survivorship of eggs that have been washed out of the nest.

Preliminary results from the model suggest that control mechanisms targeting several year classes at once are more effective than methods targeting only one age or stage class. Use of single control methods indicated that larval control every year was the most effective method for reducing the parasitic population, followed by larval control every four years. Reduction by management of the transformers alone had a somewhat greater impact than management of spawning adults, unfertilized eggs, and parasites. Simulation of nest dismantling indicated that

100% of the eggs in nests could be removed with no effect on population growth; fertilized eggs outside of the nest maintained the population. Time series analysis indicated that with low larval reduction each year, the time to reduce the parasitic population is considerable; if management efforts can reduce larval populations by at least 50% each year, a reduction in the parasitic population of 80% will take 7 years. Simulations with combined management efforts indicated that a synergistic effect could be achieved. For example, as the effect of use of sterile males increases, the need for efficient adult trapping is reduced to achieve the same result. Without the application of sterile males, adult trapping needs to be over 80% effective every year to have an impact on the parasitic population. If sterile males are used to reduce the fertilization rate by 50%, then adult trapping only needs to be 60% effective to impact the parasitic population. To achieve significant changes in the growth rate of the parasitic sea lamprey population, management efforts need to be consistent and effective. These preliminary model results indicate that understanding survivorship and proportion of eggs washed out of the nest is crucial; if estimates of survivorship at this stage are inaccurate, predictions from the sensitivity analysis in the model could be seriously skewed.

The next steps in model development include making tributary characteristics in the model specific to Lake Champlain; adding stochasticity to simulate variability found in the natural world; and simulating movements of lamprey between different natal and spawning tributaries to reflect variable production of lamprey among tributaries. **We emphasize that model results at this stage in development are highly preliminary, and should not be used to affect sea lamprey control or management decision-making**

Introduction

When the sea lamprey (*Petromyzon marinus*) became a noticeable problem in the Great Lakes in the early 1950's (Smith 1968, Smith and Tibbles 1980), a chemical treatment program was initiated to reduce the population by targeting the larval phase. TFM (3-trifluoromethyl-4-nitrophenol) and Bayluscide (Bayer-73, or niclosamide) were developed as lamprey larvicides and applied to tributaries before the ammocoetes metamorphose to the parasitic life stage and migrate to the lake. These chemical lampricides are currently the primary means of control for sea lamprey in the Great Lakes. In 1985, the sea lamprey was declared responsible for the decline in the Lake Champlain fishery (Gersmehl and Baren 1985, Plosila and Anderson 1985) and the development of a sea lamprey control program in Lake Champlain was initiated (Fisheries Technical Committee 1985).

Subsequently, lampricides were applied to the tributaries of Lake Champlain in 1990 as part of an experimental sea lamprey control program. The purpose of this program was threefold: 1) to achieve immediate and significant reduction in parasitic phase sea lamprey, 2) to assess the effects of the sea lamprey reduction at several levels, including the sport fishery, specific fish populations, and on the economic growth of the area, and 3) to formulate long-term policy and management strategies for sea lamprey control in the Lake Champlain Basin. These strategies were to utilize all forms of sea lamprey control available to optimize results for the control program in terms of fishery and economic benefits, and with environmental consciousness (Fisheries Technical Committee 1999).

At the conclusion of the experimental program an Environmental Impact Statement (EIS) was developed (Fisheries Technical Committee 2001). Chemical treatments were determined to be the most effective method of control for sea lamprey in the Lake Champlain Basin, but the

EIS also stated that alternative methods to chemical control would be further explored. Following this mandate, the Lake Champlain Sea Lamprey Alternatives Working Group was formed in 2002 to bring together a diverse group of individuals from a wide array of agencies, organizations and special interest groups (including private citizens). The mission of the Alternatives Workgroup is to review experimental projects aimed at non-chemical control for sea lamprey. The Workgroup developed research proposals with this goal in mind and forwarded their recommendations to the Lake Champlain Fish and Wildlife Management Cooperative's Fisheries Technical Committee for consideration in the sea lamprey and fisheries management plan.

One of the first decisions made by the Alternatives Workgroup was to develop a population viability model for the sea lamprey population in Lake Champlain. Population viability models are generally developed for endangered species, and are used to identify stages in the life cycle that are sensitive to changes in survivorship (Crouse et al. 1987, Mann and Plummer 1999, Reed et al. 2003). Management practices can then be focused on these life stages to improve restoration efforts for the species. For the sea lamprey, these same principles will be applied, except with the opposite goal: *limiting* the growth of the population, rather than improving it.

The objectives of this model are:

1. Determine which life stages of sea lamprey are most sensitive to control
2. Examine optimal combinations of control methods
3. Identify optimal control methods for individual streams in the Champlain Basin

With these objectives in mind, practical control options for sea lamprey at various points in the life cycle were identified (Figure 1, Table 1). This model follows the same principles as

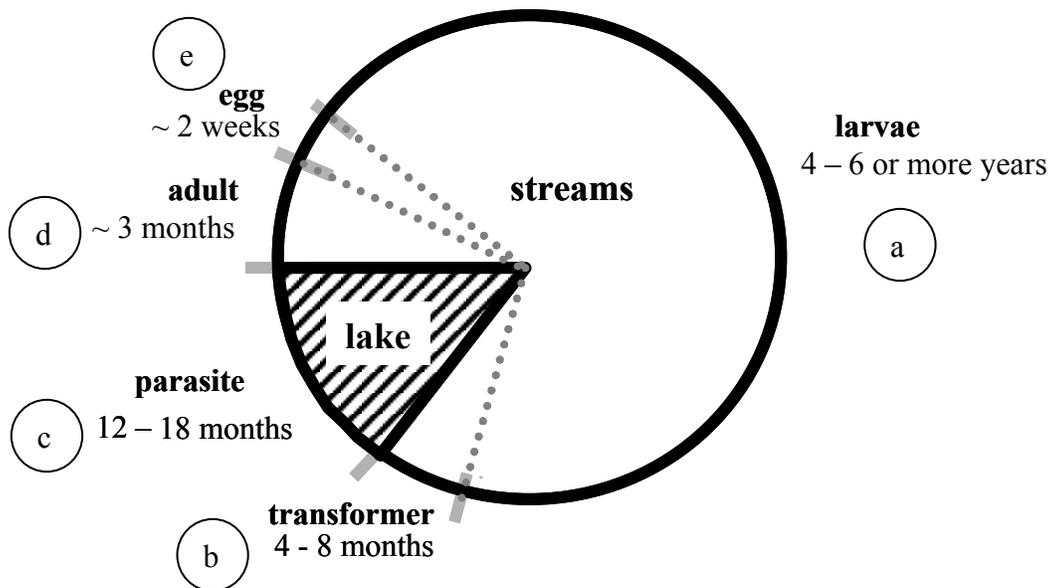
the Empiric Stream Treatment Ranking system (ESTR, Christie et al., 2003). The ESTR model is geared primarily toward determining which tributaries are the most cost-effective to treat, but does not necessarily identify suitable alternative management options for tributaries that are not suitable for chemical treatment. During the preliminary development phases of the model, a workshop was organized to discuss ideas and options for the model, and to determine the format of the model. Participants in the workshop included fisheries biology experts knowledgeable about Lake Champlain and sea lamprey issues as well as experts in the field of population modeling. Dr. Roland Lamberson, who has worked with the spotted owl and trout issues on the West coast, was hired as a consultant and participated in the workshop. It was confirmed that the model would be developed with Microsoft Excel, using a stage-based matrix format (see Model Description, p.13). The focus of this report will be Objective 1. Significant effort and further development of the model will be required for completion of Objectives 2 & 3.

Task 2 of the work plan submitted to the LCBP was reported on as an appendix within the nest dismantlement final report. It includes a comprehensive literature review for many of the species of interest in the Poultney River, such as walleye, channel darter, eastern sand darter, and state-listed freshwater mussels. This information was compiled to help the Alternatives Workgroup assess likely non-target impacts of proposed alternative control methods during its decision-making process. Non-target assessments are currently outside of the scope of the life-history model, which was designed to assess the likelihood of affecting sea lamprey population growth.

Sea lamprey life cycle

Sea lampreys have a very complex life cycle, spending the first several years of their life as a sedentary filter feeding larva (ammocoete) and then metamorphosing into an active pelagic parasite of larger fishes before becoming sexually mature (Figure 1[a]). Beginning in late fall, recently metamorphosed lampreys migrate downstream to a lake or the ocean (Figure 1[b]). During the parasitic stage, sea lampreys in lakes feed on salmonids and other high profile sport fishes, leaving wounds and often killing their hosts (Figure 1[c]). In late winter of the following year, parasitic lampreys move back into tributaries where they become sexually mature and spawn in the spring, generally between April and June, when the water in tributaries warms up to 50° F (Applegate 1950). They build crescent-shaped structures, generally thought to be nests, in well-aerated sections of the tributary with large gravel substrates (Figure 1[d]). Lampreys are generally thought of as monogamous spawners, although the rate of observed monogamy changes with the sex ratio (Applegate 1950, Hanson and Manion 1980, Manion and Hanson 1980). Eggs are deposited in the nests and hatch and emerge as ammocoetes about two weeks after fertilization (Figure 1[e]).

Figure 1. Life cycle of the sea lamprey



Potential control methods

To limit the numbers of parasitic-phase sea lamprey in the lake, several control methods have been either implemented or proposed to target different stages in the life cycle of the sea lamprey (Table 1). Sterilization of males is a feasible option, one the Alternatives Workgroup is exploring as an alternative (or supplement) for the current control program. For sterile male control, male sea lampreys would be collected as they migrate upstream, sterilized, and released. Any mating in which these males are involved will produce unviable eggs, thus reducing the number of young that hatch from a nest. This method is currently being used in the St. Mary's River and other tributaries to the Great Lakes with some success (Bergstedt et al. 2003, Jones et al. 2003).

Nest raking, or nest dismantling, is a control method that has been considered, but not implemented because it is a relatively new concept, and the efficiency of this method has yet to be demonstrated. Nest raking involves disrupting sea lamprey nests immediately post-spawning, with the goal of either killing eggs or removing them from the nest and spreading them

downstream to reduce survival. Egg survival outside of the nest is unknown, so the feasibility of this method as a possible alternative control is undetermined. The method is also highly labor intensive, because lamprey eggs have been found buried deeply within nests (Applegate 1950, W. Laroche, unpublished data), so raking to remove a majority of the eggs requires significant excavation of the nest to be successful. Non-target impacts from this method are high in terms of benthic organisms and other species that have spawned in the same habitat as the sea lamprey.

Chemical applications to tributaries are used to control the larval stages of the lamprey population. As mentioned above, this is the primary mechanism for control of sea lamprey in the Great Lakes and in Lake Champlain. Chemical applications of TFM and Bayluscide are done in the fall of every fourth year for a specific tributary. The four-year growth cycle in the larval stage of the sea lamprey allows application of chemicals to a given tributary to be minimized. This alleviates costs of the control program as well as environmental and non-target impacts of the chemical. Typical treatments of TFM to a tributary are expected to be 95-99% effective in reducing the resident larval lamprey population (this includes transformers, if the treatment occurs early enough in the fall, before out-migration begins).

Trapping can be used to target transformers, which migrate to the lake after metamorphosis, by setting fyke nets near the mouth of a tributary. However, our experience with fyke netting transformers suggests that this method would not be very successful for control. The timing of the migrations is usually keyed to a change in water flow and temperature (Applegate 1950, Manion and Smith 1978). Migrations may begin as early as the first week in October and can continue through the winter until April. Thus the effort required for this method to be effective at removing even a small percentage of lampreys from the system would be

enormous. Migratory non-target species are also impacted by this method, and subject to high mortality during elevated flow conditions.

Table 1. Life stages of the sea lamprey and potential control methods.

Life Stage	Control method
Fertilization	Sterile males
Egg survivorship	Nest raking
Hatched eggs	None
Ammocoete	Chemical (TFM, Bayluscide)
Transformer	Chemical, fyke netting
Parasite	None
Adult	Adult trapping, migratory pheromones
Sex ratio	Sex pheromones

Of the seven potential control methods identified in Table 1, only the chemical treatments and adult trapping are currently implemented in Lake Champlain; however, lamprey are restricted from spawning in several rivers by hydroelectric or other dams. Adult trapping consists of capturing adult lampreys as they migrate upstream in the spring to spawn. There is a low-head barrier dam on the Great Chazy River in New York that was installed solely for the purposes of limiting sea lamprey access to spawning habitat in the river. This is the only barrier of this type installed in a tributary to Lake Champlain. Small tributaries can be blocked off using portable assessment traps installed temporarily for the sea lamprey spawning runs. This method has been effective in tributaries where most of the water column can be blocked off (W. Bouffard, U.S. Fish & Wildlife Service, unpublished data). Some non-target species are affected by the trapping, especially larger fishes migrating upstream that are unable to pass through the opening in the trap; smaller fishes entrained in the trap are generally released alive if traps are

checked every 2-3 days. Non-target mortalities can be high if the trap is set in a high velocity area, but are generally lower than those of most chemical treatments.

Sea lamprey pheromones are the latest weapon in the control arsenal. There are two pheromones that can potentially be used as control mechanisms: migratory and sex pheromones. The migratory pheromone is an odor produced by resident larvae in a tributary. Adult sea lampreys are attracted by the larval odor and use it to select a spawning tributary (Bjerselius et al. 2000, Vrieze and Sorenson 2001). This pheromone has been isolated, identified, can be extracted from water containing larvae, and is ready for experimental use. The migratory pheromone could be used to draw adult migratory lampreys out of a major tributary that is difficult to manage and into a small secondary tributary where the lampreys can be more effectively removed from the system, or to tributaries where nesting conditions are of poor quality (e.g. an ecological trap). The sex pheromone is a compound produced in the liver of male sea lampreys to which female lampreys are attracted (Li et al. 2002). Male lampreys generally migrate upstream first and begin nest construction, followed shortly afterward by the females (Applegate 1950, Manion and McLain 1971). The sex pheromone could be used to draw female lampreys away from spawning males, perhaps into a trap, so that they can be removed from the system prior to spawning.

Model Description

The goal of the population viability model is to determine which control method, or combination of methods, would most effectively reduce the parasitic lamprey population to a minimum, given the management constraints for each option. There are five main components to this model: 1) the life stages of the sea lamprey, each with its own natural survivorship

probability; 2) management actions that may be used to lower the natural survivorship probability for each life stage; 3) carrying capacities used to limit growth of the overall population at three different levels; 4) variables that cannot be controlled by management effects, but can have a significant impact on the growth rate of the population; and 5) a stream selection matrix that incorporates the probability that an adult lamprey will select a given stream for spawning.

Currently, the model is structured to analyze population growth rates from a single stream for which different management scenarios can be set. Eventually the populations from multiple streams will be set up to mimic actual streams around the Lake Champlain Basin, and then interact with each other in an attempt to model the overall population of the lake.

Initial model simulations will determine baseline populations and growth rates for the lamprey population in the model. The key output of interest is the total number of parasites within the lake after populations have reached a stable distribution (Figure 1c). For these simulations, natural survivorship rates will be used (i.e. management will not reduce survivorship at any stage in the life cycle). Once baseline parasitic-phase populations are established, we will compare changes in parasitic-phase lamprey populations based on simulated changes in survivorship at different life stages due to some effect of a management or control option. Each management option, or combination of management options, will have some percentage reduction of survivorship at that specific life stage (or stages) required to achieve a desired reduction in the overall parasitic-phase population in the lake. Comparisons will be made to determine which management options (or combinations of management options) will provide the most effective means of reducing the parasitic-phase lamprey population in Lake Champlain.

Sea lamprey stage-based model:

The lamprey life cycle is best described through a stage-based model (Lefkovitch 1965), based on the stages described in Figure 1. The model addresses each life stage separately, and so an individual lamprey has some probability of moving from one stage to the next (i.e. parasite to spawning adult). Figure 2 is a flowchart of the model. The first oval (ue), represents a quantity of unfertilized eggs. These eggs then have some probability of becoming fertilized (surviving, designated as $S_{ue, fe}$), at which point they progress into the next life stage in the model (fe). If an egg is not fertilized, it dies and is removed from the model, and no longer plays a role in the propagation of the lamprey population. Fertilized eggs are either deposited into the nest constructed by the mating pair (en, with probability $S_{fe, en}$) or an egg may be washed out of the nest (eo, with probability $S_{fe, eo}$). Egg dispersal from the nest usually occurs during the mating process, when eggs may be fertilized, but are not adequately anchored in the nest, and end up caught in the current and are washed downstream. The data regarding survivorship of these eggs ($S_{eo, h}$) is very limited. Eggs in each of these stages (en and eo) each have a probability of surviving to hatch and emerge and then to burrow as larvae ($S_{en, h}$ and $S_{eo, h}$). Because survivorship rates are different depending on whether an egg is in or out of a nest, there are two separate states for them in the model, hence the two small circles representing this stage in Figure 2 (eo and en). The hatched eggs have some probability of burrowing as larvae ($S_{h, lo}$). There are many vulnerabilities in this stage, and so it has a separate stage in the model from the in/out of nest stage. Also, at this point in the life cycle is the first of three population growth limitations (carrying capacity K_L). There is a finite amount of habitat in each tributary, and consequently there is a maximum number of larvae that can find space to burrow. The model assumes that it is at this point in the life cycle where the larval habitat limitation takes place. If

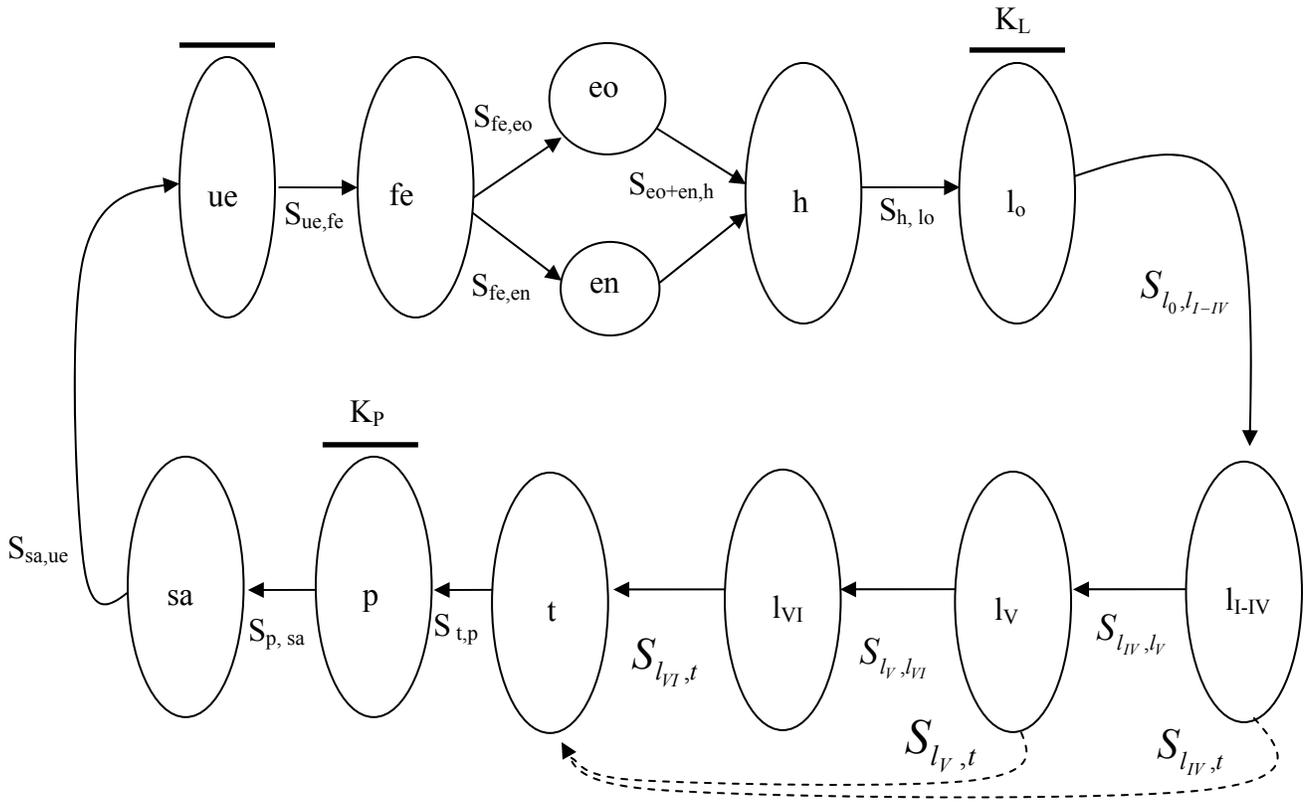
there is no room for a new ammocoete to burrow, it will die and be removed from the model. This carrying capacity is denoted in the model by a cap (K_L) over the oval for l_0 , the stage for young-of-year ammocoetes. Once in the larval stage, an ammocoete remains there for four years, with some probability of surviving through each year ($S_{l_0, l_{I-IV}}$). For simplicity, these first four full years as an ammocoete are denoted as one oval in Figure 2 (l_{I-IV}). After the fourth year as an ammocoete, there are now three possibilities: 1) an ammocoete can die and be removed from the model, 2) an ammocoete can survive and become a fifth-year ammocoete (with probability S_{l_{IV}, l_V}), or 3) an ammocoete can begin the metamorphic process into a transformer (Figure 1b). This progression into the transformer life stage is denoted by a dashed line from the l_{I-IV} oval to the t oval in Figure 2 (with probability $S_{l_{IV}, t}$). If an ammocoete survives and remains an ammocoete (moves into the l_V oval), it again has the probability of death, surviving to the next ammocoete stage (probability $S_{l_V, l_{VI}}$), or probability of transforming ($S_{l_V, t}$). For simplicity purposes, age 6 is the final year as an ammocoete in this model. Once surviving to this point as an ammocoete, the animal can then either metamorphose to the transformer stage (t oval, probability $S_{l_{VI}, t}$) or die and be removed from the model.

At the transformer stage an individual has some probability of surviving to the parasite stage (p oval, probability $S_{t,p}$); however there is another cap (carrying capacity K_P) set for the parasite stage limiting the number of transformers that can survive into the parasite stage. This cap is determined by the estimated amount of prey availability (number of lake trout and salmon, in this case) that can sustain a given parasitic population. If the number of transformers that survives to the parasite stage exceeds K_P , then K_P is returned as the number of parasites in the p oval (Figure 2). A parasite then has some probability of maturing, selecting a tributary to spawn in, and finding a mate ($S_{p,sa}$). At this point in the model, all adults are going to die and will be

removed from the model, but a certain number of them are allowed to spawn and produce eggs ($S_{sa,ue}$). The generation of unfertilized eggs is influenced by the sex ratio set for the model. The sex ratio reduces the total number of spawning adults to females (assuming that every female in the population will find a male to spawn with), so that a population of unfertilized eggs to start the next generation can be estimated.

The number of unfertilized eggs is influenced by three factors: 1) the sex ratio of the spawning adult population, 2) the fecundity of the females in the adult population (number of eggs each female carries), and 3) a cap set to limit the number of successful spawners as a result of the limited amount of spawning habitat available for spawning female lamprey in a tributary (carrying capacity K_{SH}). The assumption for K_{SH} is that there is a finite amount of spawning habitat available, and therefore the number of females that can deposit eggs there is limited.

Figure 2. Structure, parameters, and carrying capacities of the life history model (see Table 2 for definitions).



Model parameterization:

Each of the life stages identified in Figure 1 has a parameter value in the model. As stated earlier, an individual lamprey has a probability of survival through each life stage. Survivorship probability is different for each stage, and thus each of these probabilities has been assigned a value in the model (Figure 2, Table 2). The complexity of the life cycle for the sea lamprey makes accurate estimation of survivorship for each of the specific life stages difficult (Figure 2). Specific parameter values were identified for survivorship probability between each life stage, for fecundity of adults, three different carrying capacities, and for probability of metamorphosis of larvae to transformers at ages 4 and 5 (Table 2). For simplicity it was assumed that any larva surviving to age-6 would metamorphose and become a transformer the next year or die.

An extensive literature search was conducted in order to collect accurate information to develop these parameter values for sea lamprey in Lake Champlain (Appendix A). Following the EPA literature selection criteria outlined in the QAP proposal for this literature review (Martin and Howe, 2001) values from peer-reviewed literature were given highest priority. Where the peer-reviewed literature was insufficient, values were used from gray literature (technical reports) or anecdotal data (Table 3). When possible, survivorship probabilities from studies on the Lake Champlain sea lamprey population were given priority to best reflect the population that is being studied (Zerrenner 2001). In a few cases, data for specific probabilities could not be found, and so the values used for these parameters are based on educated guesses from a team of researchers experienced with lamprey and other fish populations (Table 3).

Management options:

The identified control mechanisms to date are aimed to reduce survival at a given stage, so the driving forces of the sea lamprey control matrix model are the survival parameters, which denote the ability of a subject to survive from one point in its life cycle to the next. While each life stage in the model has a natural probability of survivorship, each stage also has an additional probability of reduced survivorship based on some theoretical management action taken upon that life stage (Table 1, Table 3). Management effects are factored into the model as reductions in the natural survivorship rates established for each life stage, using a multiplicative reduction of the overall probability of survivorship for each stage. The values and justifications for management effects are further described in the justification for parameter values (Appendix C). For example, trapping adult lamprey in a tributary before they spawn is a reduction on the probability of surviving to spawn, so the natural probability of surviving to spawn ($S_{p,sa}$) is reduced by the trapping effect (M_{sa}). See the theoretical model equations section on p.23 for more detail.

Model output will be evaluated in terms of changes to the parasitic population of the lake. This is the goal of the overall management program for sea lamprey, thus the model output will reflect this goal. Model simulations will be evaluated against a background sample scenario in which all management actions are set to zero (no effective management).

Table 2. Variables used for the individual equations within the model.

Life Stage	Population at each life stage	Probability of surviving to the next life stage	Reduction by management
Unfertilized eggs	ue	$S_{sa,ue}$	M_{ue}
Sex ratio	sr		M_{sr}
Fertilization rate	fr		M_{fr}
Fertilized eggs	fe	$S_{ue,fe}$	M_e
Egg deposition rate (into nest)	edr		
Fertilized eggs, in nest	en	$S_{fe,en}$	M_{en}
Fertilized eggs, out of nest	eo	$S_{fe,eo}$	M_{eo}
Hatched eggs	h	$S_{en,h}$ and $S_{eo,h}$	M_h
Larvae age 0	l_0	S_{h,l_0}	M_l
Larvae age 1	l_I	Sl_0,l_I	M_l
Larvae age 2	l_{II}	Sl_I,l_{II}	M_l
Larvae age 3	l_{III}	Sl_{II},l_{III}	M_l
Larvae age 4	l_{IV}	Sl_{III},l_{IV}	M_l
Transformation rate, Larvae age 4	ltr_{IV}		
Larvae age 5	l_V	Sl_{IV},l_V	M_l
Transformation rate, Larvae age 5	ltr_V		
Larvae age 6	l_{VI}	Sl_V,l_{VI}	M_l
Transformer	t	$Sl_{IV,t}$ and $Sl_{V,t}$ and $Sl_{VI,t}$	M_t
Parasite	p	$S_{t,p}$	M_p
Spawning adult	sa	$S_{p,sa}$	M_{sa}
Spawning adult (fecundity)	f		
Carrying capacity, spawning habitat	K_{SH}		
Carrying capacity, larvae	K_L		
Carrying capacity, parasites	K_P		

The model is currently organized with a deterministic structure, i.e., the values for each parameter are fixed. The next step in the process of developing this model will be to apply variability to these parameters to make the model stochastic; in other words, natural variability will be incorporated into each parameter. This will be done using a beta distribution to limit the variability on the probability of survivorship between 0 and 1.

Table 3. Values used to parameterize the life history model and to simulate the effect of management. See Appendices B and C for more detail. N/A indicates that published data were not available, so a “best guess” based on experience with other fishes was used to estimate the parameter.

Parameter	Value	% Reduction by management (range)	Reference
Adult fecundity	88,000		Johnson 1987
Fertilization rate	0.90	10-90% (increments of 10%)	N/A *
Proportion of eggs washed out of nest	0.90		Manion & Hanson 1980
Survivorships			
Fertilized eggs (in nest)	0.60	0-100% (increments of 10%)	Manion & Hanson 1980, Manion 1968, Applegate 1950
Fertilized eggs (out of nest)	0.05		Manion & Hanson 1980
Hatched eggs	0.01	0 – 90% (increments of 10%)	Manion 1968, Applegate 1950
Larvae age 0	0.26	50 – 99% (variable increments)	Zerrenner 2001, Spangler 1985
Larvae age 1	0.93		Zerrenner 2001
Larvae age 2	0.95		Zerrenner 2001
Larvae age 3	0.81		Zerrenner 2001
Larvae age 4	0.88		Zerrenner 2001
Larvae age 5	0.90		Zerrenner 2001
Larvae age 6	0.90		N/A
Transformer	0.80		N/A
Parasite	0.35	0.01-0.09% (increments of 0.01%)	Mullett 2002
<i>Transformation rates</i>			
Larvae age 4	0.07		Zerrenner 2001
Larvae age 5	0.86		Zerrenner 2001
<i>Carrying capacities</i>			
Spawning adult females (K_{SH})	220,000		N/A
Larval population (K_L)	26,000,000		N/A
Parasitic phase (K_P)	650,000		N/A

Theoretical model equations:

The structure of the model is based on a classic Lefkovitch matrix (Lefkovitch 1965). The model is set up as a stage-based model in which stages consist of individuals within a certain life history stage and in which each stage experiences a survival probability (Figure 2, Table 2, Table 3). This model structure allows for estimation of the effect of management actions, which can reduce survivorship at specific life stages. For each transition from one stage to the next (Figure 2), there is a mathematical equation to estimate the number of lampreys that actually survive.

The model begins with the calculation of unfertilized eggs in the population (ue):

$$\begin{aligned} \text{ue} = & \text{if } (sa)(S_{sa,ue})(M_{sa})(sr) > K_{SH}, \text{ then calculate } (K_{SH})(f), \\ & \text{else calculate } (sa)(S_{sa,ue})(M_{sa})(sr)(f) \end{aligned} \quad (1)$$

The number of unfertilized eggs (ue) in a given tributary is calculated based on the number of spawning adults (sa), the survivorship of spawning adults to produce unfertilized eggs ($S_{sa,ue}$), effect of management on those spawners (M_{sa}), the sex ratio of the spawning population (sr) that determines the number of female lampreys that will spawn, and the fecundity of those females in that population (f). Fecundity is defined here as the number of eggs carried by an individual female prior to a spawning event. This value is limited by a density dependence on adult females based on the amount of spawning habitat available (K_{SH}). The limitation only applies to spawning females because they will release eggs into spawning substrate, and if there is not enough substrate for those females to spawn in, the eggs will not be viable.

The next step in the model is the progression of unfertilized eggs to fertilized eggs (fe). This is essentially the initial success of the mating process of the female lamprey in the system:

$$fe = (ue)(S_{ue,fe})(fr)(M_{ue}) \quad (2)$$

The number of unfertilized eggs then progresses to fertilized eggs (fe), based on a fertilization rate (fr), survivorship of unfertilized eggs to fertilized eggs ($S_{ue,fe}$) and by a management action taken to remove unfertilized eggs (M_{ue}).

The next step is the progression from fertilized eggs to hatched eggs (h). However, complications arise here due to the high percentage of eggs that are washed out of the nest during the spawning event. Consequently, there are two separate calculators to identify the overall survivorship of this stage: the number of eggs hatched within the nest, which may be reducible by management to some extent,

$$en = (fe)(edr)(S_{fe,en})(M_{en}),$$

and the number of eggs hatched outside of the nests, for which a specific management option cannot be identified at this time.

$$eo = (fe)(1-edr)(S_{fe,eo})(M_{eo})$$

To calculate the number of eggs hatched in the nest (en), there is a probability of fertilized eggs remaining in the nest, or egg deposition rate (edr), the survivorship of eggs in the nest ($S_{fe,en}$),

and management of eggs in the nest (M_{en}). To calculate the number of eggs hatched outside of the nest (eo), the number of eggs deposited outside of the nest ($1-edr$) is multiplied with the total number of eggs fertilized (fe), the survivorship of eggs outside of the nest ($S_{fe,eo}$), and any management action set to reduce survivorship (M_{on} , usually set to zero or no effect).

Using eo and en ,

$$h = en + eo \quad (3)$$

the total number of eggs that survive to hatch (h) can be calculated.

The number of hatched eggs that survive to become age-0 larvae is dependent on several events: natural survivorship, reduction due to management, and density dependence. The density dependence for larval survivorship has been fitted with a modified Beverton-Holt density dependence calculator (Beverton and Holt, 1957) as follows:

Let the sum of all resident larvae that survived into the current year be (l_a):

$$l_a = (l_0 + l_I + l_{II} + l_{III} + l_{IV} + l_V + l_{VI})$$

where l_0 is the number of larvae at age-0, l_I is the number of larvae at age-1, etc.

$$l_0 = \frac{S_{h,l_0} * h * M_h}{\left(1 + \frac{S_{h,l_0} * h * M_h}{K_L - l_a}\right)} \quad (4)$$

Equation 4 contains the Beverton-Holt density dependence calculator described above. K_L is set as the carrying capacity of larval habitat in a tributary, S_{h,l_0} is the survivorship probability of a hatched egg to burrowed larvae, h is number of hatched eggs, and M_h is reduction due to

management on hatched eggs. To set K_L in this model, the maximum number of sea lamprey larvae that can survive in a single tributary was determined by finding the maximum density in any river in the basin (Lewis Creek), and the maximum amount of larval habitat in any river in the basin (Winooski River), developing a theoretical population estimate, and expanding this value by two standard deviations. The resulting value provided a maximum ceiling for the Beverton-Holt calculator.

To calculate the number of larvae that survive to age-1,

$$l_I = (S_{l_0, l_I})(l_0)(M_I) \quad (5)$$

where (S_{l_0, l_I}) is the survivorship probability of age-0 larvae to age-1 larvae and (M_I) is a reduction by some management effect on all larvae, irrespective of age. For simplicity, the density dependence on larvae (K_L) is only applied at the age-0 level. This assumes that once an animal has survived through the age-0 stage, density is no longer a factor related to survival regardless of age or size. That is, density effects operate on the youngest of individuals such that high densities decrease the survival rate of l_0 , but not the survival of subsequent age classes.

The number of age-2 through -6 larvae are calculated in a similar fashion with the notation (l_{II}) , (l_{III}) , (l_{IV}) , (l_V) , (l_{VI}) :

$$l_{II} = (S_{l_I, l_{II}})(l_I)(M_I) \quad (6)$$

$$l_{III} = (S_{l_{II}, l_{III}})(l_{II})(M_I) \quad (7)$$

$$l_{IV} = (S_{l_{III}, l_{IV}})(l_{III})(M_I) \quad (8)$$

$$l_V = (S_{l_{IV}, l_V})(l_{IV})(M_I) \quad (9)$$

$$l_{VI} = (S_{l_V, l_{VI}})(l_V)(M_I) \quad (10)$$

Due to the variable age at which ammocoetes begin the transformation process, the model accounts for transformation at the last three age classes of ammocoetes: age-4, -5 and -6. Larvae at age-4 and -5 have a probability of transforming or a probability of remaining as ammocoetes, or else they die. In this model, age-6 larvae either transform or die; they do not remain as larvae. Consequently, the transformation rate for age-6 larvae is simply a survival probability for age-6 larvae. From this, the number of transformers (t) in a system is calculated by:

$$t = (l_{IV})(l_{trIV})(M_I) + (l_V)(l_{trV})(M_I) + (S_{l_V, l_{VI}})(l_{VI})(M_I) \quad (11)$$

where (l_{trIV}) and (l_{trV}) are transformation rates for age 4 and 5 larvae, respectively, and (l_{VI}) is the survivorship probability for age 6 larvae to the transformer stage. The transformation rate is adjusted for the survivorship probability of the metamorphic process.

The third density-dependent limitation in the model has been set for the number of parasites that can survive once they migrate out to the lake (K_P). This parameter is determined by the prey availability for the parasites, or simply the number of salmonids that can support the lamprey population. Currently, the value used for this parameter in the model is an estimate of the current parasitic population, which is presumed to be at its highest level in the history of the

population in the lake, plus two standard deviations. This population estimate is generated from a mark-recapture study conducted by the authors from 2001-2002. Consequently, the total number of parasites in the lake (p) is found to be:

$$p = \text{if } (t)(S_{t,p})(M_t) > K_p, \text{ then } K_p, \text{ else } (t)(S_{t,p})(M_t) \quad (12)$$

where $(S_{t,p})$ is the survivorship of transformers and (M_t) is reduction by management on transformers.

The final calculator in the model estimates the number of spawning adults (sa) in the population:

$$sa = (p)(S_{p,sa})(M_p) \quad (13)$$

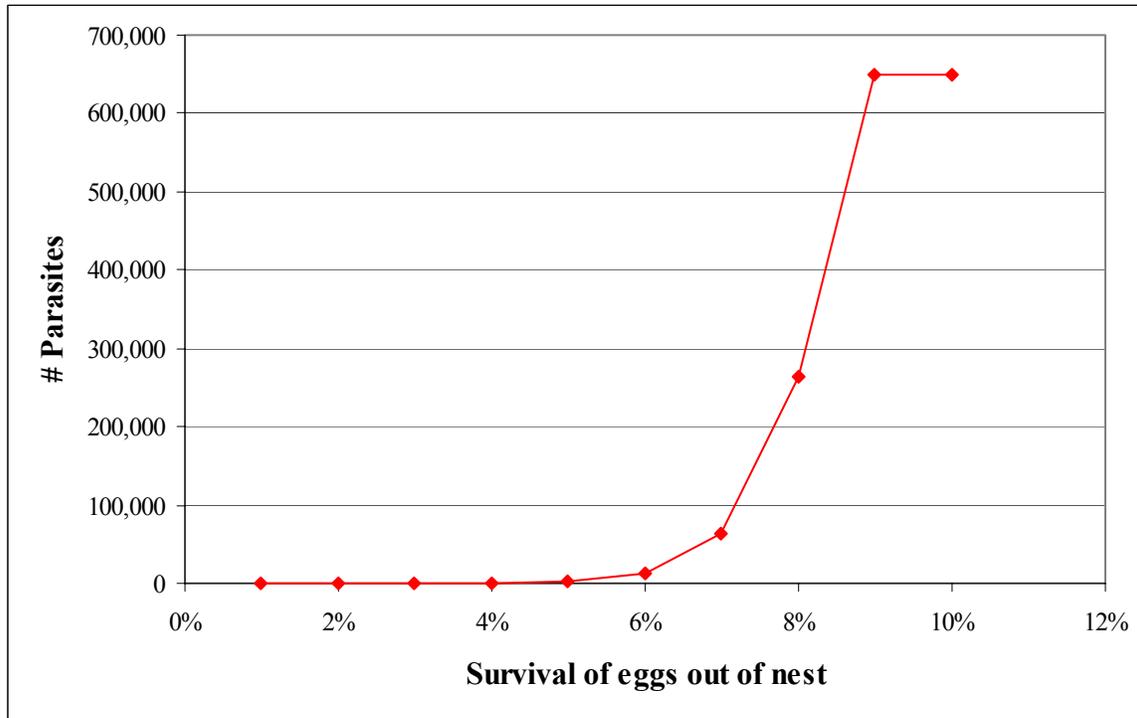
where $(S_{p,sa})$ is the survivorship probability of parasites to the spawning adult phase, and (M_p) is reduction by management of parasites.

Model simulations:

An initial simulation was run with no reduction in survivorship due to management effects to determine a baseline for the model. It immediately became apparent that the value for survivorship of eggs washed out of the nest was very important (because 90% of eggs are washed out of the nests), so simulations were run with the model at different settings for this parameter (1% to 10% survivorship), and all other parameters were held constant. Due to carrying capacity restrictions, the effect of egg contributions from outside the nests is difficult to determine with the high survivorship of eggs that stay in the nests. The question was raised: if nest survivorship were to be significantly lower than its current state, what would the contributions of eggs washed out of the nests have to be to maintain the lamprey population at the same baseline levels? To model this, survivorship of fertilized eggs in the nest was reduced from 60% to 6% to help determine the effect that egg survivorship outside of the nests would have if fertilized eggs in the nests were insignificant. Results from these simulations indicated that 5% survivorship of eggs outside of the nest was the minimum level required to have an impact on the model population, and survivorship above 9% was limited by carrying capacities (Figure 3).

Based on these findings, all further simulations were run at 5% survivorship for eggs washed out of nests because this would provide a minimum contribution of eggs outside the nest to the growth of the total population.

Figure 3. Change in the population of parasitic lamprey at stable age with increase in survivorship of eggs outside of the nest.



Using this information, simulations were run for management options at each of the stages identified in Table 1. Each management option was simulated with a minimum control level (just above 0% or no management) and a maximum control level (just below 100% effective) and some range in-between.

Given the parameter values in Table 3, an example of a management scenario would be to increase the effect of management on a given life stage and assess the change in parasitic-phase population. An example of a management scenario is provided in Table 4, where management effects on removal of spawning adults and fertilized eggs in the nests range from 0-90% effective, in increments of 10% (management effects are independent of each other).

Table 4. Example of model simulation and output for management effect on spawning adult lampreys. All other parameters held constant.

INPUT	OUTPUT
Effect of management reduction on survivorship of spawning adults	Parasitic population
0%	2,038,786
10%	2,038,786
20%	2,038,786
30%	2,038,786
40%	2,019,566
50%	1,851,191
60%	1,466,995
70%	3,911
80%	0
90%	0

Due to the possibility of eggs surviving outside of the nest, simulations for nest dismantling (management by reduction of eggs in nests) were run at a 100% effective level. This will allow for evaluation of the technique to remove enough of the egg population to significantly restrict growth, regardless of contributions from eggs out of the nests. Management of larval stages was modeled to occur every year or every four years. Control every four years would simulate the current chemical lampricide treatments.

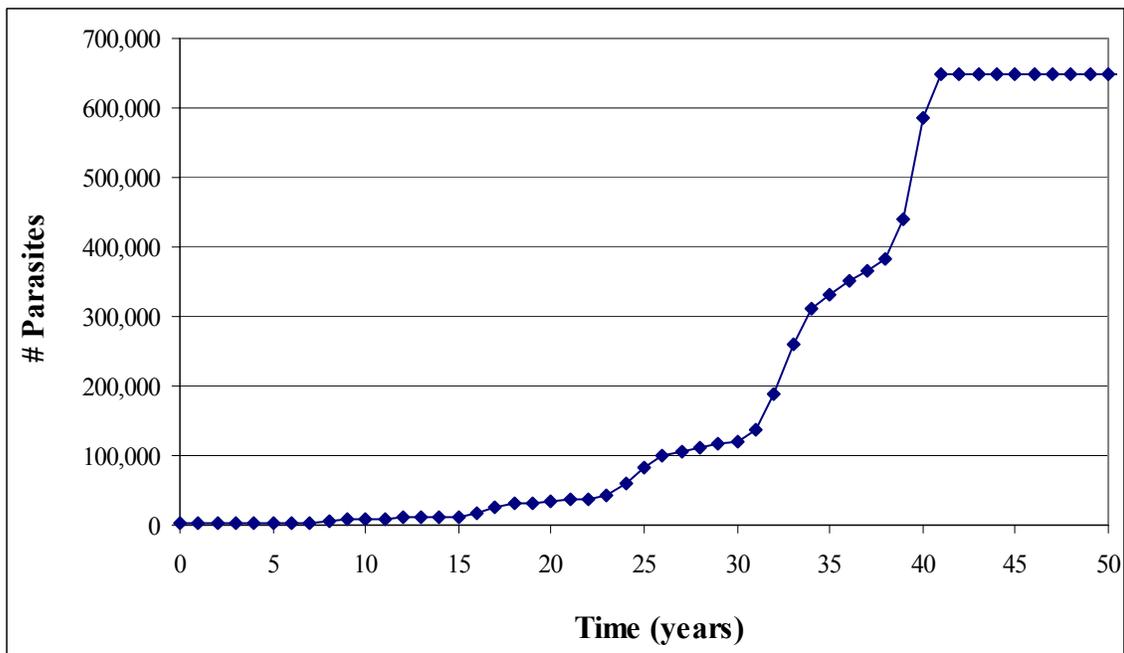
One combined simulation was run to assess the effect that adult trapping (reduction of spawning adults) could have when combined with application of sterile males to reduce the fertilization rate. A time-series analysis was also run for larval control to examine the effect the control method might have on the population initially on a short-term basis, and then over a longer period of time.

Results

Baseline simulations:

Simulations were initially run with the model set at zero reduction in survivorship due to management to set a baseline for the model. All simulations were run with seed populations at stable age distributions. The dependent variable of interest was the number of parasites in the population since this is the stage of greatest interest to management. Results from the background simulation indicated that the population reaches a maximum level of 650,000 parasites (carrying capacity) after about 40 years without control (Figure 4.)

Figure 4. Growth of the parasitic population over time without management.

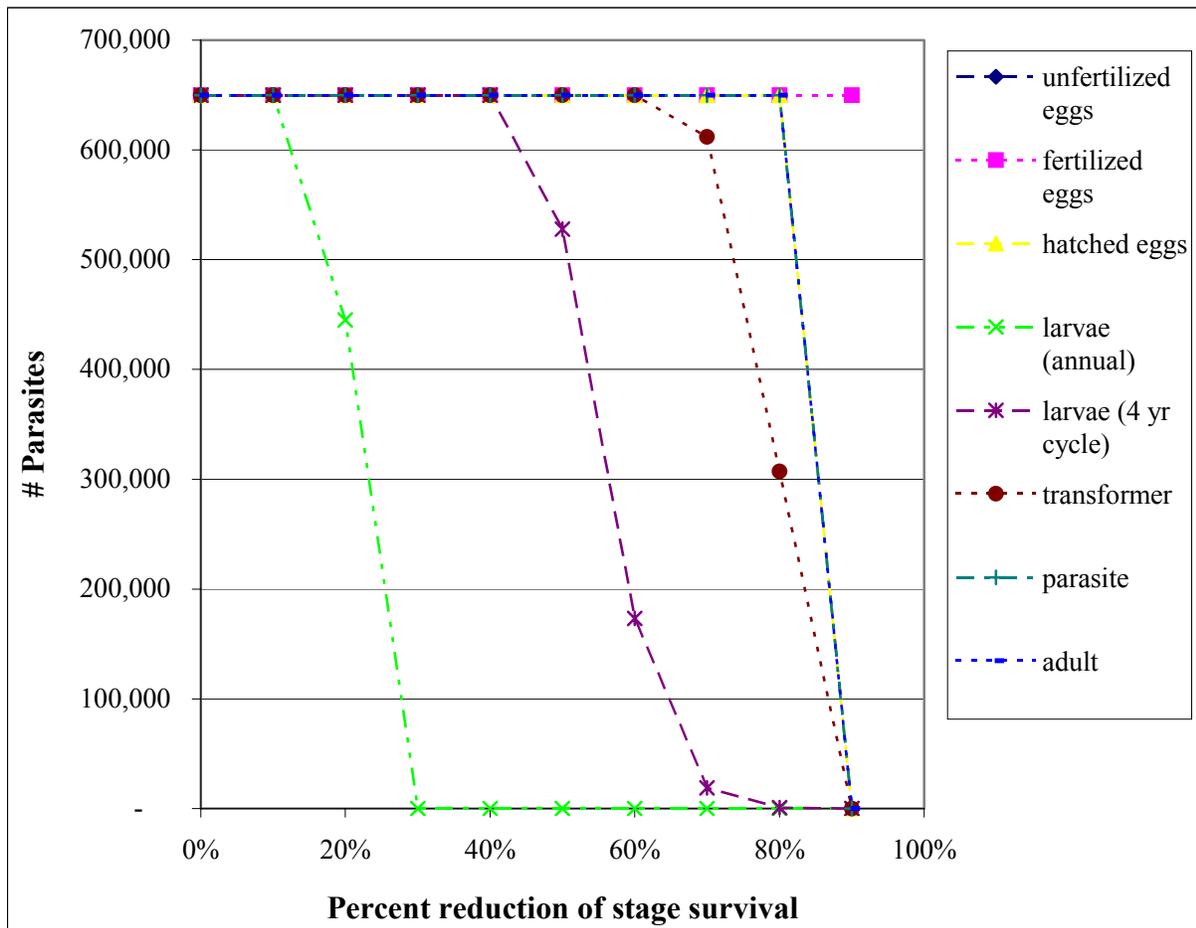


Single management efforts:

Simulations were run to examine the effects of individual management efforts on the parasitic population. These simulations indicated that larval control every year was the most

effective at reducing the parasitic population, followed by larval control every four years. Following larval control, reduction by management of the transformers alone had a somewhat greater impact than management of spawning adults, unfertilized eggs, and parasites (Figure 5). Simulation of nest dismantling indicated that 100% of the eggs in nests could be removed with no effect on population growth; fertilized eggs outside of the nest maintained the population.

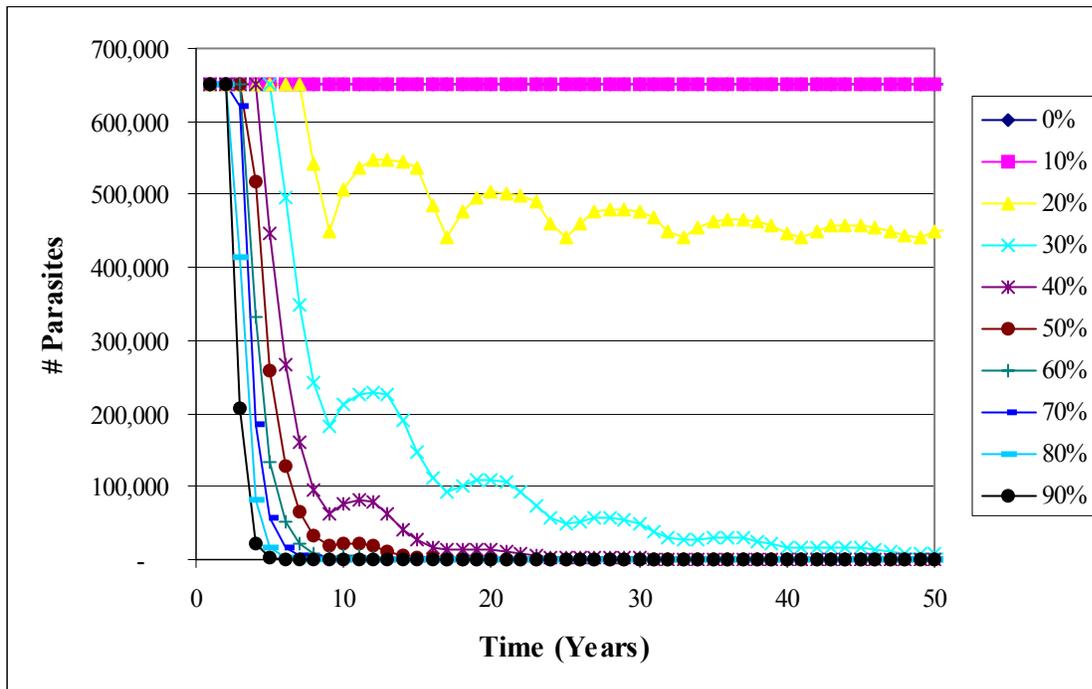
Figure 5. Impact of reduction in survivorship by management on each of the life stages in the model on the growth of the parasitic population.



Time series analysis:

The time series analysis of larval or transformer populations supports the results indicated for larval control in Figure 4, i.e. while a minimum of a 20% reduction by management efforts at the larval and transformer stages would be needed to achieve a negative growth rate in the population, almost 15 years would be required to reduce the parasitic population by 25%. Once management efforts on larvae and transformers begin to reduce the population by at least 50% every year, the parasitic population will be reduced by greater than 80% within 7 years (Figure 6).

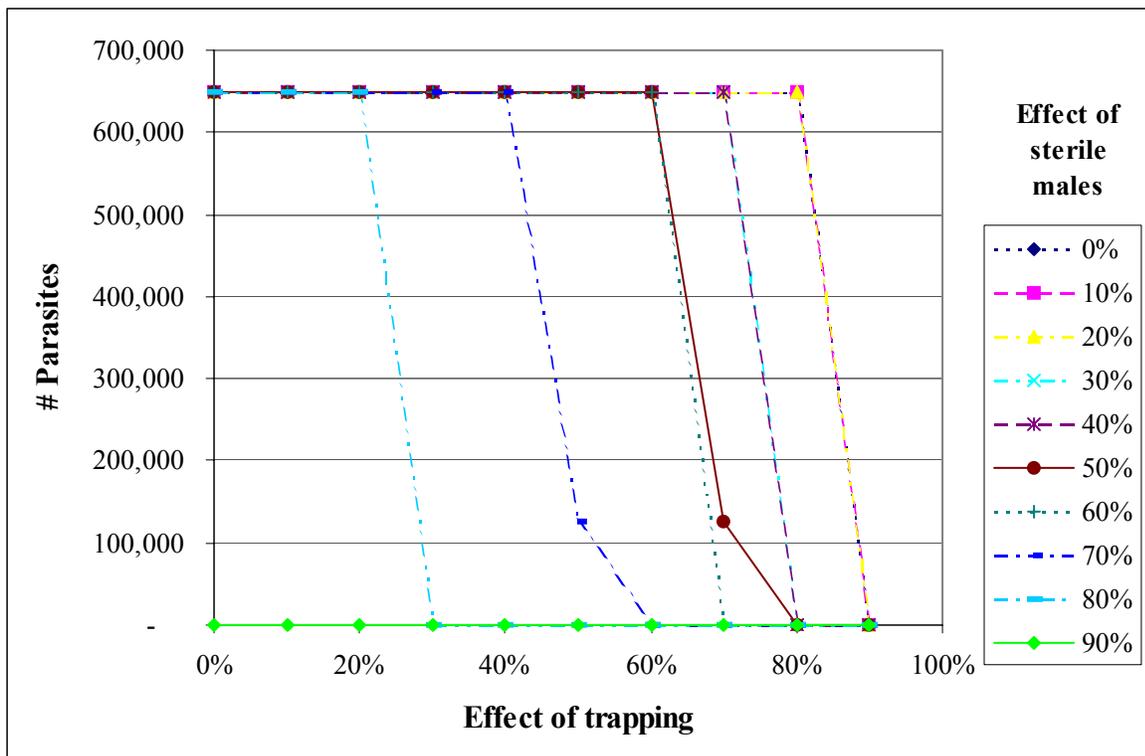
Figure 6. Time series analysis of reduction in parasitic population by management on ammocoetes and transformers annually (equal reduction on both levels).



Combined management efforts:

Simulations with combined management efforts indicated that a synergistic effect could be achieved (Figure 7). As the effect of sterile males increases, the need for efficient adult trapping is reduced to achieve the same result. For example, without the application of sterile males, adult trapping needs to be over 80% effective every year to have an impact on the parasitic population. However, if sterile males are used to reduce the fertilization rate by 50%, then adult trapping only needs to be 60% effective to impact the parasitic population.

Figure 7. Change in population growth through combined management efforts on spawning adults and their fertilization rate.



Discussion

The preliminary simulations indicate that to achieve significant changes in the growth rate of the parasitic sea lamprey population, management efforts need to be consistent and effective. This species is highly fecund, and is therefore able to recover quickly from any major reductions in survival to any single year class, as demonstrated in Figure 4. Stand-alone management efforts need to target life stages that cover several year classes (i.e., the larval and transformer stages). Hence the obvious differences in the slope of the growth curve for larval control every year, every four years, and control on transformers (Figure 5).

The result from the combination of adult trapping and sterile male release is a good indicator of the power of combined management actions. When management actions are used in combination with each other, the effect required for each management action to achieve the original goal of population reduction is likely to be much less than when the individual management tools are used alone. Combinations of the various tools can become very important in controlling the parasitic population, and need to be explored in much more detail. This effect has been demonstrated in the field when chemical treatments and adult trapping were used concordantly. A chemical treatment was applied to Stone Bridge Brook, Milton, VT to remove ammocoetes and transformers, and adult trapping has since kept the lamprey population in this brook to a minimal level (W. Bouffard, U.S. Fish & Wildlife Service, unpublished data). Results from different management simulations can also be valuable when evaluated in a time-series analysis. The time-series allows managers to assess the effect a management program might have on a short-term basis. One management technique may have desirable results for a long-term program, while some others may have desirable results on the short term. The time-series analysis will highlight which tools will achieve the desired goals within a given time frame.

Field validation will be required to verify the accuracy of the model in predicting reactions of the lamprey population in Lake Champlain. Currently, the results of the sterile male simulation (reduction in fertilization rate) indicate that an 80% reduction in the fertilization rate would be required to see an impact on the parasitic population. This value of 80% is similar to findings from other models developed to investigate the feasibility of sterile males to limit reproduction in the Great Lakes (Jones et al. 2003).

Further fieldwork needs to be done to develop estimates of the survivorship of eggs once they have been washed outside the nesting area. The preliminary results from this model indicate that this is a critical point in the sea lamprey life cycle due to the high occurrence of eggs washed out of the nests. If estimates of survivorship at this stage are inaccurate, predictions from the sensitivity analysis in the model could be seriously skewed.

The model at this point is only useful as a basic guide, and provides minimal guidance for sea lamprey managers. This report describes the potential power of the fully developed model, and highlights the gaps in our knowledge of the sea lamprey life cycle. The most obvious gap is in the egg stage: the numbers of eggs that are fertilized, washed out of the nests, and survive downstream are crucial information needs. If more than 5% of the fertilized eggs that are washed out of the nest survive, then the remaining eggs in the nest play a minor role in the maintenance of the population. Investigation into this life stage is crucial to the success of the model in assisting sea lamprey management decisions in Lake Champlain.

We acknowledge that caution should be taken when analyzing the results from these simulations. The deterministic output from the current version of the model is not without meaning, but results from a stochastic model that accounts for some natural variability in survivorship from one stage to the next would be more useful for interpretation into a

management program. The next phase of the model will include survivorship parameters that are not fixed to a certain value, but instead are randomly selected for each cycle within a given range of possibilities.

Additional steps in accurately simulating the sea lamprey life cycle include continuously updating the parameter values that are used in the model. The literature review conducted at the outset of this project in 2002 was very thorough (See Appendices A-D), but there is an extensive amount of work being conducted on these issues, and thus new information that is relevant to the parameters used in this model is published on a monthly basis. Throughout the model development phase (and afterward), parameters will be updated with the latest information pertinent to the model. This also applies to how management actions affect their target populations, i.e. for chemical treatments; are the effects uniform across all age/size classes of larvae, or should some other function be applied here to accurately reflect the kill from the treatment?

Currently the model only simulates a single stream and therefore results from the current simulations highlight management needs for the lake as a homogeneous system. The next step is to model individual tributaries in Lake Champlain and have lamprey populations in each tributary interact with each other. This is the real power of the model. To develop a better understanding of the ability of the sea lamprey to populate a system such as Lake Champlain, the model needs to be able to simulate the ability of sea lamprey to hatch in one stream and spawn in another. Each major tributary in Lake Champlain will be parameterized based on measured habitat, flow, and lamprey population characteristics, different management tools that can be applied to the stream, and how effective those tools might be. Initial seed populations will likely be different, based on the size of the tributary, known larval populations, and known adult

spawning populations. These factors will also be important for the development of the two pheromones as control methods in the model. Data from ongoing and planned research on lamprey movements among streams will be incorporated into the model. Due to our limited knowledge of stream-specific survivorship, survivorship parameters will likely remain the same among streams.

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APPENDICES

APPENDIX A. Data used in the model from the Sea lamprey literature review.

APPENDIX B. Sea lamprey literature review bibliography.

APPENDIX C. Comments on the sea lamprey literature review by Jan Janecka

APPENDIX D. Detailed account of the model parameter values and their justifications.

APPENDIX A
Sea lamprey literature review

Quantitative data on life history stages of sea lamprey, *Petromyzon marinus*, obtained from published literature, USFWS reports and GLFC reports. Annotations are provided for each estimate explaining how it was estimated, factors influencing the estimate, and validity. An estimate is recommended if it is clearly more appropriate than the others. For any inquires please contact Craig Martin, Deputy Director, Craig_Martin@fws.gov, 802-862-0729 or Jan Janecka, jjanecka@zoo.uvm.edu

Phase	Variable	Estimate	Range	Water Body	Citation	QA/QC	
<i>Parasitic</i>	survival ^a	0.35	0.2-0.5	Lake Huron & Lake Superior	Mullet 2002 [264]	C	
	survival ^b	0.66	N/A	St. Mary's model	Eshenroder <i>et al.</i> 1987 [244]	B	
	survival ^c	0.75	N/A	model	Jones <i>et al.</i> 2002 [260]	C	
	sex ratio (<i>p</i> males) ^d	0.62 (peak N) 0.32 (low N) 0.52 (stabilization)	0.53-0.71 (peak) 0.21-0.37 (low N) 0.68-0.38 (stabilization)	Lake Superior	Heinrich 1980 [93] Torblaa & Westman 1980 [94]	B B	
<i>Spawning</i>	stream allocation ^e	Proportion Allocated = 0.5*(discharge/total discharge) + 0.5*(larvae)/(total larvae)	N/A	model	Spangler <i>et al.</i> 1985 [247] Bergstedt & Seeley 1995 [101] Vrieze & Sorenson 2001 [237]	C B A	
	pre-spawn survival ^f	0.91	N/A	Big Garlic River (Superior)	Hanson & Manion 1980 [230]	C	
	females spawners (<i>p</i> of females) ^g	0.61	N/A	Big Garlic River (Superior)	Hanson & Manion 1980 [230]	B	
	mating ^h (monogamous/polygamous/polyandrous)	0.89/0.11/0.01 (59%M) 0.87/0.13 (81%M) 0.56/0.44 (50%M) 0.90/0.10 (67%M)	0.56-0.90/0.01-0.44	Big Garlic River (Superior)	Manion & McLain 1971 [229] Hanson & Manion 1980 [230] Hanson & Manion 1978 [249] Manion <i>et al.</i> 1988 [252]	B B B B	
	spawned nests ⁱ	0.86 (50%M) 0.78 (59% M) 0.34 (81%M)	0.78-0.93 N/A N/A	Salem Creek (Ontario) Big Garlic River (Superior) Big Garlic River (Superior)	Weise & Pajos 1998 [147] Manion & McLain 1971 [247] Hanson & Manion 1980 [230]	A B B	
	fecundity (eggs) ^j	89,000, Eggs = -89,428 + 367.4*length (mm) Eggs = 12, 107 + 205.6*length (mm)	56,000-121,000	Great Lakes St Mary's model (Eshenroder) model (Spangler)	Applegate 1950 [267] Vladykov 1951 [266] Manion 1972 [174] Hanson & Manion 1980 [230] Eshenroder <i>et al.</i> 1987 [244] Spangler <i>et al.</i> 1985 [247]	B B B B B C	
	egg retention ^k	0.022 0.012 0.05	0.00-0.37 N/A 0.003-0.067	Big Garlic River (Superior) Lake Huron	Manion & McLain 1971 [229] Hanson & Manion 1978 [249] Manion & Hanson 1980 [40] Applegate 1950 [267]	B B B B	
	<i>Zygote</i>	nest deposition ^l	0.10	0.06-0.12	Big Garlic River (Superior) Little Garlic River (Superior)	Manion & Hanson 1980 [40] Manion 1968 [39]	B B
		<i>in nest</i>					
		egg survival/hatching success ^m (including deposition loss)	0.06	0.053-0.078	Little Garlic, Traverse River (Superior)	Manion 1968 [39]	B
	emergence ⁿ (including deposition loss)	0.007	0.004 - 0.011	Ocqueoc River (Huron)	Applegate 1950 [267]	B	
	egg survival ^o	0.88 0.89	0.85-0.94 0.82-0.95	Big Garlic River (Superior) Laboratory	Manion & Hanson 1980 [40] Hanson & Manion 1978 [249] Piavis 1971 [239]	B B B	
	emergence ^p (excluding deposition loss)	0.074	0.044-0.11	Ocqueoc River (Huron)	Applegate 1950 [267]	B	

Zygote cont'd	<i>out of nest</i>					
	non-nest deposition ^q	0.9	0.89-0.95	Big Garlic River (Superior)	Manion & Hanson 1980 [40]	B
	deposition on suitable habitat ^q	<i>P</i>	N/A	-	Variable made by Janecka based on Manion & Hanson 1980 [40] Applegate 1950 [267] Colby <i>et al.</i> 1979 [268] Corbett & Powles 1986 [269]	B B B B
	emergence in suitable habitat ^q	0.074	0.04 -0.11	-	see above	
	non-nest emergence ^q	0.9* <i>P</i> *0.074	N/A	-	see above	
Ammocoetes	<i>Survival (t = age in years) for each age class</i>					
	Age 0 ^r	-0.006*(density) + 0.28, 0.26	N/A	model Lewis Creek Densities	Spangler <i>et al.</i> 1985 [247]	C
	Age 1 ^r	-0.013*(density) + 0.56, 0.51	N/A	model Lewis Creek Densities	Spangler <i>et al.</i> 1985 [247]	C
	Age 2, 3, 4,...,t ^r	each 0.7	N/A	model	Spangler <i>et al.</i> 1985 [247]	C
	Age 0, 1, 2, 3, 4,...,t ^s	each 0.66	N/A	Saint Mary's model	Eshenroder 1987 [244]	B
	Age 0, 1, 2, 3, 4,..., t ^t	each 0.3	N/A	model	Jones <i>et al.</i> 2002 [260]	C
	Age 1, 2, 3, 4 ^u	0.93, 0.95, 0.81, 0.88	0.85-1, 0.89-1, 0.62-1, 0.75-1	Lewis, Pike, Morpion (Champlain)	Zerrenner 2001 [270]	A
	Age 1-4.5 ^v	0.96 (age classes combined) 0.92 (age classes combined)	N/A	Jordan River (Michigan), White Rive (Michigan)	Morman 1987 [53]	B
	<i>transformation rate</i>					
	Age 0 - 3, 4, 5,...,t ^w	0, -0.01*(density)+0.1, 0.1, 0.02 in Lake	N/A	model	Spangler <i>et al.</i> 1985 [247]	C
	Yearly combined transformation rate (length > 116 mm) ^x	0.083, 0.05	N/A	Saint Mary's River, Saint Mary's model	Eshenroder 1987 [244]	B
	Yearly combined transformation rate (length > 116 mm) ^x	0.25 - fast growing 0.023 -slow growing	0.16 - 0.34 0.002 - 0.04	Great Lake	Eshenroder 1987 [244]	B
	Age 0, 1, 2, 3, 4, 5, 6 ^y	0, 0, 0.2, 0.4, 0.7, 1.0	N/A	model	Jones <i>et al.</i> 2002 [260]	C
	Age 0, 1, 2, 3, 4, 5 ^z	0, 0, 0, 0, 0.08, n/a 0, 0, 0, 0, 0.05, 0.92 0, 0, 0, 0, 0.07, 0.86	N/A	Lewis Creek (Champlain) Pike River (Champlain) Morpion Stream (Champlain)	Zerrenner 2001 [270]	C
	Proportion of all ammocoetes transformed ^{aa}	0.17, 0.02, 0.18, 0.05	N/A, N/A 0.09 - 0.32, 0.001 - 0.15	Pre-TFM Lewis Creek, Post-TFM Lewis Creek, Pre-TFM Champlain Tribs, Post-TFM Champlain Trib	FTC 1999 [271]	C
	Age 4 ^{bb}	0.042, 0.17	N/A	Jordan River (Michigan), cages White Rive (Michigan), cages	Morman 1987 [53]	B

Note :

The numbers in brackets following the years in citations refers to the catalog numbers of the articles in the literature database compiled at the Lake Champlain FWRC, Essex Junction, VT. QA/QC column refers to data information use levels based on secondary data evaluation guidelines from EPA New England (adapted from Watzin and Smyth 2001)

APPENDIX B

Sea lamprey literature review bibliography

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APPENDIX C

August 2002

Jan Janecka

Annotations to Quantitative Data on Sea Lamprey *Petromyzon marinus* Life History Stages

Note: the numbers in brackets behind the years of citations refers to the catalog numbers of the articles in the sea lamprey literature database compiled at the Lake Champlain Fish and Wildlife Resources Complex, USFWS, Essex Junction, Vermont.

For any inquires please contact Craig Martin, Project Manager, Craig_Martin@fws.gov, 802-862-0729 or Jan Janecka, jjanecka@zoo.uvm.edu

- a. *Parasitic – Survival*: I obtained the survivorship (0.35) of transformers from Mike Fodale. K. Mullet (Marquette Station, USFWS) made this estimate from mark-recapture studies. He provided me with these numbers during our conversation. He said that in Lake Superior survival (0.2) of transformers was much lower than in Lake Huron (0.5). Mike suggested that this is the limiting life stage for lampreys. However, I was not able to get a hold of K. Mullet to confirm his statement.
- b. *Parasitic – Survival*: This estimate came from a population model for the Saint Mary's River (Eshenroder 1987 [244]). The length-frequency distribution at St. Mary's River was used to construct an age-frequency distribution using the Bertalanffy growth model. From the slope of the right limb of the age distribution the survival of the ammocoete stages (0.66) was obtained. There was no available adult survival estimate and they believed survival could not be 100% even under ideal conditions. They therefore assumed that survival of adult lampreys was the same as survival of ammocoetes. One problem is that for any age class the length of ammocoetes is very variable, especially for animals over 4 years old, and so attempts to predict age distribution from body lengths are problematic. In addition, survival in adults may be different from ammocoetes because the parasitic life stage is so different in terms of both physiology and ecology. The authors noted some of these problems in the description of the model. They used this method because there were no other approaches available to them (currently still a problem) that would provide a more rigorous estimate of survival. Despite these shortcomings, their model does provide reasonable estimates for survivorship and is one of the few that is based on actual data.
- c. *Parasitic – Survival*: This estimate (0.75) came from Jones *et al.* (2002 [260]) that examined compensatory mechanisms of sea lamprey. This survival estimate was used in a population model comparing the effectiveness of TFM treatments versus male sterilization. The authors do not mention where this estimate was obtained. It is most likely just a best guess based on qualitative knowledge. I spoke to Michael Fodale (one of the authors) about the estimates for the model. However, he was not involved in obtaining any of the estimates and did not know how they were derived. Ellen Marsden e-

mailed Mike Jones concerning this, but he did not provide any more insight into the variables used in the model.

- d. *Parasitic – Sex ratio (p males)*: Estimates of sex ratio for peak abundance (0.62) and low abundance (0.32) came from Lake Superior (Heinrich *et al.* 1980 [93]). Lake Superior data was used because it is the most complete data set, represents eight tributaries, and therefore should provide the most accurate estimate. Lake Michigan was not used because there were no abundance data after 1966. Torblaa and Westman (1980 [94]) noted that sex ratios may vary between streams, and estimates based on samples from one tributary may be erroneous. Lake Huron was not used because there was only data from Ocqueoc River and no data prior to 1965. Lake Ontario was not used because there was only data from Humber River and no data prior to 1989. However, when the sex ratios of the tributaries in the Great Lakes were pooled the mean ratio was similar to that calculated from Lake Superior. In sea lamprey there is a shift towards males when abundance is high (Heinrich *et al.* 1980, Torblaa & Westman 1980). This shift occurs during the 4-5 years following TFM treatment. The sex ratio also seems to be variable at intermediate densities and when the population is not stable. Jones *et al.* (2002) discusses the ratio shift and there is also evidence from other studies that the sex ratio is partly dependent on ammocoete densities (he cites Beamish 1993, also Torblaa & Westman 1980). In Lewis Creek, after the first TFM treatment in 1990, the reported sex ratio was 75% above the falls and 53% below the falls (Zerrenner 2001 [270]). Because larval densities are lower above the falls (not many lamprey make it over the falls to spawn) it seems that sex ratio in Lewis Creek is correlated with ammocoete density. In Lake Champlain the sex ratio data is surprisingly limited. Ratios varied between Lewis Creek, Indian Brook, and Stone Bridge Brook. Indian Brook and Stone Bridge Brook had limited sample sizes. There is not enough data to calculate sex ratios for Lake Champlain from Vermont tributaries for high and low lamprey abundance. When modeling a population the sex ratio should reflect the abundance of the model population. I recommend that in the initial generations the model use ratios corresponding to high abundance and calculations for later generation in the model take into account the shift towards females (if the reduction in lamprey abundance in the model is greater than 60%).
- e. *Spawning – Stream allocation*: Lampreys do not select natal streams during spawning migration (Bergstedt & Seelye 1995 [101]; Vrieze & Sorensen 2001 [237]). However, migratory lampreys do select streams based on olfactory cues including natural stream odor and larval odor. In laboratory studies it has been found that stream water can be diluted over 1000 times and larval odor over 100,000 times before they lose their potency. Water is most attractive for migrating lampreys when it has both stream and larval odor. Therefore allocation of lamprey among tributaries is dependent on at least two factors: stream discharge and larval abundance. Spangler *et al.* (1985 [247]) developed a formula for stream allocation (portion allocated = $0.5 * (\text{discharge} / \text{total discharge}) + 0.5 * (\text{larvae} / \text{total larvae})$) that is intuitively correct.
- f. *Spawning – Pre-spawn survival*: The migration of lamprey during spawning is highly traumatic. It is possible that not all lampreys that migrate into the tributaries survive to

spawn. Lampreys do not feed during migration and spawning and so individuals with low energy reserves and body condition may die before mating. The only estimate (0.91) that I could find on pre-spawn survival is from a study on the Big Garlic River (Lake Superior) where 370 migrants were released into a section of the river (81% males) (Hanson and Manion 1980 [230]). 35 individuals were found dead before spawning commenced.

- g. *Spawning – Female spawners (p of females)*: This estimate (0.61) comes from a study on ammocoetes in the Big Garlic River (Manion & McLain 1971 [229]). Manion and McLain (1971) released 296 females into partitioned sections of the river and observed that only 182 females spawned. Based on nest counts, they did not overlook many spawning events. There were 206 nests in the sections where the released lampreys were restricted. Of these nests only 161 had eggs, and therefore they represented 161 matings. Approximately 10% of matings in lampreys are polygamous (Manion and McLain 1971, Manion *et al.* 1988 [252], Hanson & Manion 1980 [230]). Therefore based on nest data approximately 177 females (0.60 of all females) spawned. This is consistent with the estimate from the number of mating females Manion and McLain (1971) observed. Physiologically it is feasible that not all females entering a tributary in a spawning run will spawn. Loss of energy reserves during the migration may not be great enough to cause mortality, but body conditioning may be so reduced that an individual female may not spawn. This is supported by Applegate's (1950 [267]) analysis of the proportion of unspawned eggs after mating events. He observed four females (n = 40) with uncharacteristically high egg retention (19.4, 19.4, 28.6, and 37.3%). He suspected that these individuals could not complete the spawning act before their approaching death. It is possible that some females are even more exhausted and may not spawn at all. I have not seen any mention of this phenomenon in the literature. This loss from total potential spawning run fecundity has not been taken into account in any models.
- h. *Spawning – Mating (proportions monogamous/polygamous/polyandrous)*: Polygamous matings in lampreys represent around 10% of all matings (Manion & McLain 1971 [229], Hanson & Manion 1978 [249], Hanson & Manion 1980 [230], Manion *et al.* 1988 [252]).
- i. *Spawning – Spawned nests*: Not all nests observed in a spawning season have eggs (Weise & Pajos 1998 [147], Manion & McLain 1971 [229], Hanson & Manion 1980 [230]). Therefore, only a proportion of nests are successful. Although there are limited data on this, the proportion of nests with eggs is probably dependent on the sex ratio. Males initiate nest building and construct nests even with no females present. If there is an excess of males in the spawning population, there will be more empty nests that were constructed by males. Even when the sex ratio is even there seems to be an excess of nests. The sex ratio of Salem Creek (Weise & Pajos 1998) was not reported (0.86 successful nests), however, around 1989 in Lake Ontario the sex ratio was close to 50%.
- j. *Spawning – Fecundity*: There is great variability in fecundity of lampreys (Applegate 1950 [267]; Wigley 1959 [266]; Manion 1972 [174]; Heinrich *et al.* 1980 [40]; Manion & Hanson 1980 [176], Johnson *et al.* 1985 [259]; Spangler *et al.* 1985 [247]; Eshenroder *et al.* 1987 [244]). A significant portion of this variation is explained by size of females.

Therefore, there have been attempts to develop regressions that would predict fecundity based on length or weight (Spangler *et al.* 1985; Eshenroder *et al.* 1987). The regression estimates from the Spangler model (fecundity = 12,107 + 205.6*length) seem too high. The regression from St. Mary's River (fecundity = -89,428 + 367.7* length) seems closer to fecundity estimates of females (Eshenroder *et al.* 1987). Fecundity estimates vary among the Great Lakes because fecundity is tied to length/weight of a female and most likely prey abundance (resources available to apportion to reproduction). It is logical that estimates from a lake that has mean length/weight and productivity similar to Lake Champlain be used in the model. The mean length in Lake Champlain (1996-2000, based on Lewis Creek and Great Chazy River) is 460.5 mm (320-598 mm) for females and 464.0 mm (209-603 mm) for both sexes, and the average weight of female lampreys is 215 g (80-430 g) and 211 g (94-581 g) for both sexes. The mean length in Lake Champlain is closest to Lake Ontario (468 mm). The productivity of these two lakes is also similar. In Ontario fecundity was estimated to be 107,429 eggs/female (53,164-162,439) (Johnson *et al.* 1985 [268]). However, the mean weight of Lake Champlain lampreys is 211 g, much lower than in Ontario (286 g). The mean weight in Lake Champlain is closer to Lake Superior (205 g). Lake Superior has lower productivity than Champlain and shorter mean sea lamprey length (430 mm). The mean lamprey fecundity in Superior was 70,451 eggs/female, lower than in Ontario (Johnson *et al.* 1987). I recommend that an intermediate value between Lake Ontario and Lake Superior be used for Champlain. There are two reasons: 1) Lake Champlain is more productive than Lake Superior and therefore lamprey likely have higher fecundity than in Superior. 2.) Mean weight of Champlain lamprey is lower than in Ontario and so fecundity is likely lower than in Ontario. Therefore, the fecundity I list is 89,000 eggs/female, half way between the Superior and Ontario estimates. This figure seems reasonable because it is very close to the fecundity of Lake Erie females (94,344) (Johnson *et al.* 1987). This is consistent with comparison of mean length and productivity of Erie and the other three Lakes mentioned. The mean weight of Champlain lamprey is surprisingly lower than in all the Great Lakes. It may be due to the fact that the abundance of lampreys is so high that there is a very low prey/predator ratio in Champlain.

- k. Spawning – Egg retention. Egg retention (0.022) in females after spawning reduces potential fecundity (Manion & Hanson 1980 [40]). The Manion and McLain (1971 [229]) estimate of 2.2% is based on 28 females from Lake Superior. The Hanson and Manion (1978 [249]) estimate of 1.2% is based on 10 females. Applegate's (1950 [267]) estimate of 5% is based on 40 females. For several reasons the Manion and McLain (1971) estimate is the most accurate and should be used: 1) In all cases egg retention is obtained by estimating the potential fecundity of a female from a length/fecundity regression and counting eggs retained in that female after spawning. Applegate (1950) used the length of the spent female (post-spawn length) to estimate potential fecundity. However, the length of a female decreases around 17% during spawning (Manion & McLain 1971) due to gradual deterioration of the animal (about 10% for males). This spawning deterioration caused Applegate to underestimate potential fecundity and overestimate egg retention. Manion and McLain (1971) used females that were captured as they migrated up tributaries and then released to spawn. The length they measured was therefore the true length of the female and so their estimates of fecundity and egg retention are more

accurate. 2) Four of the females (19.4, 19.45, 28.6, and 37.2% egg retention) Applegate (1950) sampled were collected at the end of the spawning season and they inflated his egg retention estimate. These females were too close to death to complete spawning, and therefore the egg retentions they exhibited are not values for a typical spawning event. I therefore also recommend that these high values not be included in the range. 3) The Hanson and Manion (1978) estimate is within the range of Manion and McLain (1971), but it was obtained from a smaller sample size and therefore is not as accurate.

- l. Spawning – Egg deposition. Although lampreys have a high fecundity the fraction of zygotes that survive to emerge as pro-larvae is proportionately small (Manion & Hanson 1980 [40]). There is evidence that majority of egg loss is due to non-nest deposition. Based on eggs removed from 74 sea lamprey nests and predicted fecundity, Manion and Hanson (1980) estimated only 0.14 eggs were deposited in nests. However this calculation is not completely consistent with data on the number of eggs counted in nests by Manion (1968 [39]). The proportion overestimates the number of eggs Manion (1968) should have found by 200%. To calculate non-nest deposition Manion and Hanson (1980) used an egg retention estimate of 5% (Applegate 1950 [267]). As I describe in (i) this is an overestimate and 2.2% is a more accurate estimate of egg retention. In addition, Manion and Hanson (1968) based their predicted fecundity on the mean length of lamprey (489mm) and the fecundity regression for Lake Huron from Applegate (1950), which gave them a predicted fecundity of 79,000 eggs/female. However, the lampreys in Manion and Hanson (1980) were captured in Lake Michigan. The mean fecundity in Lake Michigan reported by Johnson *et al.* 1987 [268] was 82,000 eggs/female. The mean length and weight of the lampreys in Manion and Hanson (1980) was 489 mm/270 g. Weight seems to be more closely correlated with lamprey fecundity of different lakes than length (Johnson *et al.* 1987 [269]). I believe Manion and Hanson (1980) used an underestimate of fecundity and a value of 89,000 is more appropriate. This estimate is intermediate between means for lampreys from Michigan (452 mm/264g - 82,000) and Erie (481mm/277g - 94,000) (Johnson 1987 [268]). If this is taken into account, based on 2.2% egg retention and the higher fecundity values, the egg loss due to nest deposition is 0.12. The only other source of data available to estimate egg loss is from Manion (1968) in which he counts the number of eggs (stage 13-16) in 19 nests in the Little Garlic and Traverse River (Michigan). This is based on 27 females because in 8 nests 2 females spawned. Based on 0.88 egg survival, nest deposition observed by Manion (1968) was only 0.06. The weighted mean of these two estimates is 0.10 which is what I believe should be used.
- m. Zygote (in nest) - Egg survival/hatching success (including deposition loss): Manion (1968 [39]) estimated hatching success to be 0.06 by dismantling nests 13-15 days after deposition by the females. His estimate therefore includes loss due to non-nest deposition. At this age the lampreys are in stages 13-16 of development (Piavis 1971 [239]). Lampreys begin to emerge in stage 17 approximately 17-25 days after deposition (depending on temperature and probably some other factors) (Piavis 1971).
- n. Zygote (in nest) - Emergence (including deposition loss): Applegate's (1950 [267]) estimate (0.007) is for emergence during stage 17 (Piavis 1971 [239]) and also includes

losses due to non-nest deposition. Applegate obtained this estimate by collecting all pro-larvae that emerged and were swept into funnel nets downstream from the nests 18-22 days after deposition. For three mating events Applegate placed a barrier around the each nest to prevent escape of the pro-larvae. The barrier had no significant effect on hydrological patterns around the nest or on the spawning behavior of the two lampreys. He collected all emergent larvae (larvae leave nest 18-20 days after deposition [Piavis 1971]). Two factors account for the drastically lower emergence estimate of Applegate compared to Manion's egg survival/hatching success (1968 [39]). The first is that mortality during the last several days of stage 16 and development into stage 17 may be high. The second factor is that a large number of larvae that develop may not be able to emerge because they are trapped in the nest. I think that Applegate's emergence success should be used in the model rather than Manion's hatching success because it is of actual emerging larvae. This value is also more consistent with information on ammocoete abundance in streams (Zerrenner 2001 [270]). Eshenroder (1987 [244]) used an estimate of 0.01 for the St Mary's River sea lamprey population model.

- o. *Zygote (in nest) - Egg survival*: Egg survival to Stage 13-16 has been estimated to be high in nests (0.88) (Hanson & Manion 1978 [249], Manion & Hanson 1980 [40]). Eggs hatch in stage 14 about 10-13 days after fertilization (Piavis 1971 [239]). The egg survival estimate from the Big Garlic River was calculated from 7 nests sampled 13-22 days after deposition when lampreys were in stage 15-16 of development. (Hanson & Manion 1978, Manion & Hanson 1980). Stage 16 occurs immediately before the pro-larvae emerge during the burrowing stage (Piavis 1971). This egg survival estimate is consistent with laboratory studies (Piavis 1971). Piavis (1971) observed that 78% eggs incubated at constant "optimum" temperature (18.4°C) developed to age 17 (burrowing stage). Egg survival was drastically reduced when the constant temperature deviated from optimum temperature. At 15.5°C only 12% of eggs developed to Stage 17 and at 21.1°C only 5%. However, eggs are not as sensitive to temperature fluctuations (stream temperatures fluctuate daily). When subject to fluctuations of 18.4°C – 23.9°C (mean 18.4°C) and 15.5°C – 21.1°C (mean 18.4°C) development to Stage 17 was 95% and 82%, respectively. However, large fluctuations in stream temperature that subject eggs to drastically different temperatures for longer periods of time will significantly reduce egg survival and development. I recommend egg survival of 0.88 be used in the model.
- p. *Zygote (in nest) - Emergence (excluding deposition loss)*: This estimate (0.074) is just Applegate's (1950) emergence success modified to exclude loss due to non-nest deposition.
- q. *Zygote (out of nest) – Non-nest deposition*: Non-nest deposition occurs at a very high frequency (0.86) (Manion & Hanson 1980 [40]). There is no data on survival and development of lamprey eggs deposited outside nests. Some insight into production from eggs deposited outside of nests may be gained by considering the survival and development of walleye eggs. Walleye require spawning substrate and physiological conditions for egg development similar to lamprey. Lamprey spawn in water temperature between 10-26.1°C, in unidirectional flow (0.5-1.5m/s), over sand or gravel (0.9-5.1 cm diameter), and in depth between 13-170 cm (Applegate 1950 [266], Manion & Hanson

1980 [40]). They prefer the upstream edges of graveled riffles or riffle area proper and construct nests (Manion and Hanson 1980 [40]). Walleye spawn in water temperatures between 5.6-11.1°C, depth of 0.10-0.9 m and over many types of substrate, but are broadcast spawners (Colby *et al.* 1979 [268], Corbett & Powles 1986 [269]). Walleye primarily spawn over gravel or cobble substrate and their eggs are distributed throughout the spawning region. Significant egg production only occurs on substrate that provides protection yet allows sufficient oxygen to be transferred to the eggs. These physical parameters are mainly dependent on water flow and size of substrate. In areas with slow water velocity, material settles down on the bottom and interferes with oxygen transfer to eggs. Oxygen concentrations are low at the mud-water interface and hydrogen sulfide concentrations are high near woody debris, both of which are detrimental to egg development (Colby *et al.* 1979). In high water flow there is larger substrate and greater amount of available oxygen. Egg survival is greatest on gravel rubble, less on fine sand, and minimal on soft muck (Colby *et al.* 1979). Corbett and Powles (1986) found egg survival on gravel, sand, and mud-detritus to be 52%, 21%, and 7%, respectively. It seems reasonable that the egg survival requirements for lamprey are similar to walleye. Therefore the reduction in lamprey egg survival on sub-optimal substrate (based on walleye egg survival) would make egg development in those areas minimal. However, eggs that land on gravel-cobble substrate would have survival comparable to nest-deposited eggs. Non-nest production then will be dependent on what proportion of non-nest deposited eggs land on suitable substrate. This is going to be dependent on the hydrology of that spawning section. Many spawning sites are in runs immediately upstream from deeper pools or slower water. In these areas there will be no significant non-nest production of eggs because they will be washed onto muck after spawning. However, in areas where spawning grounds are large and on long sections of gravel-cobble riffles a significant proportion of eggs may land among gravel/cobble and develop. If this were true, it would be advantageous for lampreys to position nests on the upstream section of riffles or riffle proper – which are the nesting areas lampreys prefer (Manion & Hanson 1980). If 1 out of 100, 1 out of 50, or 1 out of 10 eggs land on favorable substrate, non-nest deposited eggs will account for 8%, 15%, or 43% of larval production. I put in a simple formula that can be used to estimate non-nest egg production. It is simply (non-nest egg production) = (proportion of eggs deposited outside nests)*(proportion of eggs that land on suitable substrate)*(emergence) = $0.9 * P * 0.074$. This allows one to include the contribution of non-nest deposited eggs in the model. If you want to simplify the model simply make $P = 0$ and only eggs in the nest emerge. If you want to examine how non-nest deposition may affect the population you can alter the proportion of eggs that land in suitable habitat.

- r. *Ammocoetes* – Survival ($t = \text{age in years}$) for each age class) age-0, 1, 2, 3, 4... t: There is evidence that survivorship of ammocoetes, especially in the age-0 class is density dependent. However, evidence for this has been found in experimental studies where the densities of larvae have been higher (25 ammocoetes/m² for low density and 75 lamprey/m² for high density, Morman 1987 [53]) than under natural conditions (around 4 larvae/m² in Lewis Creek and 1/m² in Morpion/Pike River, (Zerrenner 2001 [270]) (Mallatt 1983 [54], Murdoch *et al.* 1982 [52], Morman 1987 [53]). In natural settings, based on information following TFM treatment Purvis (1979 [248]) and Weise and Pajos

(1998 [71]) both found evidence that the first ammocoete cohort has greater growth rate and survivorship, and that this cohort reduces the growth rate of the subsequent cohorts the following years. It is hypothesized that this is due to growth inhibitors exuded by larval lamprey because food intake is not believed to be a limiting factor even at high densities. The density effect appears greatest in the age-0 age class where the larvae are theoretically most sensitive to interference. From this information Spangler *et al.* 1985 [247] created the regression of density and age-0 survival ($p = -0.006*(\text{density}) + 0.28$). He also believed that age-1 survival ($p = -0.013*(\text{density}) + 0.56$) is strongly density dependent even though overall survival may be higher. Survival of older age classes in Spangler *et al.*'s (1985) model is constant (0.7). Contrary to this model, Jones *et al.* (2002 [267]) did not find conclusive evidence for increased survival and growth rate of the first year class following decrease in density due to TFM treatment in a survey of 24 Great Lakes tributaries. It seems that in most tributaries the density of ammocoetes is not high enough to observe density dependent effects and there may be more important environmental variables that influence survival under those conditions. The age-0 survival (0.26) and age-1 (0.51) survival in the table were obtained from Spangler *et al.*'s (1985) regressions and from ammocoete densities estimated for Lewis Creek by Zerrenner (2001). It is generally agreed that survival of the age-0 class is significantly less than for succeeding age classes. Therefore age-0 should remain separate from any age classes that are combined in a model. The survival estimates from this model are consistent with knowledge about the different age classes, however, Spangler *et al.* (1985) does not describe how the estimates were obtained.

- s. *Ammocoetes – Survival (t = age in years) for each age class) age-0, 1, 2, 3, 4... t:* This estimate came from a population model for the Saint Mary's River (Eshenroder 1987 [244]). The length-frequency distribution at St. Mary's River was used to construct an age-frequency distribution using the Bertalanffy growth model. From the slope of the right limb of the age distribution the survival rate (0.66) was obtained. The main problem with this method is that for any given age class the length is very variable, especially in older age classes (4+), and so attempts to predict age distribution by length frequency data are problematic. Even predicting transformation based on length has proven to be very difficult. The authors noted these problems in the description of the model. They used this method because there were no other approaches available to them (still presently a problem) that would provide a more rigorous estimate of survival. Despite the shortcomings their model does provide reasonable estimates of both survival and transformation.
- t. *Ammocoetes – Survival (t = age in years) for each age class) age-0, 1, 2, 3, 4... t:* This estimate is from draft of Jones *et al.* (2002 [260]) and there is no information as to where this estimate was obtained. The estimate (0.3) is for survival from emergence through transformation. It is much lower than other ammocoete survival estimates (Eshenroder *et al.* 1987 [244], Spangler 1985 [247]), Zerrenner 2001 [270]), inconsistent with studies on age class distribution (Eshenroder *et al.* 1987, Zerrenner 2001), and mortality in cage studies (Morman 1987 [53]). Based on ammocoete research, it appears that larval survival (except for age-0 class) is much higher than 0.3. Jones *et al.* (2002) did make some notable observations on changes in age-0 and age-1 recruitment due to TFM

treatment in 24 tributaries. They found recruitment significantly varied among streams even when adult stock size was taken into account. This may be a result of great variability in survivorship of eggs or ammocoetes at a particular age class due to biological and/or environmental factors. They did not find conclusive evidence for compensator mechanisms in lamprey because of the variability in the data. There was also no covariance between stream type (alkalinity and temperature class) and the regression intercept. There was evidence of density dependent survival from spawning to age 1, but they concluded that density independent variation will be responsible for more inter-annual variation than density dependent variation, and so did not include density/survivorship regressions for age-0 and age-1 in their model.

- u. *Ammocoetes – Survival ($t = \text{age in years for each age class}$) age-0, 1, 2, 3, 4*: The survivorship of each age class was estimated from change in the abundance of each age class from 1999 to 2000 (Adam Zerrenner 2001 [270]). This study was conducted in Lewis Creek, Pike River, and Morpion Stream. The abundance for Pike River and Morpion Stream was combined because ammocoetes in Morpion Stream could migrate into Pike River. These estimates seem consistent with the high survivorship found in a study in which ammocoetes were kept in cages placed in tributaries for 4.5 years (Morman 1987 [53]).
- v. *Ammocoetes – Survival ($t = \text{age in years}$) for each age class) age-1 - 4.5*: Morman (1987 [53]) conducted an experiment in the Jordan River and White River that examined the effect of density on growth rate. He observed that survival was density dependent. In low-density groups he observed survivorship of 95%, and in high-density groups survivorship was around 60%. However, because even the low density (25 larvae/m²) was much higher than larval densities in Champlain tributaries, density effects are most likely minimal in Champlain (density in Lewis Creek averaged 4 larvae/m² in 1999 and 2000). His study confirms Zerrenner (2001 [53]) survivorship estimates and shows that the survivorship of ammocoetes can be very high. One factor of mortality not present in his study was predation. However, there is minimal predation on ammocoetes because they are buried in substrate and so natural survivorship should be similar to what Morman (1987) estimated.
- w. *Ammocoetes – Transformation rate age-0 – 3, 4, 5, ..., t*: Metamorphosis is believed to be in part dependent on growth rate (Eshenroder 1987 [244]). Tributaries in which ammocoetes have higher growth rates tend to have earlier transformation and higher transformation rates. In addition, there is evidence density influences transformation (through its effect on growth rate). Based on this, Spangler *et al.*'s (1985 [247]) predicts age-4 transformation ($p = -0.01 * (\text{density}) + 0.1$) is density dependent. The transformation of latter age classes (0.01 in tributaries, 0.02 in lakes) is not dependent on density in his model (Spangler *et al.* 1985).
- x. *Ammocoetes – Transformation rate Yearly combined transformation rate (length > 116 mm)*: This estimate came from a population model for the Saint Mary's River (Eshenroder 1987 [244]). Transformation was estimated to be 0.05 (for age classes with length > 116 mm) from St. Mary's River ammocoete age frequency distribution by

assuming mortality was constant and that transformation began when age class length equaled 116 mm. This model estimate is consistent with St. Mary's River data that show 8.3% of animals greater than 116 mm transform each year in this tributary. The 0.05 transformation rate from this model (for length >116 mm animals) compares favorably to other estimates from tributaries where growth is slow. Transformation rates for Big Garlic River, Deadhorse Creek, Marblehead Creek, and Hog Island Creek were estimated to be 1%, 4%, 4%, and 0.2% (Purvis 1979 [248]). These rates are lower than what has been found in tributaries with faster growth rates. Little Garlic River and Potato River (faster ammocoete growth rates) have transformation rates of 16% and 34% respectively. These ratios are cited in Eshenroder (1987), but when I examined the Purvis (1979) GLFC report there were no transformation rate estimates. I am assuming that Eshenroder obtained these rates for length > 116 mm ammocoetes from the data in Purvis (1979). The growth rates in Lewis Creek, Pike River, and Morpion Stream are similar to Little Garlic River based on mean length of age-3 and age-4 classes, and so transformation rates for tributaries with faster growth rates are probably more appropriate (Purvis 1979, Zerrenner 2001). In Lewis Creek, Pike River, and Morpion Stream, age-4 classes were longer than 116 mm and therefore these transformation estimates would be appropriate for age-class 4 and above.

- y. *Ammocoetes – Transformation rate age-0, 1, 2, 3, 4, 5, and 6:* Jones *et al.*'s (2002) transformation rates are from a model used to test control strategies. They do not describe where these estimates were obtained. It seems very unlikely that age-3 ammocoetes transform and the age-4 rate seems too high.
- z. *Ammocoetes – Transformation rate age-0, 1, 2, 3, 4, 5:* The transformation estimates are calculated simply from the proportion of age-4 and age-5 animals that were transformers in Lewis Creek (0.08 age-4, not available for age-5), Pike River (0.05 age-4, 0.92 age-5), and Morpion Stream (0.07 age-4, 0.86 age-5) (Zerrenner 2001 [270]).
- aa. *Ammocoetes – Transformation rate Proportion of all ammocoetes transformed:* These transformation rates were calculated from the percent of transformers among all ammocoetes after TFM treatment in Lake Champlain tributaries (Fisheries Technical Committee 2001). The pre-TFM (0.17 Lewis Creek, 0.18 great Lakes tributaries) values are from animals collected after the first treatment. This means that they are from an untreated population. This should be an approximation of the transformation rate for an entire larval population under age class equilibrium. If there is a shift to older age classes the proportion will be higher. If there is a shift towards younger year classes there will be a lower proportion of transformers. This is seen in the post-TFM estimates (0.02 Lewis Creek, 0.05 Great Lakes tributaries). These are estimates from animals collected in tributaries immediately after the second treatment. Because the previous TFM treatment was 4 years before, all ammocoetes were between age-0 and age-4. The transformation rate was subsequently lower than observed after the first round of treatments.
- bb. *Ammocoetes – Transformation rate age-4:* This estimate is from Morman's (1987 [53]) experimental study of density effect on growth (see annotation t). There is a large difference between the two rivers. However, the sample size was small (about 20 animals

in each tributary survived to 4 years) so it is hard to infer anything on transformation rate from his data.

APPENDIX D

Sea Lamprey Life History Model Parameter values and assumptions

- 1. Life Stage in Model:** Unfertilized eggs
Values listed below will limit (or contribute to) the number of adults that yield unfertilized eggs.
Management action: Adult trapping
Parameter entry into model: Fecundity of females
Mean and standard deviation: 88,000 ± 15,500 eggs
Justification: Mean and standard deviation from Lakes Ontario, Superior, Erie data. See Jan Janecka's literature search, section J for details.
Assumptions: Adult trapping will reduce the # of adults spawning in the tributary, and consequently the # of eggs spawned will be reduced. Carrying capacity: See carrying capacity section below.
Management effects: Management effects explored for this stage in the model would be reduction of adults in increments of 10%, from 10% to 90%.
- 2. Parameter in Model:** Sex ratio of adults
Values listed below will limit (or contribute to) the number of adults that yield unfertilized eggs.
Management action: None yet, but if it could alter the sex ratio (i.e. sex pheromones)?
Parameter entry into model: Percentage of females in adult population
Mean and Standard Deviation: 0.5 (this one isn't stochastic)
Justification: Mean of 0.5 is a default value. Local data from the USFWS adult trapping program can be applied.
Assumptions: Adult sex ratios in current spawning populations are 1:1.
Management effects: Management effects explored for this stage in the model would be altering percentage of females, in increments of 10%, from 10% to 90%.
- 3. Life Stage in Model:** Fertilization rate
Values listed below will limit (or contribute to) the number of unfertilized eggs that yield fertilized eggs.
Management Action: Sterilization of adult males
Parameter entry into model: Survivorship of unfertilized eggs to fertilized eggs (fertilization rate)
Mean and standard deviation: 0.9 ± 0.5
Justification: The literature search did not yield any information for this value, so 0.9 was applied as an "experienced estimate." Hence the high standard deviation, which will hopefully account for the unknown variable.
Assumptions: Management would involve use of sterilized males to reduce fertilization rate by some percentage.
Management effects: Management effects explored for this stage in the model would be reduction of fertilization rate in increments of 10%, from 10% to 90%.

4. **Life Stage in Model:** Hatchling (emergent larvae)

Values listed below will limit (or contribute to) the number of fertilized eggs that hatch (emerge), but have not yet burrowed.

Management action: Nest dismantling to reduce # of fertilized eggs

Parameter entry into model: survivorship of fertilized eggs into hatchling stage

Mean and standard deviation: 0.6 ± 0.3 (eggs in nest), 0.10 (eggs out of nest)

Justification: Mean and standard deviation for eggs in nest derived from Manion 1968, Manion and Hanson 1980, Hanson and Manion 1978, Applegate 1950.

- a. Eggs out of the nest – use 90% as an estimate that all eggs from a given female will be washed out of the nest, and 5% of those will survive to become age-0 larvae. This value is merely the chance that an egg washed out of the nest after fertilization will make it to become an age-0 larva. That is why the probability of survival for this one is higher than for eggs remaining in the nest, because it accounts for survival over a couple of life stages. This value is from Manion & Hanson (1980). See Janecka 2002 section Q for details.

Assumptions: There is no management for eggs that have been washed out of nest prior to nest dismantling. Nest dismantling will target *only* fertilized eggs in the nest.

Management effects: Management effects explored for this stage in the model would be reduction of fertilized eggs in nests in increments of 10%, from 10% to 90%.

5. **Life Stage in Model:** Age-0 larvae (young-of-year)

Values listed below will limit (or contribute to) the number of hatchlings that emerge and become age-0 larvae.

Management action: none (there is nothing we know of to reduce hatchlings, as they are defined in this model, but the model will tell us what an effect of management will be on them if something does come up in the future).

Parameter entry into model: Survivorship of hatchlings to age-0 larvae

Mean and standard deviation: 0.01 ± 0.005

Justification: Manion (1968) lists a value of 0.06 for lamprey just before they emerge, and Applegate (1950) has a value of 0.007 for after they emerge and have burrowed, and accounts for fertilized eggs, hatchlings, and age-0 larvae. Based on this information, a mean value of 0.01 ± 0.005 is used.

Assumptions: If an egg survives hatching, it has an equal chance to survive to age-0 despite if it hatched in or out of the nest. Management activities on hatchlings will be equally effective on hatchlings in or out of the nest. Carrying capacity: See carrying capacity section below.

Management effects: Management effects explored for this stage in the model would be reduction of hatchlings in increments of 10%, from 10% to 90%.

6. **Life Stage in Model:** Age-1 larvae

Values listed below will limit (or contribute to) the number of age-0 larvae that become age-1 larvae.

Management action: Chemical treatment of tributary (effective on age-0 larvae)

Parameter entry into model: survivorship of age-0 larvae to age-1

Mean and standard deviation: 0.26 ± 0.5

Justification: Mean value from Spangler model (1985) and Zerrenner data from Lewis Creek

(2001). See Janecka 2002 section R for details. Standard deviation is arbitrary.
Assumptions: Chemical treatment is equally effective on all larvae year classes and transformers, and is applied every 4 years.
Management effects: Management effects explored for this stage in the model would be reduction of age-0 larvae in increments of TFM or chemical toxicities of 50%, 60, 70, 80, 90, 95, 97, 98, and 99%.

7. **Life Stage in Model:** Age-2 larvae

Values listed below will limit (or contribute to) the number of age-1 larvae that become age-2 larvae.

Management action: Chemical treatment of tributary (effective on age-1 larvae)

Parameter entry into model: Survivorship of age-1 larvae to age-2

Mean and standard deviation: 0.93 ± 0.5

Justification: Mean value from Zerrenner data (2001). See Janecka 2002, section U for details. Standard deviation is arbitrary.

Assumptions: Chemical treatment is equally effective on all larvae year classes and transformers, and is applied every 4 years.

Management effects: Management effects explored for this stage in the model would be reduction of age-1 larvae in increments of TFM or chemical toxicities of 50%, 60, 70, 80, 90, 95, 97, 98, and 99%.

8. **Life Stage in Model:** Age-3 larvae

Values listed below will limit (or contribute to) the number of age-2 larvae that become age-3 larvae.

Management action: Chemical treatment of tributary (effective on age-2 larvae)

Parameter entry into model: Survivorship of age-2 larvae to age-3

Mean and standard deviation: 0.95 ± 0.5

Justification: Mean value from Zerrenner data (2001). See Janecka 2002, section U for details. Standard deviation is arbitrary.

Assumptions: Chemical treatment is equally effective on all larvae year classes and transformers, and is applied every 4 years.

Management effects: Management effects explored for this stage in the model would be reduction of age-2 larvae in increments of TFM or chemical toxicities of 50%, 60, 70, 80, 90, 95, 97, 98, and 99%.

9. **Life Stage in Model:** Age-4 larvae

Values listed below will limit (or contribute to) the number of age-3 larvae that become age-4 larvae.

Management action: Chemical treatment of tributary (effective on age-3 larvae)

Parameter entry into model: Survivorship of age-3 larvae to age-4

Mean and standard deviation: 0.81 ± 0.5

Justification: Mean value from Zerrenner data (2001). See Janecka 2002, section U for details. Standard deviation is arbitrary.

Assumptions: Chemical treatment is equally effective on all larvae year classes and transformers, and is applied every 4 years.

Management effects: Management effects explored for this stage in the model would be

reduction of age-3 larvae in increments of TFM or chemical toxicities of 50%, 60, 70, 80, 90, 95, 97, 98, and 99%.

10. Life Stage in Model Age-5 larvae

Values listed below will limit (or contribute to) the number of age-4 larvae that become age-5 larvae.

Management action: Chemical treatment of tributary (effective on age-4 larvae)

Parameter entry into model: Survivorship of age-4 larvae to age-5

Mean and standard deviation: 0.88 ± 0.5

Justification: Mean value from Zerrenner data (2001). See Janecka 2002, section U for details. Standard deviation is arbitrary.

Assumptions: Chemical treatment is equally effective on all larvae year classes and transformers, and is applied every 4 years. For transformation rates, see transformer stage (12) below.

Management effects: Management effects explored for this stage in the model would be reduction of age-4 larvae in increments of TFM or chemical toxicities of 50%, 60, 70, 80, 90, 95, 97, 98, and 99%.

11. Life Stage in Model: Age-6 larvae

Values listed below will limit (or contribute to) the number of age-5 larvae that become age-6 larvae.

Management action: Chemical treatment of tributary (effective on age-5 larvae)

Parameter entry into model: Survivorship of age-5 larvae to age-6

Mean and standard deviation: 0.9 ± 0.5

Justification: Mean value is based on “educated estimates”, as there is not any data available on survivorship for age-5 to 6 larvae. Standard deviation is arbitrary.

Assumptions: Chemical treatment is equally effective on all larvae year classes and transformers, and is applied every 4 years. For transformation rates, see transformer stage (12) below.

Management effects: Management effects explored for this stage in the model would be reduction of age-5 larvae in increments of TFM or chemical toxicities of 50%, 60, 70, 80, 90, 95, 97, 98, and 99%.

12. Life Stage in Model: Transformer

Values listed below will limit (or contribute to) the number of age-4, 5, and 6 larvae that become transformers.

Management action: Chemical treatment of tributary (effective on Ages 4,5, and 6 larvae)

a. *Parameter entry into model:* transformation rate of age-4 larvae to transformer

Mean and standard deviation: 0.07 ± 0.03

Justification: Mean and standard deviation from Zerrenner (2001) for Morpion Stream data. See Janecka 2002, section Z for details.

Assumptions: This value is based on a rate from Lake Champlain data. Density, size, and other factors that may induce transformation are not specifically accounted for within the model. Any of those assumptions must be incorporated into the parameter entry above. Chemical treatment is equally effective on all larvae year classes and transformers, and is applied every 4 years.

- b. *Parameter entry into model:* transformation rate of age-5 larvae to transformer
Mean and standard deviation: 0.86 ± 0.05
Justification: Mean and standard deviation from Zerrenner (2001) for Morpion Stream data. See Janecka 2002, section Z for details.
Assumptions: Same as larvae becoming transformers after age-4 above
- c. *Parameter entry into model:* Survivorship of larvae age-6 to transformer
Mean and standard deviation: 0.9 ± 0.5
Justification: Mean value is based on “educated estimates”, as there is not any data available on survivorship for age-5 to 6 larvae. Standard deviation is arbitrary.
Assumptions: If a larva makes it through age-6, it will become a transformer, or it will die. Chemical treatment is equally effective on all larvae year classes and transformers, and is applied every 4 years.

Management effects: Management effects explored for this stage in the model would be reduction of Ages 4, 5, and 6 larvae that are going to become transformers in increments of TFM or chemical toxicities of 50%, 60, 70, 80, 90, 95, 97, 98, and 99%.

13. **Life Stage in Model:** Parasite

Values listed below will limit (or contribute to) the number of transformers that become parasites.

Management action: Chemical treatment on transformers.

Parameter entry into model: Survivorship of transformers to parasites

Mean and standard deviation: 0.8 ± 0.5

Justification: Mean value is based on “educated estimates”, as there are no data available on survivorship for transformers to parasites. Standard deviation is arbitrary.

Assumptions: Chemical treatment is equally effective on all larvae year classes and transformers, and is applied every 4 years. Transformers that make it to the lake and begin life as a parasite will not have any fidelity to their natal tributary, and parasites from all tributaries will mix into a pool before selecting a tributary to spawn in as an adult.

Management effects: Management effects explored for this stage in the model would be reduction of treatments in increments of TFM or chemical toxicities of 50%, 60, 70, 80, 90, 95, 97, 98, and 99%.

14. **Life Stage in Model:** Adult spawner

Values listed below will limit (or contribute to) the number of parasites that become adult spawners.

Management action: Capture of parasites by anglers (?)

Parameter entry into model: Survivorship of parasite to adult spawner

Mean and standard deviation: 0.35 ± 0.30

Justification: Mean and standard deviation from Mullett (2002) for Lakes Huron and Superior data. See Jan Janecka’s literature search, section A for details.

Assumptions: Parasites will mature to adults before selecting a stream to spawn in. Effect of anglers removing lamprey they catch on boats, fish, etc. is probably minimal with regard to the overall population in the entire lake, so the management effects explored for this stage will be substantially lower than those for previous stages.

Management effects: Management effects explored for this stage in the model would be reduction of # of parasites in increments of 0.01%, from 0.01% to 0.09%.

CARRYING CAPACITY

Remember, these values are to be the *extreme maximum* number that could possibly be used to limit the respective life stage.

1. Limitation on # of female spawners by spawning habitat:

This is merely a cap on the number of females that can spawn in a given tributary because there is a finite amount of habitat for lamprey to spawn in. This will, in effect, limit the number of eggs that can be deposited.

The assumptions to calculate this value are as follows:

- a. 4 nests/m²
- b. each spawning pair will work on a nest for 2 days
- c. period of entire spawning run is 4 weeks (28 days). This means that a given nesting site will be utilized by a maximum of 14 spawning pairs, or 7 females (in 1:1 sex ratio).
- d. multiply amount of m² spawning habitat as determined by USFWS QAS surveys by 4 nests/m², then by 7 females.

For example, on the Poultney River, the QAS survey estimates 7,966 m² of spawning habitat. This works out to (7,966 m²)* (4 nests/m²) * (7 females/nest) = 223,048 females as a maximum number that can effectively lay eggs in the Poultney River. There may be more than that coming in, but anything beyond the K will kill the eggs spawned there previously. Hence, this is actually a limit on the number of eggs that the tributary can hold (to find this, simply multiply 223,048 by fecundity, but the model doesn't need this value.)

2. Limitation on # of hatchlings that become age-0 larvae by larval habitat availability:

Here we use a Beverton-Holt carrying capacity calculator. The formula for this is:

$$(a) / [(1+(a))/(K_L - b)]$$

where (a) is the number of hatched eggs trying to move into age-0, (b) is the number of resident larvae from the previous year that will remain as larvae in the current year.

The sum all of the larvae from the previous year that want to stay as larvae is then subtracted from the returned value of the formula above. This returns the number of hatched eggs that will move into age-0 for a respective tributary.

This formula essentially creates an asymptotic curve from the beginning of the population, so that the population is somewhat limited by density, no matter how close

the population is to K . However, the closer the population gets to K , the more impact the formula has on limiting the number of lamprey moving into age-0.

The K_L is determined by taking the highest densities observed in a tributary, increasing this value by two standard deviations, and multiplying by the total amount of larval habitat in the respective river. By default, the K_L for the Winooski River will be used (26,000,000 larvae). This assumes that all age classes of larvae require the same amount of space.

3. Limitation on # of transformers that become parasites:

This is another straight cap, similar to the spawning K . This one comes into effect as transformers move into the parasite stage. To determine the K_p , the mark-recapture values to date from the tagging experiment were used in a Lincoln-Peterson estimator to calculate the current population of parasites, which is estimated to be at the highest level ever seen in the lake. The value from the population estimate was then increased by 2 standard deviations to return a maximum number of 650,000.

Each tributary is then limited, if K_p is reached, by the proportion of parasites that it is trying to contribute to the lakewide population. In later versions of the model, we will probably try to use a K_p set by the number of salmonids in the lake that can support a given parasitic lamprey population, rather than the method currently applied.