



A life cycle approach to modeling sea lamprey population dynamics in the Lake Champlain basin to evaluate alternative control strategies

Eric A. Howe ^{a,*}, J. Ellen Marsden ^{b,1}, Therese M. Donovan ^{c,2}, Roland H. Lamberson ^{d,3}

^a Rubenstein School of Environment and Natural Resources, University of Vermont, Burlington, VT 05405, USA

^b Rubenstein School of Environment and Natural Resources, University of Vermont, Burlington, VT 05405, USA

^c U.S. Geological Survey, Vermont Cooperative Fish and Wildlife Research Unit, University of Vermont, Burlington, VT 05405, USA

^d Department of Mathematics, Humboldt University, Arcata, CA 95521, USA

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ABSTRACT

Sea lamprey (*Petromyzon marinus*) is a nuisance species in the Laurentian Great Lakes and Lake Champlain that has devastated native fish populations and hampered sport fisheries development. We developed a modified stage-based life history matrix for sea lamprey to analyze the effects of various management efforts to suppress sea lamprey population growth in Lake Champlain. These efforts targeted different life stages of the sea lamprey life cycle. A beta distribution was used to distribute stochastic larval populations among twenty sea lamprey-bearing tributaries and five deltas to Lake Champlain, from which sea lamprey that survive through larval metamorphosis were then pooled into a lake-wide parasitic-phase population. Parasitic-phase survival to the spawning stage was evaluated based on proximity to the natal tributary and on the size of the resident larval population in each tributary. Potential control strategies were modeled at egg to emergence, larval, and spawning stages to reduce vital rates at each stage, with the goal of suppressing parasitic-phase production. Simulations indicate that control of the larval stage was essential to achieving this goal, and with supplemental effort to reduce the vital rates at early life stages and at the spawning stage, the parasitic-phase population can be further suppressed. Sensitivity simulations indicate that the life history model was sensitive to egg deposition rate, abundance of parasitic-phase sea lamprey from unknown, uncontrolled sources, and the method in which parasitic-phase sea lamprey select tributaries for spawning. Results from this model can guide management agencies to optimize future management programs.

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Introduction

Sea lamprey (*Petromyzon marinus*) parasitize lake trout (*Salvelinus namaycush*) and other commercially and recreationally important fishes in the Great Lakes and Lake Champlain. This parasitism has had significant ecological and economic impacts, and has inhibited restoration of sport fisheries. Early methods to restrict sea lamprey population growth included the application of two chemical pesticides highly selective for sea lamprey, TFM (3-trifluoromethyl-4-nitrophenol) and Bayluscide (Bayer-73, or niclosamide; Smith and Tibbles, 1980), and the construction of barriers to spawning habitat in tributaries. More recently, concerns have arisen about potential

impacts of TFM on non-target species (e.g., the mudpuppy, *Necturus maculosus*; Boogaard et al., 2003; Matson, 1990).

Although modern sea lamprey control programs still rely heavily on these lampricides, management agencies have adopted integrated pest management (IPM) principles, which have proven to be successful in managing insect pest populations (Sawyer, 1980; Smith and Swink, 2003). For example, managers in the Great Lakes and Lake Champlain now use multiple control methods to reduce survival at different stages in the sea lamprey life cycle (Christie and Goddard, 2003; Marsden et al., 2003).

Currently, 25 tributaries and six deltas in the Lake Champlain basin are known to contain larval populations of sea lamprey. Permanent barriers to sea lamprey spawning migrations are in place on two rivers (Great Chazy River, NY and Lewis Creek, VT); these barriers limit the amount of spawning habitat available to sea lamprey (Fig. 1). Five other tributaries (Sunderland Brook, Malletts Creek, Trout Brook, Pike River, and Morpion Stream) are blocked on a seasonal basis and trapped sea lamprey are removed to reduce the number of spawning-stage adult sea lamprey (Wayne Bouffard, USFWS, pers. comm, 2005; Fig. 1). As of 2005, lampricides had been applied to 14 tributaries and five deltas to reduce survivorship at the larval

* Corresponding author at: Lake Champlain Basin Program, 54 West Shore Rd., Grand Isle, VT 05458, USA. Tel.: +1 802 3723213.

E-mail addresses: ehowe@lcbp.org (E.A. Howe), Ellen.Marsden@uvm.edu (J.E. Marsden), Therese.Donovan@uvm.edu (T.M. Donovan), rhl1@humboldt.edu (R.H. Lamberson).

¹ Tel.: +1 802 656 0684.

² Tel.: +1 802 656 2516.

³ Tel.: +1 707 826 4926.

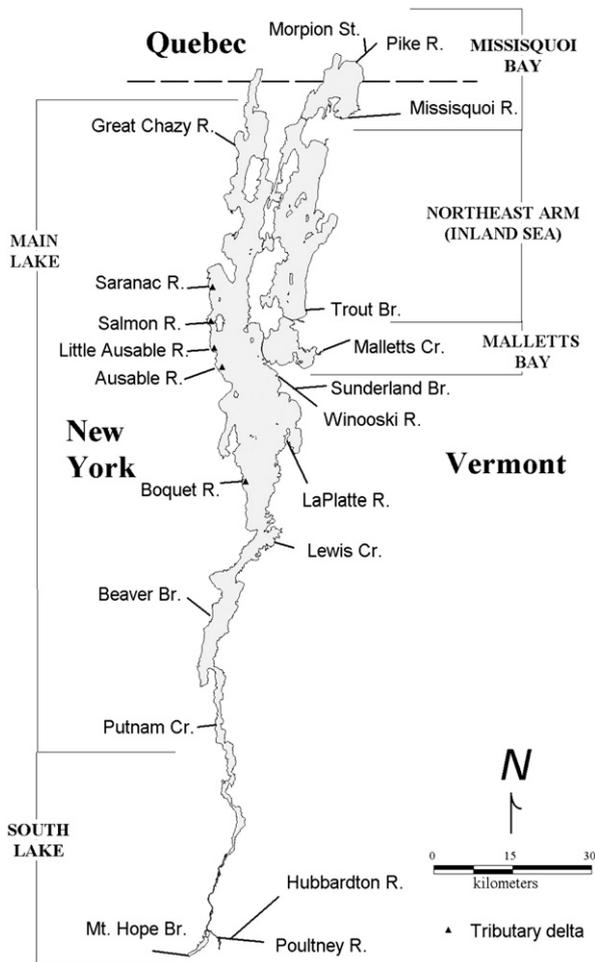


Fig. 1. Map of Lake Champlain with the tributaries, deltas, and basins in the sea lamprey life history model.

and transformer stages of the life cycle. These efforts are coordinated by the Lake Champlain Fish and Wildlife Management Cooperative, representing three of the U.S. jurisdictions managing the Lake Champlain fishery: the U.S. Fish & Wildlife Service, New York State Department of Environmental Conservation, and Vermont Agency of Natural Resources. Collectively, this Cooperative establishes sea lamprey wounding rate targets on Lake Champlain sport fishes, identifies funding priorities for managing the fishery, and coordinates management of the fishery (Marsden et al., 2010).

One tool for optimizing an integrated management approach is population modeling. Matrix modeling has proven useful in highlighting which vital rates in the life cycle of a particular organism are most likely to change the population trajectory, particularly through the application of sensitivity analysis (Caswell, 1989, 2005). This form of population modeling has been used frequently for endangered species management (Crouse et al., 1987; Norris and McCulloch, 2003), but is increasingly applied to management of nuisance species (Blackwell et al., 2003; Hein et al., 2006; Shi et al., 2002).

In this paper, we developed a population matrix modeling framework (Lefkovich, 1965) to optimize basin-wide management for controlling sea lamprey in Lake Champlain and to identify the spatial extent and temporal frequency of TFM applications needed to achieve management targets. The matrix model described the life cycle of the sea lamprey, tracking the deposition of eggs in Lake Champlain tributaries, the transition of fertilized eggs to larval and transformer stages within streams and associated deltas, and the migration of parasitic-

phase sea lamprey into Lake Champlain, culminating in the selection of streams for spawning to complete the life cycle.

The objectives for the development and manipulation of this sea lamprey life history model were: 1) determine which life stages of sea lamprey were most sensitive to changes in survivorship and fecundity through management activities, and 2) examine optimal combinations of control methods to drive down the rate of population growth. We begin with a description of the stages in the general sea lamprey life cycle, then describe the full model, which was a modified Lefkovich (1965) matrix incorporating multiple tributaries and the effects of density-dependence at specific stages. Lastly, we use the full model to evaluate the effects of various management scenarios. A similar modeling approach was used by Vélez-Espino et al. (2008) to accomplish these objectives for sea lamprey populations in each of the Great Lakes. Both models incorporate density-dependence on young-of-year survival. Because our model focuses on a single, small lake, we were able to build tributary-specific density-dependence functions for young-of-year survival, a population ceiling on spawning females in specific tributaries, and a ceiling on the lake-wide parasitic-phase population in Lake Champlain.

Methods

Model description

In this population viability analysis (PVA), a series of 25 individual stream-based, stage-based matrix models were designed to represent 17 main-stem and three secondary tributaries with five associated deltas in Lake Champlain (Table 1; Fig. 1). The model matrices and all subsequent model simulations were built in Microsoft® Office Excel 2003 (© Microsoft Corporation). Specific tributaries and deltas were chosen based on their inclusion in the control program at the time the model was constructed. The model began by allocating spawning adults among tributaries. Two tributary selection schemes were developed: a natal-basin tributary selection scheme (see below for detailed description), in which tributaries were grouped by proximal location, and assigned a proportion of the lake-wide parasitic-phase population to be selected by spawning adults. Tributaries were grouped by location: south lake, Malletts Bay and the Northeast Arm, Missisquoi Bay, and the main lake basin (Fig. 1). The second tributary selection scheme was constructed based on larval density. These two schemes are described in further detail, below (see Model parameterization and spawning tributary selection).

Each of the 25 matrices in the full model contained designated stages summing to annual time-steps in the sea lamprey life cycle; however, due to the complexity of the sea lamprey life history, age is a unique stage in the model for the larval period because each age class has different survivorship and transformation probabilities and the egg fertilization, hatched eggs, and age-0 ammocoete stages all occur within the same annual time step. The model was constructed using a generalized sea-lamprey life cycle, beginning with the egg stage (Fig. 2, and see Table 2 for stage durations used in the model). Unfertilized eggs (u ; Fig. 2, Table 2) were released during spawning, a percentage of which were fertilized (f). A percentage of fertilized eggs (π) was deposited into a nest (f_n); the remainder ($1 - \pi$) were flushed downstream (f_o). The eggs hatched (h) and remained in this stage for 10–15 days, after which they emerged from the substrate and became stage l_0 larvae (Piavis, 1962, 1971), completing the first time step in the model. The ammocoetes then burrowed in the sediments of the tributary, where they remained for 4–6 years (l_1 – l_6 ; Morkert et al., 1998). At the end of the larval life stages, the ammocoetes metamorphosed from a filter-feeding life strategy into a parasitic strategy. Sea lamprey at this stage are called transformers (T) and metamorphosis generally requires about 8 months for completion (Applegate, 1950; Youson, 2003). Newly metamorphosed sea lamprey then migrated to the open lake where they sought hosts to

Table 1

Tributaries simulated in the sea lamprey life history model, with most recent QAS survey year, quantity of larval habitat and upper limit of QAS larval population estimate (K_L ; 95% CI), percent of larval lamprey within each tributary to the total number within the basin, spawning habitat and female abundance limit (K_a), lampricide treatments, discharge, distance of accessible sea lamprey habitat, and potential management options. The option for no management is also considered for all tributaries. Tributaries are listed in counter-clockwise orientation around the lake, beginning with the northwest corner. The lake-wide carrying capacity for the parasitic-phase (K_p) is 378,135. All data were current through 2005. Survey or treatment data collected after 2005 are not included in this model.

Tributary	Survey year ^a	Larval habitat (m ²)	Larval abundance (K_L)	Percent of total larval lamprey population	Spawning habitat (m ²)	Female abundance (K_a)	Most recent lampricide treatment applied to model	September mean discharge (m ³ /s) ^b	River access to lamprey (km) ^b	Management options ^c
<i>New York</i>										
Great Chazy R.	2003	988,015	2,027,033	43.98	31,453	125,812	2004	2.46	33.2	1, 2
Saranac R.	ns	na	391 ^b	0.01	31,453 ^{**}	125,812	1992	13.91	3.3	1
Saranac R. delta	2004	1,651,117	443,088	9.61	na	na	2004	na	na	1
Salmon R.	2005	25,599	132,119	2.87	11,568	46,272	2002	0.62	6.4	1
Salmon R. delta	2003	218,530	1938	0.04	na	na	1995	na	na	1
Little Ausable R.	2005	58,542	314,129	6.82	16,261	65,044	2002	0.6	9.8	1
Little Ausable R. delta	2003	218,530	10,685	0.23	na	na	1991	na	na	1
Ausable R.	2005	305,341	839,799	18.22	31,453 ^{**}	125,812	2002	9.6	11.3	1
Ausable R. delta	2002	1,339,509	62,890	1.36	na	na	2003	na	na	1
Boquet R.	2002	200,255	82,995	1.80	9441	37,764	2003	3.06	4.2	1
Boquet R. delta	2003	2,120,553	35,632	0.77	na	na	1995	na	na	1
Beaver Br.	2002	8736	1949	0.04	379	1516	2003	(<0.300)	4	1, 3
Putnam Cr.	2005	31,902	22,352	0.48	8203	32,812	2002	0.4	8.4	1
Mt. Hope Br.	2002	23,575	1957	0.04	1379	5516	2003	(0.14–0.28)	1.4	1, 3
<i>Vermont</i>										
Poultney R.	2000	207,036	23,338	0.51	7966	31,864	1996	2.61	16.9	1, 2 (?), 4
Hubbardton R.	2000	5200	873	0.02	18,844	75,376	1996	(0.28–0.71)	3.2	1, 4
Lewis Cr.	2005	123,236	120,411	2.61	7222	28,888	2002	1.19	15.3	1, 2
LaPlatte R.	2002	15,430	5090	0.11	3870	15,480	None	0.4	5.3	1
Winooski	2002	1,313,267	54,085	1.17	2350	9400	2004	20.39	17.7	1, 4
Sunderland	2000	16,076	8494	0.18	379 [*]	1516	None	(<0.28)	5.1	3, 4
Mallets Cr.	2005	9359	28,874	0.63	891	3564	None	(0.14–0.28)	2.7	3
Trout Br.	2005	9778	9964	0.22	379 [*]	3032	1995	(<0.28)	2.1	3
Missisquoi R.	2004	1,086,631	26,389	0.57	379 [*]	1516	None	18.12	12.9	1 (?), 4
<i>Québec</i>										
Pike R.	2000	139,441	83,491	1.81	5828	23,312	None	2.07	13.2	2
Morpion Str.	2000	128,062	270,951	5.88	5503	22,012	None	(0.14–0.42)	27.5	2 (?)

1 = lampricide, 2 = permanent barrier, 3 = seasonal trapping, 4 = pheromone (potential), ? = indicates method is in consideration, na = information not available, ns = not surveyed.

^a USFWS, unpublished data from lampricide treatments (2005).

^b Fisheries Technical Committee (2001).

^c Management options:

* Estimate from Beaver Br.

** Estimate from Great Chazy R.

parasitize for 12 months (p). The total lake-wide parasitic-phase population was the sum of p across all tributaries and deltas, plus a number of parasites from unknown sources, Θ (Table 3). Sea lamprey are semelparous; the parasites began the adult maturation process (a), and a portion of adults (S_i) selected tributary i for spawning in the spring, after which they died, thus completing the life cycle (Fig. 2).

The number of stages that occurred within tributary ($n = 20$) and delta matrices ($n = 5$) varied. Spawning, fertilization, emergence and growth through age-0 occurred in tributaries, after which a portion ($\Delta_{i,j}$) migrated from tributary i to the delta j and the rest ($1 - \Delta$) remained within the tributary (Fig. 2). The delta matrices received immigrants from their respective tributaries, where they remained through metamorphosis. Thus, the seven stages in the delta matrices represented the ammocoete (l_1 – l_6) through transformer (T) stages only. Transformers from both tributaries and delta matrices then joined the lakewide parasitic-phase population.

Three of the stages included a carrying capacity (Table 2). $K_{a,i}$ was the carrying capacity of spawning habitat for adult females, $K_{L,i}$ was the carrying capacity of larval habitat availability across larval age classes l_1 – l_6 , and K_p was the carrying capacity of parasites in Lake Champlain. The spawning limitation ($K_{a,i}$) was a ceiling limit to the

the maximum number of adult female sea lamprey that could spawn in tributary i (Dawson and Jones, 2009). Density-dependence at the larval stage ($K_{L,i}$) has been documented for sea lamprey populations (Zerrenner and Marsden, 2006). The limitation to parasitic-phase sea lamprey (K_p) was based on host (prey) availability (general parasite–host limitation, Anderson and May, 1978).

Modified Lefkovich matrix model transition probabilities

The progression in the matrix was similar to that of an age-based model, in which an individual must proceed to the next stage, or else it was no longer included within the population. There were two occasions at which an individual could skip stages; these occurred when l_4 or l_5 ammocoetes entered metamorphosis and skipped ahead to the transformer stage (Fig. 2). The equations used in the life history model were as follows, beginning with the number of unfertilized eggs at time t and tributary matrix i (see Table 2 for stage notations and Table 3 for parameter descriptions):

$$u_{t,i} = a_{t-1} S_i \Omega m, \quad (1)$$

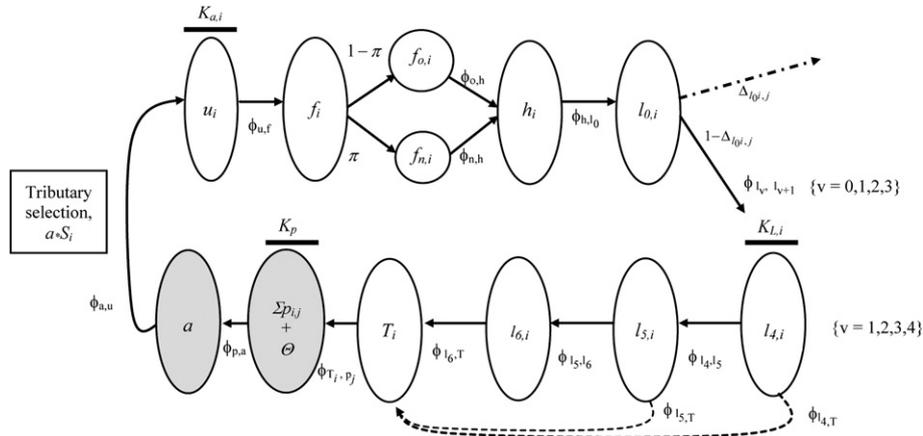


Fig. 2. Structure, parameters, and carrying capacities of the life history model (see Table 2 for definitions). Ovals represent specific life stages; ovals with a bar above them indicate stages with density-dependence. Arrows represent transition (survivorship) probabilities from one stage to another. Grayed ovals indicate life stages that occur in the lake; open ovals represent stages occurring in tributaries.

where a_{t-1} was the number of adults in the preceding time step, S_i was the probability of an adult spawning in tributary i (as established by the stream selection parameters described below), Ω was the proportion of females in the population, and m was the fecundity rate per female (Table 3). The number of fertilized ($f_{t,i}$) and hatched ($h_{t,i}$) eggs at time t and tributary i was given by:

$$f_{t,i} = u_{t,i}\psi, \tag{2}$$

$$h_{t,i} = f_{n,t}\phi_{n,h} + f_{o,t}\phi_{o,h}, \tag{3}$$

where ψ was the fertilization rate, f_n denotes eggs deposited immediately into the nest after fertilization ($f_{t,i}*\pi$), and f_o denotes eggs washed out of the nest after fertilization ($f_{t,i}*(1-\pi)$). Eggs in the nest and eggs out of the nest differed in their probability of surviving to hatching, designated by $\phi_{n,h}$ and $\phi_{o,h}$, respectively (Table 3). The number of l_0 ammocoetes at time step t , tributary i was

$$l_{0,t,i} = h_{t,i}\phi_{h,l_0}(1-\Delta_{ij}), \tag{4}$$

Table 2
Life stage description, population stage notation, stage duration, and carrying capacity values used in the sea lamprey life history model for Lake Champlain. n/a denotes not applicable.

Life stage	Population at stage	Stage duration or value
Unfertilized eggs	u	1 day
Fertilized eggs	f	n/a
Fertilized eggs, in nest ($f*\pi$)	f_n	2 weeks
Fertilized eggs, out of nest ($f*(1-\pi)$)	f_o	2 weeks
Hatched eggs	h	2 weeks
Larvae age 0	l_0	11 months
Larvae age 1	l_1	12 months
Larvae age 2	l_2	12 months
Larvae age 3	l_3	12 months
Larvae age 4	l_4	12 months
Larvae age 5	l_5	12 months
Larvae age 6	l_6	12 months
Transformer	T	12 months
Parasite	p	12 months
Spawning adult	a	1 month
Carrying capacity, spawning habitat	K_a	See Table 1
Carrying capacity, ammocoetes	K_L	See Table 1
Carrying capacity, parasites	K_P	378,135

where Δ_{ij} is the proportion of individuals that drift to the adjoining delta j , thus populating the appropriate delta matrix, where they had the same probability of survivorship to the parasitic-phase as their counterparts in the tributary sediments. Eqs. (1) through (4) all occurred at the same time step, given the short duration of these stages in the life cycle, so the model time step remained a 1-year step. We assumed that survivorship through each of these stages is successive, summing to one year, therefore were not adjusted (scaled) to fit into a 1-year stage.

Following larval emergence, a modified Beverton–Holt stock-recruitment function was used (Beverton and Holt, 2003; Mousalli and Hilborn, 1986), such that the number of l_1 ammocoetes at time step t , tributary i was:

$$l_{1,t,i} = \frac{l_{0,t-1,i}\phi_{l_0,l_1}}{1 + \left(\frac{l_{0,t-1,i}\phi_{l_0,l_1}}{(K_{L,i}-b_{t,i})} \right)}, \tag{5}$$

The density-dependence function was applied as age-0 larvae entered age-1, reduced by the sum of all larvae currently present in the tributary ($b_{t,i}$). After the transition into the age-1 stage, progression through the larval stages was simply a function of the abundance at time $t-1$ and survival (ϕ) into the respective stage. For brevity, these functions were compressed into Eq. (6), where v represented the age of the ammocoetes:

$$l_{v,t,i} = l_{v-1,t-1,i}\phi_{l_{v-1},l_v}\{v = 2, 3, 4, 5, 6\} \tag{6}$$

Ammocoetes had a probability of moving to the transformer stage (T) from the age-4, -5 and -6 larval stages, and the total number of transformers, T , at time step t for tributary i was:

$$T_{t,i} = l_{4,t-1,i}\phi_{l_4,T} + l_{5,t-1,i}\phi_{l_5,T} + l_{6,t-1,i}\phi_{l_6,T} \tag{7}$$

Transformers had a probability of surviving to become parasites, ($\phi_{T,p}$), and the total number of potential parasites in the lake was calculated as y_t , which summed all transformers from tributaries and deltas that survived to the parasite stage. This number was adjusted

Table 3

Stage transition probabilities, transition notation, parameter values, percent reduction of transition probabilities due to management effects, and possible management control options considered for each respective stage in the Lake Champlain sea lamprey life history model. For stage notation description, see Table 2.

Transition		Parameter name	Parameter value (±SD)	% Reduction by management, M_i (increment)	Control option	Reference ¹
From stage	To stage					
u	F	ψ	0.95 (0.032)	10–90	Sterile males	
f	f_n	π	0.15			1, 2, 3, 5
f	f_o	$1 - \pi$	0.85			
f_n	H	$\phi_{n,h}$	0.80 (0.08)	0–100 (by 10%)	Nest dismantling	1, 2, 3, 5
f_o	H	$\phi_{o,h}$	0.025 (0.00)	None	None to date	4, 4
h	l_o	ϕ_{h,l_o}	0.06 (0.01)	(50, 75, 90, 95, 99% effective, on 3, 4, 6, 10 year cycles), applied to larvae age-0 to -6 and transformers	Chemical (TFM, Bayluscide)	2, 3
l_o	l_1	ϕ_{l_o,l_1}	0.26 (0.022)			7, 8
l_1	l_2	ϕ_{l_1,l_2}	0.93 (0.078)			8
l_2	l_3	ϕ_{l_2,l_3}	0.95 (0.079)			8
l_3	l_4	ϕ_{l_3,l_4}	0.81 (0.068)			8
l_4	l_5	ϕ_{l_4,l_5}	0.88 (0.073)			8
l_4	T	$\phi_{l_4,T}$	0.07 (0.007)			8
l_5	l_6	ϕ_{l_5,l_6}	0.90 (0.075)			
l_5	T	$\phi_{l_5,T}$	0.86 (0.072)	None	None to date	
l_6	T	$\phi_{l_6,T}$	0.90 (0.075)			
T	P	$\phi_{T,P}$	0.35 (0.029)	None	None to date	
p	A	$\phi_{p,a}$	0.35 (0.029)			
Fecundity		m	67,642 (18,072)	None	None to date	5
Proportion of females		Ω	0.50 (0.00)	None	Sex pheromones	
Probability of a migratory adult spawning in tributary i		S_i	(Tables 4, 5)			
Migration of larvae from tributary i to delta j sediments	Δ		0.25	None	None to date	
Parasite population from unknown sources	Θ		18,828 (7349)	None	None to date	9

¹ 1. Applegate, 1950; 2. Manion, 1968; 3. Manion and Hanson, 1980; 4. Smith, 2006; 5. Smith and Marsden, 2007; 6. Smith and Marsden, 2009; 7. Spangler et al., 1985; 8. Zerrenner, 2001; 9. Estimated by sea lamprey control agents

based on a lake-wide carrying capacity, K_p , to yield the total number of parasites in the lake at time t as:

$$p_t = \left(\frac{T_{t-1,t}\phi_{T,p} + \Theta_t}{y_{t-1}} \right) z_{p,t-1}, \tag{8}$$

where

$$z_{p,t-1} = \frac{y_{t-1}}{1 + (y_{t-1}/K_p)},$$

and

$$y_{t-1} = \sum_{i=1}^{i=20} T_{t-1,i}\phi_{T,p} + \sum_{j=1}^{j=5} T_{t-1,j}\phi_{T,p}$$

and Θ was a randomly generated population of parasitic-phase sea lamprey to represent contributions from unknown sources (Table 3).

Finally, the number of spawning adults in the population at time t , was:

$$a_t = p_t\phi_{p,a} \tag{9}$$

Again, Eqs. (8) and (9) occurred in the same time step due to the relatively short duration of the spawning adult stage to maintain the one-year time step within the model. These adults were then distributed to tributaries for spawning (see below); some of these adults were unable to spawn if the spawning carrying capacity ($K_{a,i}$) was exceeded.

Model parameterization and spawning tributary selection

Parameter values obtained from the published literature for this model were weighted, with highest ranking given to values from peer-reviewed papers, technical reports, and unpublished data, in that order (Martin and Howe, 2003). Data specific to Lake Champlain were given priority over information derived from studies in other geographic regions.

The fecundity of sea lamprey is very high, but less than 15% of their eggs are retained by the nests they construct during the spawning period ($\pi = 0.15$, Table 3; Applegate, 1950; Manion, 1968; Manion and Hanson, 1980; Smith and Marsden, 2009). Eggs that remain in the nests appear to have a high probability of surviving to the larval stage (Manion, 1968); survivorship of those eggs that leave the nests is not well studied, although recent research suggests that probability of surviving to the emergence stage is less than 2.5% (Smith, 2006). Smith (2006) also estimated fecundity rates of sea lamprey from Lake Champlain; these estimates were used for fecundity in the model.

The probability that tributary i would be selected for spawning (S_i) is not well understood; yet this selection probability was a critical part of the model as it established the number of spawning females could potentially spawn in each tributary. Two approaches were used to partition the adults into tributaries: 1) natal basin-based selection, and 2) larval population-based selection. The natal basin-based selection scheme allocated adult sea lamprey to tributaries based on the most likely natal basin (Howe et al., 2006; Table 4). In this scheme, sea lamprey that made the transition from parasitic-phase to spawning adults selected spawning tributaries according to the proportion of parasites that emerged from a given basin (Table 4). Table 4a indicates the proportion of sea lamprey selecting a given tributary in New York for spawning and Table 4b

Table 4a

Natal basin stream selection scheme for spawning-phase sea lamprey that select New York tributaries. Row indicates the tributary of larval origin; column indicates the tributary the lamprey select to spawn in. Values are the proportion of the spawning population. Boldface indicates sea lamprey returning to their natal tributary. “–” indicates no lamprey were allocated to the respective tributary.

Natal tributary	Spawn in:									
	Great Chazy R.	Saranac R.	Salmon R.	Little Ausable R.	Ausable R.	Boquet R.	Beaver Br.	Putnam Cr.	Mt. Hope Br.	Poultney R.
Great Chazy R.	0.059	0.059	0.059	0.059	0.059	0.059	0.059	0.059	–	–
Saranac R.	0.059	0.059	0.059	0.059	0.059	0.059	0.059	0.059	–	–
Salmon R.	0.059	0.059	0.059	0.059	0.059	0.059	0.059	0.059	–	–
Little Ausable R.	0.059	0.059	0.059	0.059	0.059	0.059	0.059	0.059	–	–
Ausable R.	0.059	0.059	0.059	0.059	0.059	0.059	0.059	0.059	–	–
Boquet R.	0.083	0.083	0.083	0.083	0.083	0.083	0.083	0.083	–	–
Beaver Br.	0.083	0.083	0.083	0.083	0.083	0.083	0.083	0.083	–	–
Putnam Cr.	0.075	0.075	0.075	0.075	0.075	0.075	0.075	0.075	0.030	0.030
Mt. Hope Br.	–	–	–	–	–	–	–	0.100	0.300	0.300
Poultney R.	–	–	–	–	–	–	–	0.100	0.300	0.300
Hubbardton R.	–	–	–	–	–	–	–	0.100	0.300	0.300
Lewis Cr.	0.071	0.071	0.071	0.071	0.071	0.071	0.071	0.071	–	–
LaPlatte R.	0.083	0.083	0.083	0.083	0.083	0.083	0.083	0.083	–	–
Winooski R.	0.083	0.083	0.083	0.083	0.083	0.083	0.083	0.083	–	–
Sunderland Cr.	0.083	0.083	0.083	0.083	0.083	0.083	0.083	0.083	–	–
Malletts Cr.	0.042	0.042	0.042	0.042	0.042	0.042	0.042	0.042	–	–
Trout Br.	–	–	–	–	–	–	–	–	–	–
Missisquoi R.	0.050	0.050	–	–	–	–	–	–	–	–
Pike R.	0.050	0.050	–	–	–	–	–	–	–	–
Morpion Str.	0.050	0.050	–	–	–	–	–	–	–	–

indicates the proportion spawning in Vermont and Québec tributaries; S_i was allocated proportionately according to basin contribution of parasites, where a basin consisted of a grouping of proximal tributaries.

In the larval population-based scenario, a selection scheme was developed to allocate spawning-stage sea lamprey to streams in proportion to larval distributions based on $K_{L,i}$, which used larval population estimates from recent Quantitative Assessment Sampling (QAS) surveys (Tables 1, 5). This scenario assumed parasitic-phase sea lamprey were more likely to select a tributary with larger larval populations based on pheromone production, a hypothesis currently under investigation (Vrieze et al., 2011; Wagner et al., 2009). The larval selection scheme (Table 5) provided the initial selection scheme for the first time step; a new selection scheme was generated for each

successive time step based on the number of sea lamprey (l_{0-6}) in each tributary for the respective time step.

The parameterization of carrying capacities at different stages was as follows: $K_{a,i}$ was a tributary-specific carrying capacity for spawning females, where we assumed that no more than four females could spawn in 1 m² of suitable spawning habitat. For tributaries for which habitat data were not available, these data were extrapolated based on comparison with similar tributaries in the region, and best professional judgment was used to generate population limits for these parameters. The carrying capacity of a tributary's larval population, $K_{L,i}$, was the upper bound of the 95% confidence interval for the larval estimate for tributary i based on recent survey data, which assumed an equal quantity of habitat was required for all larval age classes (Table 1). Survey data for the Saranac

Table 4b

Natal-basin selection scheme for spawning-phase sea lamprey that select Vermont and Québec tributaries. Row indicates the tributary of larval origin; column indicates the tributary the lamprey select to spawn in. Values are the proportion of the spawning population. Boldface indicates sea lamprey returning to their natal tributary. “–” indicates no lamprey were allocated to the respective tributary.

Natal tributary	Spawn in:									
	Hubbardton R.	Lewis Cr.	LaPlatte R.	Winooski R.	Sunderland Br.	Malletts Cr.	Trout Br.	Missisquoi R.	Pike R.	Morpion Str.
Great Chazy R.	–	0.059	0.059	0.059	0.059	0.059	0.059	0.059	0.059	0.059
Saranac R.	–	0.059	0.059	0.059	0.059	0.059	0.059	0.059	0.059	0.059
Salmon R.	–	0.059	0.059	0.059	0.059	0.059	0.059	0.059	0.059	0.059
Little Ausable R.	–	0.059	0.059	0.059	0.059	0.059	0.059	0.059	0.059	0.059
Ausable R.	–	0.059	0.059	0.059	0.059	0.059	0.059	0.059	0.059	0.059
Boquet R.	–	0.083	0.083	0.083	0.083	–	–	–	–	–
Beaver Br.	–	0.083	0.083	0.083	0.083	–	–	–	–	–
Putnam Cr.	0.030	0.075	0.075	0.075	0.075	–	–	–	–	–
Mt. Hope Br.	0.300	–	–	–	–	–	–	–	–	–
Poultney R.	0.300	–	–	–	–	–	–	–	–	–
Hubbardton R.	0.300	–	–	–	–	–	–	–	–	–
Lewis Cr.	–	0.071	0.071	0.071	0.071	0.071	0.071	–	–	–
LaPlatte R.	–	0.083	0.083	0.083	0.083	–	–	–	–	–
Winooski R.	–	0.083	0.083	0.083	0.083	–	–	–	–	–
Sunderland Cr.	–	0.083	0.083	0.083	0.083	–	–	–	–	–
Malletts Cr.	–	0.042	0.042	0.042	0.042	0.400	0.100	–	–	–
Trout Br.	–	–	–	–	–	0.200	0.500	0.100	0.100	0.100
Missisquoi R.	–	–	–	–	–	0.050	0.100	0.250	0.250	0.250
Pike R.	–	–	–	–	–	0.050	0.100	0.250	0.250	0.250
Morpion Str.	–	–	–	–	–	0.050	0.100	0.250	0.250	0.250

Table 5

Proportion of the initial spawning population that selects each tributary in the larval stream selection scheme.

Tributary	Proportion of spawning population
Great Chazy R.	0.457
Saranac R.	0.068
Salmon R.	0.030
Little Ausable R.	0.073
Ausable R.	0.195
Boquet R.	0.029
Beaver Br.	0.000
Putnam Cr.	0.005
Mt. Hope Br.	0.000
Poultney R.	0.005
Hubbardton R.	0.000
Lewis Cr.	0.027
LaPlatte R.	0.001
Winooski R.	0.012
Sunderland Br.	0.002
Malletts Br.	0.007
Trout Br.	0.001
Missisquoi R.	0.006
Pike R.	0.019
Morpion Str.	0.061

River were not available; larval abundance estimates were extrapolated from mortality estimates from a 1992 lampricide application to this tributary (Fisheries Technical Committee, 1999). The limit of lakewide parasites (K_p) was based on a population estimate of the number of transformers that migrated to the lake as the 2002 parasitic-phase cohort (Howe et al., 2006). Wounding rates on lake trout were the highest during this period that had ever been recorded in Lake Champlain (102 wounds per 100 lake trout; Fisheries Technical Committee, 2005), so we assumed that the parasitic-phase sea lamprey population was near carrying capacity, as wounding on lower-quality prey increased (Howe et al., 2006). The parasitic-phase population estimate was 269,139 (160,143–378,135; 95% CI). The upper limit (378,135) was used as the maximum number of parasitic-phase sea lamprey that could survive in Lake Champlain (K_p).

Population projections

Simulations of 1000 time steps were run prior to implementation of management scenarios to allow the tributaries in each model to equilibrate ($\Delta\lambda_{t,t+1}=0$). The final equilibrated population was assumed to consist of a stable stage distribution and became the seed population for all management simulations.

The beta distribution is a function commonly used when modeling natural survivorship variability (Fieberg and Ellner, 2001; Hutchings, 1999; Kaye and Pyke, 2003) and was used in this model to introduce stochasticity for survivorship parameters (ϕ). The normal distribution (NORMINV function in Microsoft® Excel 2003; © Microsoft Corporation) was used for fecundity, m .

For each simulation, 100 model runs were executed, where key output was the abundance of parasitic-phase sea lamprey generated by each tributary. The mean and standard deviation of these outputs were recorded across the 100 model runs.

Model evaluation

Few data were available to benchmark the results of this model, and none of the existing data are well-suited for model validation. As in the Great Lakes, success of the sea lamprey control program in Lake Champlain is measured by reductions in wounding rates on stocked lake trout; there is no recruitment of wild lake trout in Lake Champlain (Marsden et al., 2003). Therefore, a simulation was constructed to represent the lampricide applications to Lake Champlain

tributaries from 1989 to 2005. Model output of the parasitic-phase population for this time period was plotted with the observed trends in sea lamprey wounding on lake trout (number of wounds per 100 lake trout). Finally, we plotted an estimate of the out-migrating transformer population derived for 2001 and 2002 (Howe et al., 2006). Howe et al. (2006) estimated that $269,139 \pm 55,610$ (SD) and $111,807 \pm 23,511$ (SD) transformers out-migrated to Lake Champlain as part of the 2002 and 2003 parasitic-phase cohorts, respectively. These estimates were reduced by 35%, our assumed probability of transformers surviving to the parasitic phase ($\phi_{t,p}$; Table 3), to provide a parasitic-phase population estimate for comparison to the model-derived parasitic-phase population for these two years.

Sensitivity analyses

Model sensitivity is a measure of the response of the population growth rate to a change in any of the parameters that drive the population (Caswell, 1989; Crouse et al., 1987). Given the complexity of the internal factors driving these population models, such as the spawning tributary allocations of the parasitic-phase population, traditional sensitivity analyses could not be estimated.

As an alternative to traditional sensitivity analysis of the matrix, we examined the sensitivity of p (the number of parasites in a year) to changes in egg deposition rate into nests (π), fecundity (m), and contributions from unknown sources (Θ). To measure sensitivity of egg deposition, π was extended by 0.1 from the base values (e.g., $\pi=0.15$; Table 3), so the sensitivity simulations included setting this parameter to 0.05 and 0.25. Sensitivity of the model output to fecundity inputs (m) was evaluated by increasing the base rate, $67,642 \pm 6764$ eggs per female, by $\pm 25\%$ of this value ($50,732 \pm 13,554$ and $84,552 \pm 22,590$). The contributions of unknown (Θ), and therefore uncontrollable, populations to the parasitic-phase population were evaluated as 50% decreases and two-fold increases in the mean of the baseline values used for the unknown population Θ ($18,828 \pm 7,349$ decreased to 9414 ± 3674 and increased to $37,656 \pm 14,698$) for both spawning selection schemes (natal-based and larval). Sensitivity of this parameter was also evaluated for Control Scenarios 3a and 3h (Table 6). Sensitivity for each estimate on the full matrix model (pre-management) was evaluated while the remaining parameters were held constant at baseline values.

Management scenarios

The effects of management actions (M_i) were modeled as reductions on the natural survivorship of a given life stage or as a reduction to the fecundity of spawning females (m). Thus, the simulated survivorship value was the product of the natural survival (ϕ) and the management effect ($1 - M_i$). Management effects were designed to reflect current management practices, such as 4-year lampricide treatments and adult trapping, as well as possible future management practices, such as the application of pheromones to draw migratory adults from one tributary into another (Table 6). An initial baseline simulation (Scenario 1) was executed to determine the population growth rate and stabilized parasitic-phase population level without the influence of management effects on the population.

Management scenarios were explored to investigate the effect of lampricide treatments to tributaries and their deltas on the overall parasitic-phase population, with treatment efficiencies of 95% and 99%, and with 3-, 4-, 5-, 6-, and 10-year cycles for all tributaries that are currently managed (Table 6). Scenario 1 represented the baseline model with no control measures. We then explored 95% and 99% effective treatments on a suite of tributaries, and on five deltas to those tributaries (scenarios in group 2). Scenarios in group 3 explored the current control program (3a) and variations thereof. In the current control program through 2005, tributaries and deltas are treated on a 4 year cycle, and were simulated to be 95% effective. Variations

Table 6
Hypothetical management scenarios simulated with the Lake Champlain sea lamprey life history model.

Scenario	Description
1	No control
2a	95% reduction by lampricide, 4-yr cycle, to Great Chazy R., Salmon R., Little Ausable R., Ausable R., Boquet R., Beaver Br., Putnam Cr., Mount Hope Br., Lewis Cr., Winooski R.
2b	95% reduction by lampricide (as above) including the deltas of Saranac R., Salmon R., Little Ausable R., Ausable R., Boquet R.
2c	As above, except 99% reduction by lampricide treatments
3a	Current control program: Scenario 2b with adult trapping on Great Chazy R. (40%), Beaver Br. (95%), Sunderland Br. (80%), Malletts Cr. (80%), Trout Br. (80%)
3b	Current program, without control on deltas
3c	Current program, with 99% reduction by lampricide
3d	Current program, with 40% effect of nest dismantling on Poultney R., Boquet R., Malletts Cr.
3e	Current program, with effect of pheromones to draw 100% migratory adults from Winooski R. into Sunderland Br. trap, increase trapping efficiency to 90% on Great Chazy R., Trout Br., Sunderland Br.; no TFM on Winooski R.
3f	Current program, with 100% effective trap for adult lamprey on Morpion Str.
3g	Current program, with 95% reduction by lampricide on Poultney and Hubbardton rivers
3h	Current program, with 95% reduction by lampricide on Poultney and Hubbardton rivers, 100% effective trap for adult lamprey on Morpion Str.
3i	Current program, with 95% reduction by lampricide on Poultney and Hubbardton rivers, 100% effective trap on Morpion St., no delta treatments
4	Trapping migratory adults, with effects on: Great Chazy R. (40%), Salmon R. (40%), Little Ausable R. (30%), Beaver Br. (95%), Mount Hope Br. (50%), Sunderland Br. (80%), Malletts Cr. (80%), Trout Br. (80%)
5	95% reduction by lampricide treatments on all 20 modeled tributaries, all 5 deltas, 4-yr cycle

on Scenario 3a explored combined management scenarios, in which the effect of adult trapping, nest dismantling, and variations in lampricide effectiveness were used to reduce survivorship at multiple life stages (Table 6). Pheromone applications to draw sea lamprey from one tributary into another for more effective control were also simulated. Scenario 4 simulated trapping of spawning adults on a suite of tributaries as a single control method, and Scenario 5 represented 95% effective lampricide applications to all tributaries and deltas in the model. The mean annual abundance of lake-wide parasites was calculated for the last 20 time steps in each simulation. The number of parasites generated in the simulations for each of

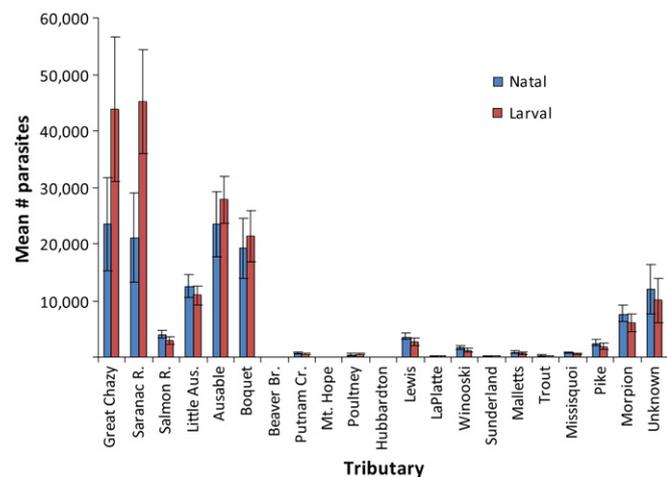


Fig. 3. Base model abundance of parasitic-phase sea lamprey from each tributary from the natal basin-based and larval-based tributary selection schemes, including parasites from unknown sources.

the treatment rotations was compared over this 20-year period, for 100 iterations in each rotation, to estimate a mean and standard deviation for each simulation.

Results

Baseline model

The base model, without reductions in survival due to management efforts, yielded a lake-wide parasitic-phase sea lamprey abundance of $136,557 \pm 11,433$ (SD) in the natal basin-based selection scheme, and $176,758 \pm 10,645$ (SD) in the larval-based selection scheme. The Great Chazy River, Saranac River, Ausable River, and Putnam Creek in New York and the Winooski River in Vermont contributed the greatest number of sea lamprey to the parasitic-phase population in the natal basin-based tributary selection scenario, and the Great Chazy and Ausable Rivers were the major contributors to the parasitic-phase population in the larval-based selection scenario (Fig. 3).

Model evaluation

The model-predicted parasitic-phase sea lamprey population followed a trend similar to that of the actual wounding record for the period 1989–1998 (Fig. 4). Following 1999, wounding rates began increasing on an annual basis, whereas the model predictions continued on a downward trend for both the natal basin-based and larval stream selection scheme (Howe, 2006). The model-derived parasitic-phase population estimate was $37,739 \pm 6272$ (SD) and $37,792 \pm 6297$ (SD) for 2002 and 2003, respectively.

Sensitivity analyses

The sensitivity analysis (pre-management effects) indicated that the population was minimally sensitive to changes in the survivorship parameters, and less sensitive for the larval selection scheme than for the natal basin matrix. For both selection schemes, all stages had $\pm 10\%$ or less change in survivorship or rate of transformation from the baseline value.

The model was most sensitive to changes in the egg deposition rate (π), though the magnitude of the response was higher for the natal basin selection scheme than the larval selection scheme (Table 7, Fig. 5). For the natal basin selection scheme, an egg deposition rate of 25% resulted in a 13.7% increase in the mean number of parasites over the baseline egg deposition rate of 15%, while a 5% egg deposition rate yielded a 75.7% decrease in number of parasites (Table 7, Fig. 5a). The mean number of parasites produced with the

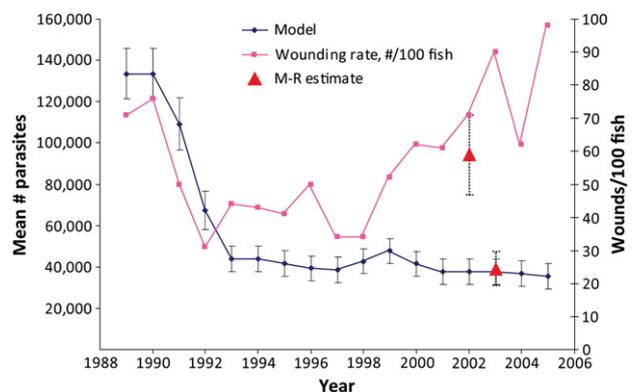


Fig. 4. Model predictions for the parasitic-phase sea lamprey population (natal basin selection scheme), wounding rates on lake trout in Lake Champlain, predicted number of wounds on 3 year old lake trout, 1989–2005, and parasitic-phase population estimate for 2002 and 2003 from Howe et al. (2006). Error bars for model values are ± 1 SD.

Table 7

Model-predicted lakewide parasite production with changes in egg deposition rate, number of parasites contributed by unknown sources, and fecundity for the natal basin-based and larval-based selection scheme.

Simulation	Natal basin matrix			Larval matrix		
	Mean	SD	% difference from baseline	Mean	SD	% difference from baseline
<i>Egg deposition</i>						
25% deposition	158,307	12,113	15.9	183,521	7622	3.8
15% (baseline)	136,557	11,433		176,758	10,645	
5% deposition	77,738	13,131	-43.1	145,615	18,051	-17.6
<i>Parasites from unknown sources</i>						
Scenario 1 (no control)						
100% increase	139,449	14,231	2.1	181,169	9453	2.5
Baseline	136,557	11,433		176,758	10,645	
50% decrease	132,766	12,826	-2.8	174,375	9440	-1.3
Scenario 3a (current control)						
100% increase	47,566	10,535	44.7	48,801	11,540	44.7
Baseline	32,877	6982		33,726	6364	
50% decrease	24,347	4428	-25.9	24,580	4330	-27.1
Scenario 3h (increased control)						
100% increase	38,720	12,731	64.3	38,650	11,975	78.0
Baseline	23,570	6809		21,713	6656	
50% decrease	14,221	3542	-39.7	13,847	3759	-36.2
<i>Fecundity</i>						
25% increase	149,804	11,828	9.7	180,365	10,397	2.0
Baseline	136,557	11,433		176,758	10,645	
25% decrease	115,972	14,131	-15.1	169,137	11,666	-4.3

larval selection scheme was +3.7% and -21.4%, respectively, from the baseline egg deposition rate (Table 7, Fig. 5b).

The model was also more sensitive to changes in fecundity under the natal-based selection scheme than for the larval selection scheme. A 25% increase in fecundity using the natal-basin selection scheme increased the parasitic-phase population by 9.3%, while a 25% decrease lowered the parasitic phase population by 16.3%. For the larval

selection scheme, changes in fecundity of plus or minus 25% yielded a +2.0 and -4.4% change, respectively (Table 7, Fig. 5).

The model was not highly sensitive to changes in the abundance of parasites from unknown (and therefore uncontrolled) sources for either selection scheme in an unmanaged sea lamprey population. When the number of parasites from unknown sources was doubled in Scenario 1 (unmanaged population), the mean parasitic-phase population increased by 2.1% for the natal-basin selection scheme and by 2.4% for the larval selection scheme (Table 7, Fig. 5). These minimal responses are likely because the population is already limited by the three carrying capacities, so adding more sea lamprey to the uncontrolled population (Scenario 1) was ineffective. However, the model was highly sensitive for this parameter under the management scenarios, when population sizes for lamprey were depressed well below the carrying capacity limitations. For the two management scenarios evaluated by adding unknown sources (Scenarios 3a, current control program, and 3h, current control plus control of the Poultney River system and Morpion Stream), the mean parasite population

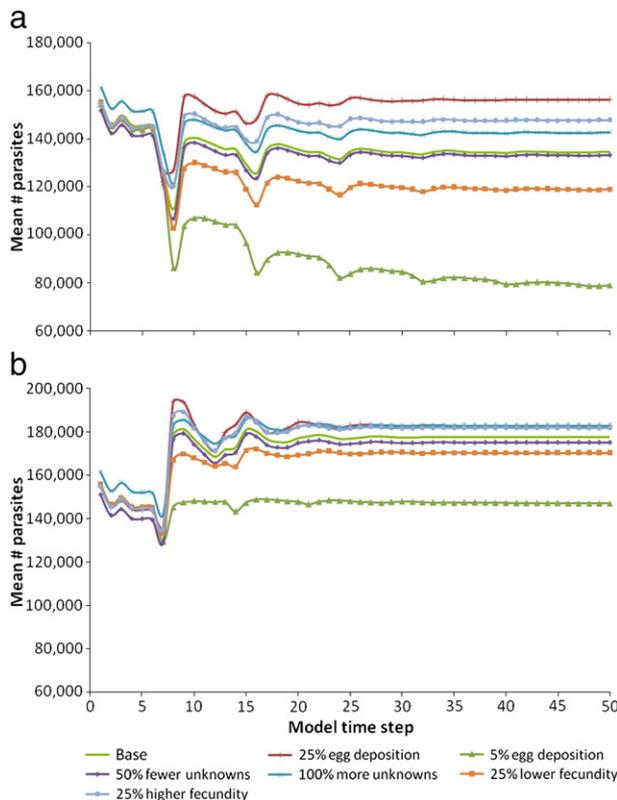


Fig. 5. Sensitivity of the Lake Champlain sea lamprey life history model to altered egg deposition rates, fecundity, and number of parasites from unknown, unmanaged sources for the (a) natal basin selection scheme and the (b) larval selection scheme.

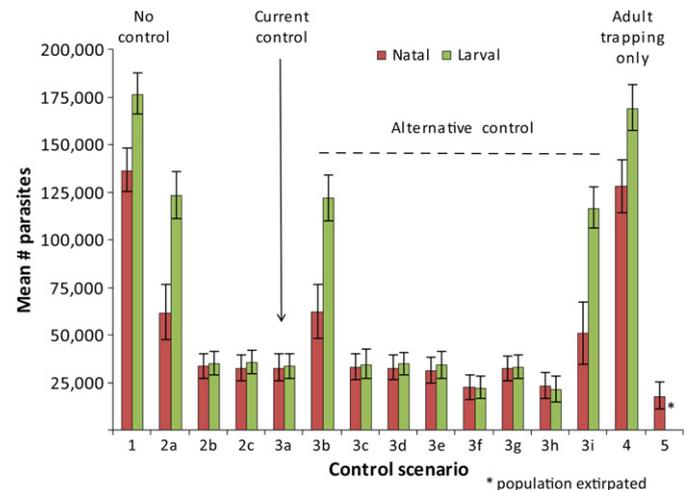


Fig. 6. Projected mean number of parasitic-phase sea lamprey for each of the control scenarios identified in Table 6, for the two selection schemes (natal basin and larval). Error bars are ± 1 SD. "*" denotes population extirpation.

increased 30.9% for both the natal and larval selection schemes in Scenario 3a and increased 39.1% and 43.8%, respectively for Scenario 3h (Table 7).

Management scenarios

The management scenarios reflecting control with the natal basin and larval stream selection schemes suggested that as more comprehensive control was applied to limit the population growth, the stabilization point of the population dropped to smaller parasitic-phase abundance levels, and dropped more for the larval selection scheme than the natal basin scheme (Fig. 6). The natal basin and larval selection schemes yielded parasitic-phase populations at the current control level (Scenario 3a) that were 75.9% and 80.9%, respectively, below the uncontrolled population for each stream selection scenario. Scenario 5, which represented the most complete management of sea lamprey, (95% reduction by lampricide control on all tributaries, not including the unknown population Θ), drove the population down to 18,146 +/- 7071 for the natal based selection scheme and to extinction for the larval selection scheme. Second only to Scenario 5, Scenarios 3f (addition of a 100% effective adult trapping in Morpion Stream) and 3h (95% reduction by lampricide treatments in the Poultney and Hubbardton Rivers, 4-year cycle, with 100% effective adult trapping in Morpion Stream) had the greatest effect on the parasitic-phase population, with a mean abundance that was 31.3 and 28.3% lower than that of the current control program (3a) for the natal basin and 33.3% and 35.6% lower for the larval selection schemes, respectively (Table 8, Fig. 6).

Simulations of 3-, 5-, and 6-year treatment cycles were not substantially different from the 4-year treatment cycle for the natal-basin selection scheme over a 20-year period. In the simulation of a 10-year treatment cycle, the population rose dramatically prior to each treatment event (Fig. 7).

Discussion

Simulations of management scenarios for sea lamprey in Lake Champlain using a population viability analysis (PVA) model largely conform to expectations of effectiveness at reducing the parasitic-phase sea lamprey population. Baseline model simulations indicate that the Great Chazy and Ausable Rivers in New York would be the two greatest contributors of sea lamprey to the parasitic-phase population in Lake Champlain without any form of control on the population, regardless of the manner in which sea lamprey select a tributary for spawning. The model appears to be robust, as simulations of

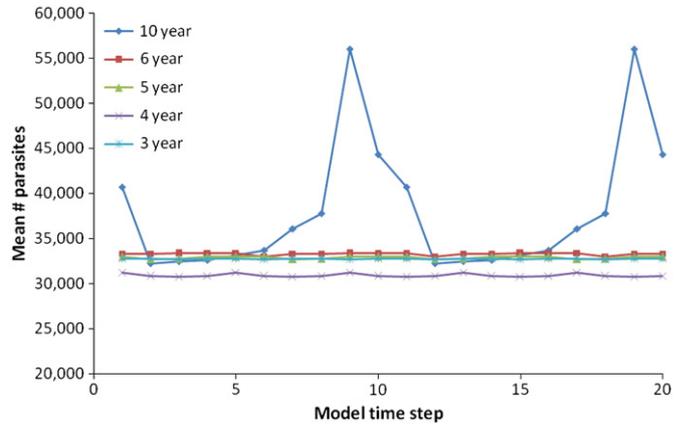


Fig. 7. Annual parasite production for the natal basin selection scheme over a 20-year period for 3-, 4-, 5-, 6-, and 10-year treatment cycles.

historic control levels produce parasitic-phase sea lamprey populations that closely echo trends of sea lamprey wounding rates on salmonids in Lake Champlain from 1989 to 1998. Simulations of various management scenarios largely conform to expectations of effectiveness at reducing the parasitic population. Similar to other PVA models used for nuisance species management (e.g. Blackwell et al., 2003; Govindarajulu et al., 2005; Shi et al., 2002), this model can be used to identify the stages in the life cycle of sea lamprey that are the most vulnerable to management effects (larval sea lamprey); the model can then be used to optimize the control program by designing combinations of individual stream treatments that maximally reduce parasitic populations while simultaneously reducing costs, TFM use, and non-target mortality (Fisheries Technical Committee, 2001; Parker, 2000).

Model evaluation

The lake trout wounding data used as a surrogate for parasite abundance in this study are an index. Wounding rates may be influenced by several factors, including host:parasite ratio, host survival, parasite attack rates, host selection, and availability of alternate host species, and therefore do not predict actual numbers of the parasite population. The trends for the number of parasitic-phase sea lamprey predicted by the model and the observed wounding rates for the period between 1989 and 1998 are similar. After 1998, observed wounding rates began to increase, while the predicted sea lamprey

Table 8 Mean number of parasitic-phase sea lamprey with standard deviation, percent difference from no control (Scenario 1), and percent difference from the current control program (Scenario 3a) for each scenario in the natal basin and larval selection schemes. “-” indicates population extirpation.

Scenario	Natal basin matrix				Larval matrix			
	Mean # parasites	SD	% difference from no control (Scenario 1)	% difference from current control (Scenario 3a)	Mean # parasites	SD	% difference from no control (Scenario 1)	% difference from current control (Scenario 3a)
1	136,557	11,433	0.0	315.4	176,758	10,645	0.0	424.1
2a	61,808	14,547	-54.7	88.0	123,320	12,218	-30.2	265.6
2b	33,693	6488	-75.3	2.5	35,462	6151	-79.9	5.1
2c	32,492	6768	-76.2	-1.2	35,757	6308	-79.8	6.0
3a	32,877	6982	-75.9	0.0	33,726	6364	-80.9	0.0
3b	62,267	14,091	-54.4	89.4	121,922	12,011	-31.0	261.5
3c	33,198	6932	-75.7	1.0	34,862	7596	-80.3	3.4
3d	32,932	6544	-75.9	0.2	34,906	5699	-80.3	3.5
3e	31,599	6772	-76.9	-3.9	34,388	6996	-80.5	2.0
3f	22,596	6403	-83.5	-31.3	22,502	5794	-87.3	-33.3
3g	32,517	6641	-76.2	-1.1	33,341	6080	-81.1	-1.1
3h	23,570	6809	-82.7	-28.3	21,713	6656	-87.7	-35.6
3i	51,000	16,259	-62.7	55.1	116,953	10,563	-33.8	246.8
4	128,213	13,785	-6.1	290.0	169,379	12,040	-4.2	402.2
5	18,146	7071	-86.7	-44.8	-	-	-100.0	-100.0

population in the model continued on a downward trend (Fig. 4). This loss of congruity may be due in part to a change in the lake trout stocking program beginning in 1994, when lake trout stocking was reduced to compensate for increased survival and thus protect the forage base (Fisheries Technical Committee, 2005; Fig. 4). By 1999, there may have been fewer prey available for parasitic-phase sea lamprey to attack, thus the same number of wounds would be concentrated on fewer lake trout, leading to increased wounding rates per lake trout. A parallel shift in predator and prey abundance may not alter the wounding rates, thus masking any changes in the parasite population. These confounding factors make it challenging to understand why wounding rates increased so dramatically from 1998 to 2005, in divergence from the model prediction. In addition, two new spawning populations discovered recently in tributaries in Vermont may also have contributed to increased parasite abundance. Reproducing sea lamprey populations in the Lamoille and LaPlatte Rivers (Vermont) were large enough to merit chemical control (Lamoille) and consideration of a semi-permanent spawning barrier (LaPlatte) after these modeling exercises were complete. It is possible that these populations had been contributing to the parasitic-phase population in the late 1990s; earlier surveys did not detect a significant sea lamprey presence in these tributaries.

The comparison between model-predicted and mark-recapture derived (Howe et al., 2006) population estimates for parasitic-phase sea lamprey population in 2001 and 2001 was somewhat indeterminate. The model and mark-recapture estimates for 2001 were quite disparate; the 2002 estimates were very close, reflecting the need for more accurate information to populate the model. One source of uncertainty in this validation exercise is the efficacy of the lampricide treatments. Lampricide treatments are often estimated to be 95–99% effective; these management efficiencies were set to be deliberately conservative in the model simulation for this validation exercise. Another source of uncertainty may be the degree of influence of compensatory mechanisms, which have been challenging to resolve in sea lamprey population dynamics (Jones et al., 2003). Zerrenner and Marsden (2005, 2006) observed evidence of increased rates of transformation in smaller sea lamprey in Lewis Creek, VT under high larval density conditions. These elevated transformation rates may be higher than are currently used in this life history model. High larval density conditions were observed in Lewis Creek in years prior to 2001, before the 2002 lampricide application (the previous application had been more than five years earlier). A greater number of ammocoetes may have metamorphosed and migrated to the lake to join the 2002 parasitic-phase cohort than are accounted for in the model. However, this would not likely be enough to make up the difference between the mark-recapture estimate from Howe et al. (2006) and the model-predicted parasite population for the 2002 parasitic-phase cohort.

Sensitivity analysis: survivorships and transformation rates

Sensitivity analysis of the survivorship parameters indicates that while there is no specific life-stage during which the population is substantially more susceptible to changes in survivorship, there is some evidence that certain stages are less susceptible. Specifically, a 10% increase or decrease in survivorship of sea lamprey that metamorphose at age-4 and -5 or ammocoetes at age-5 and -6 results in minimal change in the parasitic-phase population abundance. This indicates that control methods specifically targeting these stages would not be as effective as methods that target other stages in the sea lamprey life cycle. Intuitively, this would appear to contradict conclusions from this model that demonstrate the efficacy of targeting larval populations; however, the lifecycle of the sea lamprey is such that the amount of time spent in the larval stage is substantially greater than in the parasitic stage. Therefore, a control program targeting

the entire larval period affects the greatest percentage of the population (age-1 larvae through the transformer stage).

Sensitivity analysis: egg deposition into nests

The model is highly sensitive to the number of eggs retained in the nest (π). The number of parasitic-phase sea lamprey decreased by more than 40% for the natal basin selection scheme and by nearly 20% for the larval selection scheme when the egg deposition rate was decreased from 15 to a 5% egg deposition rate (Fig. 5). When the egg deposition rate was increased from 15 to 25%, there was an increase of 4 to 16% in parasitic-phase sea lamprey abundance, dependent upon which selection scheme is used (natal basin or larval). These results highlight the importance of this parameter in governing the population growth rate, and illustrate the potential utility of nest dismantling as a control mechanism to supplement lampricide treatments. Laroche et al. (2004) evaluated the effect of dismantling sea lamprey nests on Lewis Creek, Vermont and determined that extensive use of this technique would be extremely labor-intensive. Nest dismantling success is also dependent on the percentage of fertilized eggs that are not retained in the nest, and survive to become age-0 ammocoetes. This model assumes that 85% of the fertilized eggs are not deposited in the nest ($1 - \pi$), based on Smith (2006), and that 3% of these eggs survive to the emergence or hatched stage. Any increase in this rate could significantly alter the population growth rate. Very little work has been conducted to explicitly examine the survival rate of fertilized eggs washed out of the nest, with the exception of recent work by Smith (2006), who estimated that survivorship of fertilized eggs that leave the nest is 2.5% (Table 3).

Sensitivity analysis: fecundity

The model was more sensitive to changes in fecundity for the natal-basin selection than the larval selection scheme. A 25% increase in fecundity yielded nearly a 10% increase in the parasite abundance for the natal-basin selection, but only a 2% increase for the larval selection scheme. Decreasing the fecundity by 25% from the base value yielded similar results. Vélez-Espino et al. (2008) found, through similar matrix modeling efforts, that reduction of sea lamprey fecundity could result in reduction of lampricide applications to maintain current levels of control in the Laurentian Great Lakes. If fecundity, fertilization rate or the survivorship of eggs deposited in or out of the nest can be reduced through an effective control program, then a proportional reduction in lampricide use might be feasible if wounding rates have been achieved.

Sensitivity analysis: parasite contributions from unknown sources

The life history model was sensitive to the abundance of parasites from unknown sources. The model was not sensitive to this parameter for Scenario 1 (uncontrolled population), most likely due to the fact that the population in this scenario is largely limited by the density-dependence limitations of the model. However, not surprisingly, the model increased in sensitivity to this parameter as the level of control increased from zero control in Scenario 1, to the current control program (3a), to a more comprehensive control program (3h). As more parasites are contributed by uncontrolled sources, the success of the control program diminishes because the remaining parasitic-phase population surviving to the spawning adult stage will carry the population through the next cycle. This highlights the importance of monitoring (and managing) all sources of parasitic-phase sea lamprey in Lake Champlain.

One source of parasitic-phase sea lamprey that is unaccounted for in this model is the potential increase in larval density over time in many tributaries within the Lake Champlain basin. A study investigating the effect of water quality on ammocoete populations highlighted

the importance of this variable on sea lamprey survivorship in the early life history, as well as throughout the larval growth period (Ferreri et al., 1995). Increased focus on watershed management has led to the restoration or improvement in water quality of several tributaries in the Lake Champlain basin, such as the LaPlatte (Vermont) and Pike River (Québec) systems. The improved water quality—i.e., increased dissolved oxygen in the water column and reduced sedimentation over gravel beds—could explain the recent increases in larval populations within these tributaries (USFWS, Essex Junction, VT; unpubl. data, 2007). The importance of this factor may be mitigated by the carrying capacity ($K_{L,i}$) that was set for the ammocoete population; however, given some of the low densities that were observed in some tributaries (i.e. LaPlatte R., 0.32 lamprey/m² in 2002; Table 1), it is feasible that future larval populations within these systems could exceed the carrying capacity used in this model. Tributaries within the Lake Champlain basin need to be surveyed at regular intervals to verify larval densities.

Proportion of females

The proportion of females (Ω) used in all model simulations presented in this paper was unbiased (0.5). The current Lake Champlain sea lamprey management program does not plan to use sterilization programs to alter the proportion of females in the spawning population; consequently this variable was not manipulated in model simulations prepared for this paper and held constant throughout all model exercises. Application of pheromones to draw one sex away from the other may be considered, and adjustments to this parameter could be incorporated into the model in future model simulations.

Management scenarios

Results from the management scenarios simulated in this model indicate that populations of parasitic-phase sea lamprey can be decreased most efficiently by targeting those tributaries that have the highest larval populations. Simulations that included control on tributaries with large larval populations were most successful in reducing the parasitic phase population; these conclusions support the current policy of the sea lamprey control program, which chooses management options for a tributary based on the number of sea lamprey present in a given tributary that are predicted to become parasites in the following year (Christie et al., 2003; Slade et al., 2003). However, simulations from this model demonstrate that the sea lamprey life cycle is sensitive to the distribution or allocation of parasitic-phase sea lamprey into spawning tributaries. Management scenarios that assume spawning tributary selection based on resident larval population size have different outcomes than those scenarios which assume selection based on natal basin-based distribution; additional scenarios based on random selection of spawning streams also had different outcomes than those presented here (Howe, 2006). Because of this phenomenon, the results from this study and therefore usefulness of this PVA model cannot be fully maximized until tributary contribution to the parasite population can be more accurately determined.

In both tributary selection schemes, parasitic-phase populations were only suppressed by reduction in the vital rates of the larval stages (i.e. simulated lampricide applications). In Scenario 4, for example, which included only the trapping of spawning-phase sea lamprey, parasitic-phase populations were not suppressed. It is also clear that control of the delta populations is necessary in order to maintain the current parasitic-phase population, as illustrated in Scenarios 3b (current control, no delta treatments), 3i (95% effective lampricide on Poultney/Hubbardton rivers, 100% effective barrier on Morpion Stream, no delta treatments), and 4 (adult trapping only). The importance of targeting the larval stages over the spawning stage has also been demonstrated by Jones et al. (2003) through the use of stock-

recruitment models and by Vélez-Espino et al. (2008) via matrix models, demonstrating that suppression of the sea lamprey population growth rate is more effective at the larval stage than at the spawning stage.

Lampricide application to larval populations in streams was the most successful approach based on these model simulations (scenario 5: 95% effective lampricide on all tributaries). When lampricide is applied to all streams at similar levels, there is complete extirpation of the population within 25–30 generations (Scenario 5). Scenario 5 was proposed by Smith and Swink (2003), in which they present a hypothesis to eradicate sea lamprey from Lake Superior by conducting lampricide treatments on all lamprey-bearing tributaries within the Lake Superior basin in a single year. This strategy was implemented in Lake Erie in 2009, as part of a strategy to use whole-lake, consecutive treatments to severely suppress sea lamprey populations (Sullivan and Adair, 2009). At the time of writing, results of this strategy were not available.

An alternative to applying lampricides to all tributaries (Scenario 5) is Scenario 3h, which illustrates the anticipated plan for sea lamprey management that managers hope will address the majority of remaining sources of parasitic-phase sea lamprey (current control, with 95% effective lampricide on the Poultney/Hubbardton rivers, and a 100% effective trap on Morpion Stream). Scenario 3h follows integrated pest management theory, which has demonstrated that by changing the vital rates of a species at multiple points in the life cycle, the population growth rate can be altered much more dramatically than when only a single stage in the life cycle is targeted (Sawyer, 1980). Scenario 3f, using a combination of control mechanisms (lampricide applications, partially effective trapping of spawning-phase sea lamprey, and installation of 100% effective spawning barriers), illustrates the potential to reduce the parasitic-phase population an additional 25–35% beyond the current control program (Scenario 3a). This reduction demonstrates the effect that a control program targeting multiple life stages can have on the parasitic-phase sea lamprey population in Lake Champlain. Implementation of alternative control strategies can be supported by cost-benefit analyses of the alternate strategies against the current sea lamprey control program. For example, Scenario 3h would require increased costs for lampricide applications and a one-time cost for barrier construction, which would impact migration of native species that are of concern in this tributary, such as redbone (Moxostoma sp.). Other management scenarios simulating control at these alternate life stages can also be explored.

Alternative lampricide treatment rotations: 3-, 5-, 6-, and 10-year cycles

Parasitic-phase populations generated in the 3-, 5-, and 6-year treatment rotations were not substantially different from that of the 4-year cycle over the short-term (20 generations; differences $\pm 8\%$ of the 4-year cycle), but the 10-year treatment cycle resulted in parasite abundances more than 22% greater than those in the 4-year rotation. Given that the majority of larval sea lamprey in this model metamorphose after five years, these results from the extended rotations are not surprising, as they allow several cohorts of lamprey into the parasitic-phase population before the next cycle of treatments suppresses the next larval cohorts. These observations are similar to those from the larval growth model of Ferreri et al. (1995), in which transformer production was estimated for 4-, 5-, and 6-year treatment rotations. The percent differences of the 5- and 6-year treatment rotations in our model were substantially lower than those found by Ferreri et al. (1995); however, the Ferreri et al. (1995) model simulated the effect of treatment on a single population, so the management effect was applied to the entire population. In our model, the current control scenario (3a) only simulated the effect on tributaries that are managed in the current sea lamprey management program. Additionally, lampricide treatments were applied in

our model to simulate 95% mortality, and Ferreri et al. (1995) simulated 99% lampricide mortality. The residual sea lamprey from simulated treatments in our model and parasite contributions from unmanaged sources likely account for the small differences observed among the various treatment rotations. In practice, increasing the treatment interval above four years may be a risky strategy; although the number of sea lamprey spawners attracted to a stream may decline in the first year or two after treatment due to the reduced larval pheromone signal, larval survival may increase considerably as a consequence of reduced competition (Zerrenner and Marsden, 2006).

Conclusions

Simulations generated by this sea lamprey life-cycle model for Lake Champlain clearly indicate that if any one tributary with a significant proportion of the larval sea lamprey population within the basin is not controlled, it can act as a source population to all other tributaries to which control has been applied. This is made evident by the fact that the abundance of the parasitic population did not decrease substantially in any management scenario for this model except for those in which control was applied to all major contributors. If any major contributing streams were left uncontrolled, survival to the parasitic-phase from that tributary increased substantially, compensating for any decrease that was achieved elsewhere. An economic injury level model that has been devised for application to each of the Great Lakes also indicates the importance of uncontrolled populations, either in the form of deferred lampricide treatments, reduced treatment effectiveness, or contributions from unknown sources, in accurately predicting the impact of parasitic-phase sea lamprey on the lake trout fishery (Christie and Goddard, 2003; Koonce et al., 1993; Larson et al., 2003; Sawyer, 1980).

Simulations from this model also highlight the importance of the method in which the parasitic-phase sea lamprey population is allocated to tributaries for spawning. The contributions of several tributaries to the parasite population may be mitigated if in fact these parasites remain local, rather than distributing freely among the lake tributaries. This observation is especially evident when assessing the results from the larval selection scheme, where large quantities of parasites are distributed to tributaries that may in fact not be contributing parasites to a lake-wide population. However, the model did demonstrate that with the natal basin selection scheme, even a small proportion (<10%) of the parasites from one major tributary can be enough to maintain the overall population. Developing theories suggest that parasitic-phase sea lamprey may select tributaries based on presence of larval populations (Vrieze et al., 2011; Wagner et al., 2009); if so, it is highly possible that the true allocation of parasites from the lake to the tributaries is some combination of the natal basin and larval selection schemes simulated in this study.

The model presented here is capable of optimizing the integrated pest management approach to sea lamprey control in Lake Champlain. Results from the management scenarios simulated present evidence that, with the appropriate management strategy, the parasitic-phase sea lamprey population could be significantly decreased. This model should be used as a guide for fisheries managers, not as a final answer on the demography of the Lake Champlain sea lamprey population. The model will require updating over time as new information becomes available in the form of demographic data specific to Lake Champlain, in our understanding of sea lamprey biology, or as new management options are considered. While results from this model should not be used to forecast the future parasitic-phase sea lamprey population in Lake Champlain, the model does provide a mechanism for guiding fisheries managers toward a more efficient management program by evaluating the relative contribution of different management activities in reduction of the parasitic lamprey population.

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