Demographic analysis of trade-offs with deliberate fragmentation of streams: Control of invasive species versus protection of native species

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Abstract
Tools restricting the movements of invasive species (e.g. barriers) and reducing habitat fragmentation for native species (e.g. corridors, fishways) provide examples where actions taken to address one environmental concern can hinder efforts to address another environmental concern. We used perturbation analysis of stage-structured projection matrices to evaluate the efficacy of seasonally operated barriers and fishways for controlling non-native sea lamprey (Petromyzon marinus) in the Laurentian Great Lakes while minimizing effects on non-target fishes. For non-jumping fishes migrating in spring, seasonally operated barriers without a fishway will not balance the management objectives satisfactorily. Migration phenologies of the seven common non-target fishes considered in our analyses overlapped considerably with the migration phenology of sea lamprey, with peaks in migration typically being 7–43 days (median 12) from the peak in the sea lamprey migration. Consequently, across species, years, and tributaries, 44–100% of the migratory runs of non-target fishes would be blocked under the 75-day operation period required to block 99% of the sea lamprey spawning run, on average. Reductions in the production of non-target fishes due to blocking were also projected to be similar in magnitude to reductions projected in the production of sea lamprey, unless density-dependent compensation was strong or overlap in migration phenologies between a non-target species and sea lamprey was low. Even under density-dependent compensation, providing a fishway is advisable and passage of non-target fishes may have to be highly effective to avoid population declines in non-jumping species that migrate between a Great Lake and its tributaries.

1. Introduction

Ecosystem-based management requires that decision makers weigh opposing environmental concerns. For example, barriers to movement can provide an effective, economical ecosystem tool restricting the movements and reproduction of invasive species and facilitating protection or restoration of native communities (Sharov and Liebhold, 1998). They can also restrict the movements and reproduction of non-target, native species (Benstead et al., 1999; Porto et al., 1999). Conversely, provisioning movement corridors or fishways, or removing barriers to movement (e.g. dams) can reduce habitat fragmentation (Levey et al., 2005; With, 2002), but facilitate the spread of invasive species and their unwanted effects on native ecosystems (Proches et al., 2005). The need to evaluate the effectiveness of management tools restricting or facilitating movement in light of both perspectives has been recognized for some time (Saunders and Hobbs, 1991; With, 2002), but overlooked in prominent studies (Proches et al., 2005). This need will likely to increase as concerns regarding invasive and sensitive native species heighten (e.g. Fausch et al., 2009).

This study examines tensions between control of invasive species and habitat fragmentation surrounding the use of in-stream barriers to control sea lamprey (Petromyzon marinus) in the Laurentian Great Lakes. The sea lamprey is a fish that feeds on the blood and tissue of host fishes. Its status in Lake Ontario remains the subject of debate (Bryan et al., 2005), however, its invasion of the upper lakes following modifications to the Welland Canal (Christie and Goddard, 2003) was arguably one of the largest ecological disasters in North America during the 20th century. Sea lamprey parasitism, combined with habitat alteration and overfishing, caused significant declines in populations of large native fishes, altering food webs within the lakes (Eshenroder and...
Sea lamprey control began in the 1950s and is overseen by the Great Lakes Fishery Commission (GLFC) with field operations contracted to Fisheries and Oceans Canada (DFO) and the United States Fish and Wildlife Service (USFWS).

Control efforts over the past 50 years relied heavily on periodic application of the selective lampricide 3-trifluoromethyl-4-nitrophenol (TFM) to streams and rivers where larval sea lamprey rear for their first four or more years of life. Lampricides remain the key component of the sea lamprey management program (Great Lakes Fishery Commission, 2001). Physical and electrical barriers to movement provide an effective control alternative. They deny maturing sea lamprey access to spawning habitat. Barriers played a significant role in early efforts to control sea lamprey (Hunn and Youngs, 1980), but their use declined due to maintenance needs of early designs and the success of chemical control. In 2001, the GLFC pledged to reduce its reliance on TFM and increase its use of alternative control methods such as barriers (Great Lakes Fishery Commission, 2001). It operates 69 sea lamprey barriers. It also monitors several hundred de facto dams that function as sea lamprey barriers, but were constructed for other purposes, and are owned and operated by other agencies and corporations (Lavis et al., 2003). Until 2007, the GLFC was considering construction of up to 100 more barriers over 20 years. In 2007, these expectations were reduced to a smaller number of tributaries where other control options are not viable, a barrier would be more cost-effective than lampricide control, or a barrier would be competitive with local watershed management plans (Burkett et al., 2007). The change was made to direct resources to the restoration or replacement of deteriorating de facto dams and to address growing, basin-wide demand for dam removal or provisioning of fish passage, which can increase spawning habitat available to sea lamprey and add to chemical treatment costs (e.g. Furlong et al., 2006).

The barrier design used most extensively for sea lamprey control is a permanent, fixed-crest barrier where the crest is a constant height relative to the stream bottom providing a drop of ~0.5–2 m. This design is effective at blocking sea lamprey, but can also restrict movements of common non-jumping fish species (Porto et al., 1999), and alter the composition of fish assemblages above the barrier (Dodd et al., 2003). To avoid these outcomes, newer seasonal barrier designs have been developed that block movements of sea lamprey and other non-jumping fishes during the period of sea lamprey migration, but allow passage of non-target fishes at other times of the year (McLaughlin et al., 2007). These seasonal barriers involve either elevating crest height or turning on an electrical field across the tributary during the period of sea lamprey migration and lowering crest height or turning off the electrical field at other times. Newer fixed crest and seasonal barriers may also be outfitted with a trap or fishway where sea lamprey and non-target fishes are captured, sorted, and the latter released. Optimal operation of these devices, and their effectiveness in terms of blocking sea lamprey while passing non-target fishes, have been key uncertainties. The uncertainties are significant. Across the basin over 100 non-target fishes co-occur with sea lamprey in streams (Mandrak et al., 2003) and migration phenologies of migratory, non-target fishes overlap with that of sea lamprey (Klinger et al., 2003).

This study modeled the effectiveness of seasonally operated sea lamprey barriers and fishways in terms of blocking sea lamprey and passing non-target fishes. We first quantified overlap in migration phenologies of sea lamprey and seven migratory non-target teleost fishes that co-occur with sea lamprey. We then used stage-structured matrix population models to project how blocking the reproductive migrations of sea lamprey was expected to affect the production of sea lamprey and the non-target fishes. Last, we projected how population sizes of non-target species change proportionally over time under different levels of fish passage.

2. Methods

2.1. Modeling migration phenologies of sea lamprey and non-target fishes

Data quantifying the migration phenology of sea lamprey were obtained from the DFO and USFWS. These data sets consisted of daily catches from traps and trap-and-sort fishways used to remove sea lamprey from the spawning run. Data were obtained for 149 sample years from 13 tributaries (Table 1 and Fig. 1). Annual catches ranged from 7 to 21 107 individuals (median = 997). Our analysis is based on 145 sample years where 30 or more individuals were captured during a run.

For sea lamprey, a single migration phenology was constructed by standardizing daily captures ($C_{th}$) for day $i$ into proportions of the total run for year $j$ and tributary $k$, calculating mean daily proportions across years, and repeating these steps across tributaries to obtain the proportion of the run expected on a given Julian date. The resulting phenology did not differ significantly from a normal distribution (Kolmogorov–Smirnov test: $p > 0.05$). Mean date of the phenology was calculated as $\mu = \frac{\sum_{i=\text{first}}^{\text{last}} C_{th} f_i}{\sum_{i=\text{first}}^{\text{last}} C_{th}}$, where $(f)$ represents daily frequencies computed from standardized daily catches, $\mu$ represents the Julian day and $C_{\text{first}}$ and $C_{\text{last}}$ are the first and last capture days, respectively, across all sea lamprey runs. Standard deviation of the phenology was calculated as

$$\sigma_X = \left( \sum_{i=\text{first}}^{\text{last}} (f(X_i - \mu))^2 \right)^{1/2}.$$ 

Mean and standard deviation of the fitted distribution were used in our model to estimate the proportions of the migration run blocked by barrier operations.

<table>
<thead>
<tr>
<th>Tributary</th>
<th>Lake</th>
<th>Period</th>
<th>Catch</th>
<th>Years of data</th>
</tr>
</thead>
<tbody>
<tr>
<td>Big Carp River</td>
<td>Superior</td>
<td>1997–2000</td>
<td>10 (8–301)</td>
<td>2</td>
</tr>
<tr>
<td>Carp River</td>
<td>Superior</td>
<td>1988–1997</td>
<td>117 (91–221)</td>
<td>6</td>
</tr>
<tr>
<td>Bridgeland Creek</td>
<td>Huron</td>
<td>1979–2001</td>
<td>1033 (178–5181)</td>
<td>24</td>
</tr>
<tr>
<td>Echo River</td>
<td>Huron</td>
<td>1987–2001</td>
<td>2045 (105–5716)</td>
<td>15</td>
</tr>
<tr>
<td>Ocqueoc River</td>
<td>Huron</td>
<td>1980–1998</td>
<td>2771 (473–9836)</td>
<td>15</td>
</tr>
<tr>
<td>Big Creek</td>
<td>Erie</td>
<td>1996–2001</td>
<td>212 (7–997)</td>
<td>5</td>
</tr>
<tr>
<td>Cobourg Brook</td>
<td>Ontario</td>
<td>1998–2001</td>
<td>219 (168–258)</td>
<td>4</td>
</tr>
<tr>
<td>Duffins Creek</td>
<td>Ontario</td>
<td>1981–2001</td>
<td>1059 (149–2414)</td>
<td>21</td>
</tr>
<tr>
<td>Humber River</td>
<td>Ontario</td>
<td>1987–1996</td>
<td>2117 (473–9836)</td>
<td>10</td>
</tr>
</tbody>
</table>
A single sea lamprey migration phenology was calculated because (i) control agents organize operations based on the long-term knowledge about a tributary, and possibly neighboring tributaries, given that the agents cannot accurately predict the migration phenotype for a given tributary in a specific year due to annual variation in run timing, (ii) comparison of Julian dates for 10% 25% 50% 75% and 90% of a season’s catch (Q10 Q25 Q50 Q75 and Q90 respectively) across tributaries failed to detect consistent inter-tributary differences in these phenotype features against the year to year variation within tributaries (one-way multivariate analysis of variance: Wilk’s = 0.64, p = 0.19) and (iii) simple models that aggregate data to estimate fewer parameters can perform better than models where more parameters are estimated (Hilborn and Mangel, 1997). Annual phenologies were expressed as proportions so that phenologies from years and locations where run size was high were given the same weight as phenologies from years and tributaries where run size was low. For an operation period of 75 days, a period predicted to block 99% of migrating sea lamprey on average, the estimated proportion blocked each year did not differ systematically with annual catch (mean Spearman rank correlation between % blocking and catch by tributary following z transformation = 0.16; 95% confidence limits: –0.16 to 0.49; N = 13 tributaries). Control agents are concerned about infrequent observations of sea lamprey moving in streams outside of the normal period of barrier and trapping operations. Reproductive fates of these individuals are unknown (McLaughlin et al., 2007). The normal distribution accommodates this concern because the tails of the distribution extend outside of the period of normal trap operations.

For non-target species, we quantified migration phenologies for brown bullhead (~nus robustus), longnose sucker (~ostomus catostomus), white sucker (~ostomus commersoni), channel catfish (~ctalurus punctatus), yellow perch (~erca flavescens), walleye (~ander vitreus), and creek chub (~emotilus atromaculatus). Data for migration phenologies of brown bullhead, longnose sucker, white sucker, yellow perch, and creek chub were obtained from trap records for seven of the same tributaries used for sea lamprey. Data for migration phenologies of the remaining non-target species were obtained from records provided by Michigan Department of Natural Resources for the St. Joseph River, Lake Michigan (channel catfish) and the Otter River, Lake Superior (walleye). This generated 97 sample years of data from nine tributaries (Table 2 and Fig. 1).

These non-target species were selected based on (i) their co-occurrence with sea lamprey (Dodd et al., 2003; Furlong et al., 2006; Porto et al., 1999), (ii) the availability of catch records during upstream spawning migrations, and (iii) the availability of estimates for stage-specific vital rates for the population models (Vélez-Espino et al., 2006). We considered channel catfish and walleye in our analyses despite lacking corresponding sea lamprey data for the St. Joseph and Otter Rivers because these species are of fishing and conservation interest (e.g. Furlong et al., 2006) and because sea lamprey occur in the St. Joseph River, and the Sturgeon River, of which the Otter River is a tributary. Sea lamprey barriers affect migratory fishes more so than resident fishes (R. McLaughlin, University of Guelph, unpublished data). All fishes considered here except creek chub migrate from lakes to rivers to spawn (Becker, 1983; Scott and Crossman, 1973). Creek chub migrate within streams and rivers to spawn (Dinsmore, 1962; Stock and Momot, 1981). Longitudinal (along a stream course) abundances of white sucker, yellow perch, and creek chub are sensitive to low-head barriers (McLaughlin et al., 2006).

For each non-target species, a single migration phenology was constructed by standardizing daily captures (N for day j into proportions of the total run for year k and tributary j, calculating mean daily proportions across years, and repeating these steps across tributaries to quantify the proportion of the run expected on a given Julian date. As with sea lamprey, each species’ migration phenotype did not differ significantly from a normal distribution (Kolmogorov-Smirnov test: all p’s > 0.05). One phenology per species was considered appropriate because for each species multivariate analyses of variance for Q10, Q25, Q50, Q75, and Q90 revealed no significant differences among tributaries (one-way multivariate analyses of variance for each species, all p’s > 0.05) and because simple models using the data to estimate fewer parameters often outperform more complex models. One phenology for all non-target species was considered inappropriate because two-sample t tests comparing capture dates indicated the timing of migration differed significantly among species (p < 0.05) in 19 of 21 possible pairwise comparisons. Annual phenologies were expressed as proportions so that phenologies from different years and locations were weighted the same. For a 75 day operation period, the estimated level of non-target blocking each year did not differ systematically with annual non-target catch (Spearman rank correlation between % blocking and catch following z transformation = 0.27, 95% CL’s: −0.02 to 0.57, N = 17 species-tributary combinations).
Proportions of non-target fishes that would be blocked ($B$) by barrier operation of a given duration were predicted from the probabilities ($Pr$) from the normal distributions characterizing the average phenologies for each species by using the overlap between the duration of barrier operation used to prevent sea lamprey passage and the migration phenology of each non-target species:

$$B = Pr(x_l \leq X \leq x_r) \quad \text{for} \quad X = N(\mu_x, \sigma_x)$$

(1)

where $x_l$ and $x_r$ are the Julian days representing the beginning and the end of the operation period, respectively, centered on the mean of the migration phenology for sea lamprey, and $\mu_x$ and $\sigma_x$ represent the mean and standard deviation of the phenology for a given non-target species.

We assessed the predictions of this blocking model for sea lamprey by comparing the proportion of blocking expected for each annual run from a tributary, assuming a barrier was operated for 75 days centered on the median of the averaged sea lamprey migration phenology for the tributary, against the predicted value of 99% obtained from the blocking model. Seventy-five days (99%) was selected because the control agents strive to block the entire sea lamprey run and this was considered the shortest duration that might be acceptable from a control perspective. Seasonal barriers are typically operated for 90–110 days corresponding with ~99.9% blocking of sea lamprey. We assessed the predictions of the blocking model for non-target species by comparing the proportion of blocking expected for each annual run of each species from a tributary, assuming a barrier was operated for 75 days centered on the median of the averaged sea lamprey migration phenology for the tributary, against predicted values obtained from Eq. (1).

We assessed whether the levels of blocking quantified for the seven non-target fishes were representative of other non-target species co-occurring with sea lamprey in the Great Lakes basin by comparing the overlap between Julian dates of operation required to block 99% and 99.99% of sea lamprey, respectively, based on the blocking model, against the Julian dates of first and last capture for migratory runs made by an additional 18 species for which there were less than 30 records for each annual migratory run. Data for these species were obtained from trapping records from Big Carp River, Big Creek, Bridgeland Creek, Cobourg Brook, Duffins Creek, Echo River, Otter River, and St. Joseph River.

### 2.2. Modeling effects of blocking on production

Population responses to blocking were modeled using stage-structured matrices with a 1-year projection interval.

$$A = \begin{bmatrix} P_2 & 0 & 0 & E_5 \\ G_2 & P_3 & 0 & 0 \\ 0 & G_3 & P_4 & 0 \\ 0 & 0 & G_4 & 0 \end{bmatrix} \quad B = \begin{bmatrix} P_2 & 0 & E_4 & E_5 \\ G_2 & P_3 & 0 & 0 \\ 0 & G_3 & P_4 & 0 \\ 0 & 0 & G_4 & P_5 \end{bmatrix}$$

(2)

Elements of $A$ and $B$ are stage-specific fecundity rates ($E_k$), probabilities of surviving and remaining in the same stage ($P_k$), and probabilities of surviving and moving to the next stage ($G_k$; transition probabilities). Matrix $A$ summarizes the life cycle in five stages: individuals less than a year old (young-of-the-year, YOY), larvae (ammoecetes), individuals undergoing metamorphosis from larval to parasitic form (transformers), parasitic individuals (juveniles), and adults ($Vélez-Espino et al., 2008$). This model structure corresponds to life stages with different ecological roles and vital rates, except for the YOY stage which is set apart in fish population models because of differences in survival probabilities for the first and later years of life ($Vélez-Espino et al., 2008$). Matrix $B$ summarizes the life cycles of non-target fishes in five life stages: YOY, early juvenile, late juvenile, early adult, and late adult ($Vélez-Espino et al., 2006$). The juvenile period refers to the period from the end of the first year of life to the age-at-maturity ($T_{max}$). Early juvenile stage refers to fish during the first half of the juvenile period. Late juvenile refers to the second half. The adult period refers to the period from age-at-maturity to last observed reproductive age. Early adult stage refers to the first half of the adult period. Late adult stage refers to the second half. Juvenile and adult periods were subdivided to avoid loss of information caused by averaging values of vital rates with high variance in species with long juvenile or adult periods ($Crouse et al., 1987$). Stage-structured models assume that individuals in a given stage are subject to identical rates of mortality, growth, and fecundity ($Crouse et al., 1987$). Even when age-specific information is available, a stage-structured approach can be simpler and equally efficient providing rates of mortality, growth, and fecundity are similar across age classes. Annual population growth rate ($\lambda$) is represented by the largest eigenvalue of the projection matrices. A $\lambda$-value of 1.0 represents a population at equilibrium, $\lambda$ of 1.1 a
population growing 10% annually, and $\lambda$ of 0.9 a population declining by 10% annually.

In matrices $A$ and $B$, $P_1 = 0$ because the length of stage 1 is equal to the projection interval. In the sea lamprey matrix, $P_5 = 0$ because adult sea lamprey die after spawning and stage duration is less than the projection interval. Matrix elements $E$, $P$ and $G$ were estimated from a pre-breeding model (Caswell, 2001) with fecundity rate ($E_S$) computed as the product of proportion of females ($p_f$, assumed to be 0.5), annual offspring per adult female ($m_f$), and YOY survival. Matrix dimensions are reduced by one order because $YOY$ would be 1 year of age at the time of census in the model and their survival rate is included in the fecundity rate (Caswell, 2001). This is why $P_1$ is not explicit in the matrices. $\sigma_S$ is the annual survival probability of an individual in stage $S$ and $\gamma_S$ is the probability of moving from $S$ to $S + 1$ given $\sigma_S$. Parameters $P_5$ and $G_S$ were defined as $\sigma_S(1 - \gamma_S)$ and $\sigma_S \gamma_S$, respectively. $\gamma_S$ was calculated using a geometric-distribution with $\gamma_S = T_S^{-1}$, where $T_S$ is the duration (years) of stage $S$, assuming the age distribution within stages is stable (Lefkovitch, 1965). Specific values of vital rates and corresponding matrix elements for the sea lamprey matrix ($A$) were compiled from Vélez-Espino et al. (2008) and for the non-target matrices ($B$) from Vélez-Espino et al. (2006) (Table 3). These are species averages considered to be representative for populations in the Great Lakes. Values for specific non-target populations were not available.

For sea lamprey and the non-target fishes, reductions in population growth rates due to barrier operations were modeled by assuming the reduction in fecundity rate was directly proportional to the proportion of the run blocked by the barrier and that early and late adult stages of non-target fishes were affected equally. Effects on population growth rates were calculated through direct perturbation of projection matrices:

$$\lambda' = \lambda_M |B|$$

where $\lambda'$ is the new population growth rate, $\lambda_M$ the dominant eigenvalue of original projection matrices of sea lamprey and non-target species, and $B$ the reduction in fecundity. For the sea lamprey, we used the Ricker function in the fecundity coefficient of the matrix ($E_S = \xi_S p_f m_f$) to model density-dependent compensation in the form of proportional increases in YOY survival arising from reductions in fecundity as:

$$\xi_S = \sigma_S (1 + Be^{-\beta})$$

where $\xi_S$ is the density-dependent YOY survival and $\beta$ is the index of density dependence. $\beta$ was estimated from analyses of time series of spawner abundances (Vélez-Espino et al., 2008).

For non-target fishes, we used life history correlates of density dependence to predict the compensation ratio ($CR$) for the Ricker model. $CR$ is a standardized measure of density-dependent recruitment (Goodyear, 1997) used to compare the relative strength of density dependence across populations or stocks. It is the ratio of maximum recruit survival and recruit survival at equilibrium for an unexploited spawning stock (Goodwin et al., 2006). $CR$ was estimated from maximum weight ($W_{max}$: kg) and age-at-maturity ($T_{mat}$; year) following Goodwin et al. (2006):

$$\log CR = 0.18 \log W_{max} + 1.06 \log T_{mat}$$

Values of $W_{max}$ and $T_{mat}$ for each species were obtained from Vélez-Espino et al. (2006), Winemiller and Rose (1992), and FishBase (www.fishbase.org) (Table 3).

Changes in population growth rates were modeled as proportional, rather than absolute, changes. For non-target species, we lacked population abundances needed to estimate actual population growth rates. Using proportional changes has the advantage of calculating changes in population growth rates without having to know the value of $\lambda$ prior to a perturbation. It also serves to standardize individual matrices for the effect that population state lacked population abundances needed to estimate absolute changes. For non-target species, we calculated changes in population growth rates without having to know the value of $\lambda$ prior to a perturbation.

Proportional change in population growth rate ($\psi$) was computed as:

$$\psi = (\lambda' - \lambda_M)/\lambda_M$$

If $\psi_{DD}$ is the proportional density-independent reduction in population growth rate, and $\psi_{DD}$ the proportional density-dependent reduction in population growth rate, the ratio between these parameters represents a density-dependent compensation ratio. Eq. (5) was developed for marine fishes, so sea lamprey (SL) parameters $\psi_{DD}$, $\psi_{DD}$, and $CR$ were used to calibrate the predictive relationship and infer $\psi_{DD}$ for each non-target fish (NTF) as:

$$\psi_{DD,SL} = \frac{\psi_{DD,SL} CR_{NTF}}{\psi_{DD,SL} CR_{SL}}$$

The trade-off between harm to non-target fishes and gains in sea lamprey control was characterized by plotting the projected

### Table 3

<table>
<thead>
<tr>
<th>Vital rate</th>
<th>Species</th>
<th>Sea lamprey</th>
<th>Brown bullhead</th>
<th>Channel catfish</th>
<th>Creek chub</th>
<th>Longnose sucker</th>
<th>Walleye</th>
<th>White sucker</th>
<th>Yellow perch</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\sigma_1$</td>
<td></td>
<td>0.0006</td>
<td>0.005</td>
<td>0.0027</td>
<td>0.005</td>
<td>0.0037</td>
<td>0.001</td>
<td>0.003</td>
<td>0.001</td>
</tr>
<tr>
<td>$\sigma_2$</td>
<td></td>
<td>0.53</td>
<td>0.098</td>
<td>0.24</td>
<td>0.15</td>
<td>0.02</td>
<td>0.017</td>
<td>0.21</td>
<td>0.22</td>
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<tr>
<td>$\gamma_2$</td>
<td></td>
<td>0.16</td>
<td>1</td>
<td>0.5</td>
<td>1</td>
<td>0.5</td>
<td>0.5</td>
<td>0.33</td>
<td>1</td>
</tr>
<tr>
<td>$\sigma_3$</td>
<td></td>
<td>0.53</td>
<td>–</td>
<td>0.48</td>
<td>0.31</td>
<td>0.46</td>
<td>0.48</td>
<td>0.49</td>
<td>0.37</td>
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<tr>
<td>$\sigma_3$</td>
<td></td>
<td>1</td>
<td>–</td>
<td>1</td>
<td>1</td>
<td>0.5</td>
<td>0.5</td>
<td>0.5</td>
<td>1</td>
</tr>
<tr>
<td>$\gamma_4$</td>
<td></td>
<td>0.6</td>
<td>0.22</td>
<td>0.64</td>
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<td>0.69</td>
<td>0.65</td>
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<tr>
<td>$\sigma_4$</td>
<td></td>
<td>0.69</td>
<td>0.5</td>
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<tr>
<td>$\sigma_5$</td>
<td></td>
<td>0.25</td>
<td>0.64</td>
<td>0.46</td>
<td>0.25</td>
<td>0.25</td>
<td>0.69</td>
<td>0.65</td>
<td>0.55</td>
</tr>
<tr>
<td>$\gamma_5$</td>
<td></td>
<td>–</td>
<td>0.5</td>
<td>0.33</td>
<td>0.25</td>
<td>0.2</td>
<td>0.5</td>
<td>0.2</td>
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<tr>
<td>$m_4$</td>
<td></td>
<td>5868</td>
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<td>4043</td>
<td>20,972</td>
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<td>80,245</td>
<td>58,196</td>
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<tr>
<td>$m_5$</td>
<td></td>
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<td>11,415</td>
<td>57,596</td>
<td>4514</td>
<td>40,629</td>
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<td>$W_{max}$</td>
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<td>2.7</td>
<td>9.3</td>
<td>0.3</td>
<td>3.3</td>
<td>11.3</td>
<td>2.9</td>
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<td>$T_{mat}$</td>
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</tr>
<tr>
<td>$CR$</td>
<td></td>
<td>66.3</td>
<td>32.2</td>
<td>54.7</td>
<td>21.7</td>
<td>57.5</td>
<td>71.7</td>
<td>68.1</td>
<td>30.3</td>
</tr>
</tbody>
</table>
proportional decrease in production of each non-target species against the projected proportional decrease in production of sea lamprey. For all species, the plots provide projections based on the blocking model. For brown bullhead, creek chub, longnose sucker, white sucker, and yellow perch, the plots also provide projections based on the levels of blocking expected for the non-target species in each year for a given tributary when blocking durations for sea lamprey control were determined based on the average migration phenology across years for that tributary. For channel catfish and walleye, where sea lamprey data were not available for the specific tributary, annual projections were based on the levels of blocking expected for channel catfish and walleye in each annual run for the tributary where data were collected against blocking dates for sea lamprey based on the average sea lamprey phenology across years for each tributary located within the geographic ranges of channel catfish and walleye within the Great Lakes. These projections should bracket the range of possible annual outcomes given the yearly variation in non-target phenologies within tributaries.

We used fecundity elasticities to assess whether the relative changes in population growth rates projected for the seven non-target species in response to barriers were representative of changes expected for 41 other migratory, non-target fishes co-occurring with sea lamprey in the Great Lakes basin (Vélez-Espino et al., 2006). Elasticities ($\varepsilon_{ij}$) approximate how population growth rates change in response to perturbation of a given vital rate (e.g. the effect of barriers on fecundity). They are demographic partial derivatives that indicate the sensitivity of $\lambda$ to changes in the matrix elements ($m_{ij}$):  

$$\varepsilon_{ij} = \frac{\partial \log \lambda}{\partial \log m_{ij}}$$

For example, a 20% decrease in the fecundity rate for a population with a fecundity elasticity of 0.1 will decrease population growth rate by 2% (Brault and Caswell, 1993; De Kroe et al., 1986). Our assessment tested whether the variance in fecundity elasticities for the seven non-target species examined here differed significantly from that of a random sample of seven taken from the 48 non-target species, using the randomization test of Sokal and Rohlf (1981, Chapter 18) with 9999 randomizations.

### 2.3. Population responses to fish passage

We calculated how fish passage during a period of barrier and fishway operation could affect population growth rates of non-target fishes by simulating fish passage efficiencies of 10%, 50%, and 90% of the non-target run, respectively, for hypothetical population growth rates before barrier construction ($\lambda_{M}$) of 1.00, 1.05, and 1.10. We did not consider $\lambda_{M} < 1.00$ because the non-target species considered here are common in the Great Lakes basin. Population growth rates were projected over 20-years as:

$$\lambda = \lambda_{M}(B, \zeta)$$

where $\zeta$ represented the proportion of the spawning run passed by a hypothetical fish passage device. Proportional changes in population size relative to time (t in years) were estimated as ($\lambda > 0$) under continuous and constant annual perturbation rates $1 - \zeta$ and including density-dependent increases in YOY survival due to reductions in spawner abundances. These projections did not include equilibrium population sizes (i.e. carrying capacities) for increasing trajectories ($\lambda > 0$) because our analyses pertain to scenarios where barriers cause population declines. All matrix computations were conducted using MATLAB version 6.5.1 (The Mathworks, Inc., Natick, Massachusetts).

Our analyses assumed that in-stream barriers affect the population dynamics of sea lamprey and non-target species by blocking upstream migrations of spawning individuals and that blocked animals do not spawn successfully elsewhere or after the barrier is no longer in operation (Schilt, 2007). For sea lamprey, barriers are typically situated so that the stream section below the barrier lacks suitable spawning habitat. When spawning habitat is present downstream, the section is treated chemically, as are neighboring streams with spawning habitat. For non-target fishes, movements between streams are rare. A study tracking 4100 non-target fish (from 25 species), tagged with passive integrated transponder (PIT) tags, for movements between six adjacent Lake Ontario tributaries over 3 years revealed that 0–4% of individuals moved between streams, depending on the species (Dolinske et al., 2008). The species tracked included four of the seven non-target species considered here. Percentages of individuals exhibiting inter-stream movements were 1%, 1%, 3%, and 4% for brown bullhead, creek chub, white sucker, and yellow perch, respectively.

Our analyses focused on the level of individual tributaries because the decision to build a barrier is made on the perceived advantages and disadvantages of control options at that spatial extent and because of evidence that juvenile and adult non-target fishes move little between streams within and across years (Dolinske et al., 2008). Sea lamprey, however, do not home (Bergstedt and Seeley, 1995) and can move from one stream to another during the spawning season (Kelso and Gardner, 2000). Estimates of the relative change in $\lambda$ for sea lamprey represent the decrease in sea lamprey production expected from the tributary targeted for a barrier. This production is repeatable over the long term prior to barrier construction because barriers are placed on tributaries where control actions are needed consistently.

### 3. Results

#### 3.1. Differential blocking of sea lamprey and non-target fishes

Averaged migration phenologies calculated for the seven non-target species overlapped considerably with the averaged phenology for sea lamprey (Fig. 2). Peaks in the migration of longnose sucker, white sucker, and walleye occurred 8, 8, and 25 days earlier than sea lamprey, respectively, on average. Peaks in the migration of creek chub, yellow perch, brown bullhead, and channel catfish occurred 7, 12, 16, and 43 days later, respectively, on average. Durations of migration were also relatively long (Fig. 2).

The blocking model predicted that proportions of sea lamprey blocked by a barrier increase at a decreasing rate as the period of barrier operation increases (Fig. 3). Operation periods of 25, 50, 75, and 115 days were predicted to block 60%, 90%, 99%, and 99.99% of migrating sea lamprey, respectively. For a 75-day opera-

![Fig. 2. Averaged migration phenologies (see Section 2) for the sea lamprey, brown bullhead, channel catfish, creek chub, longnose sucker, walleye, white sucker, and yellow perch used to predict levels of blocking for different periods of barrier operation.](image-url)
tion period, the blocking model made good predictions of the level of blocking estimated for annual sea lamprey runs (Fig. 4). Operation periods of 75 days or more were also predicted to block substantial proportions of the non-target species (Fig. 3). For a 75 day blocking period, the blocking model also made good predictions of the level of blocking estimated for annual non-target runs, although there were infrequent years where blocking was considerably lower than predicted (Fig. 4).

The high levels of blocking predicted for the seven species considered here are likely for other migratory fishes inhabiting the Great Lakes. Earliest and latest catches for the additional non-target species with information available on migration timing overlapped considerably with the dates for the 75 and 115 day operation periods predicted to block 99% and 99.99% of a sea lamprey run in the blocking model (Fig. 5).

3.2. The trade-off between sea lamprey control and non-target species

Plots relating annual decreases in production projected for the non-target species to the annual decrease in production projected for sea lamprey revealed four salient features. First, reductions in the production of non-target fishes can be expected to increase at an accelerating rate with increased blocking of sea lamprey and corresponding reductions in sea lamprey production (Figs. 6 and 7). This curvilinear shape arises because, as the period of barrier operation is increased to block more early and late migrating...
Our application to sea lamprey in the Great Lakes has three additional, noteworthy features. First, it provides an explicit case study exemplifying the tension between restricting the movements of harmful, non-native species and reducing habitat fragmentation foreseen in earlier publications (Saunders and Hobbs, 1991; With, 2002) and responds to recent publications stressing the need for mechanistic studies assessing management tools restricting or facilitating animal movements in light of both environmental concerns (Fausch et al., 2009; Proches et al., 2005). Second, itvaluably extends earlier research indicating migration phenologies of sea lamprey and non-target fishes could overlap significantly (Klinger et al., 2003) by explicitly modeling how this overlap is expected to influence production of sea lamprey and non-target fishes. Third, the application to sea lamprey control provides an example where the trade-off between management concerns is occurring over a broad geographic extent and is of significant ecological and economic importance, given the value of the Great Lakes' fishery (US Department of the Interior, 2006), the crucial role of sea lamprey control in managing the ecological health and economic success of the fishery (Koonce et al., 1993; Lupi et al., 2003), and growing basin-wide concern about habitat fragmentation by small dams (Cumming, 2004; Sarakinos and Johnson, 2003).

Our model suggests it could be possible to operate barriers for less than the typical 90–110 days and still achieve sea lamprey control; however, any reduction in the duration of operation is unlikely without further empirical testing. Sea lamprey control is the primary management objective of the Great Lakes Fishery Commission and its contract agents. Managers are concerned about effects of control actions on non-target species (Great Lakes Fishery Commission, 2001), but remain cautious about the risk associated with reducing durations of barrier operation. In fact, control agents have recommended operation periods of 180 days (Burkett et al.,...
2007), because of infrequent observations of sea lamprey moving in streams outside of the migration period and uncertainty surrounding the reproductive success of those lamprey (McLaughlin et al., 2007). In addition, gains in production of non-target fishes for shorter periods of operation (e.g. 75 days) are projected to be small.

Efforts to minimize the effects of barriers on spring migrating fishes by providing selective fish passage will need to be highly effective unless the non-target fishes exhibit compensatory responses larger than those considered here. This conclusion is consistent with evidence that fewer non-target species are found in stream segments above barriers than expected from corresponding reference locations (Dodd et al., 2003; Porto et al., 1999) and evidence that non-target fishes using lentic and lotic habitats are more likely to be under-represented above barriers while lotic specialists are not (DePasquale, 2005). For some non-target species, population fragments isolated above a barrier can persist for decades (e.g. Furlong et al., 2006); however, it is not yet possible to predict when and where this will happen for the fishes considered here. Studies examining how fishes respond demographically and genetically to isolation are still emerging, have focused on salmonids, and suggest that population responses vary due to the complex interplay between adaptation and the reduced survival associated with isolation caused by fragmentation (Letcher et al., 2007; Morita and Yokota, 2002). The efficiency of initial efforts to pass fishes using trap-and-sort fishways is encouraging. A wide variety of species use the fishways, high passage efficiencies can be achieved, and delays are relatively short (Pratt et al., 2009).

There are assumptions and limitations with our analyses that deserve additional consideration. Acknowledging them can ensure our conclusions are interpreted and applied appropriately and identify avenues for further research.

First, our calculations assumed in-stream barriers affect the population dynamics of sea lamprey and migratory non-target spe-

Fig. 6. Proportional annual decreases in the production of each non-target fish in relation to proportional annual decreases in production of sea lamprey under different levels of blocking when young-of-the-year (YOT) survival is assumed to be density independent. The thick black line represents projections based on the blocking model (Fig. 2). The thin gray lines represent projections based on migration phenologies for individual years. The top right closed circle represents projections for a permanent barrier (100% blocking of sea lamprey and the non-target species). The lower left circle represents projections for blocking 99% of the sea lamprey run: (a) brown bullhead, (b) creek chub, (c) longnose sucker, (d) white sucker, (e) yellow perch, (f) channel catfish, and (g) walleye. When shown, the dashed diagonal line denotes 1:1 reductions for non-target fishes and sea lamprey.
cies by blocking the upstream migrations of spawning individuals. We did not consider how alteration of flow, and water temperature and chemistry (Poff et al., 1997; Poff and Hart, 2002; Pringle et al., 2000), might influence non-target fishes, because sea lamprey barriers have minimal effect on local habitat features (Dodd et al., 2003). The possibility that barriers act as hotspots for predation on small migrating fishes (Martin, 1987; Schwalme et al., 1985) was also not considered because we lacked the information needed to examine it satisfactorily. These other mechanisms could be incorporated into our models as adequate information becomes available.

Second, our analysis was carried out at a tributary scale. A valuable, future extension would be to scale up the model to consider the trade-off between sea lamprey control and fragmentation of non-target fish populations over a larger geographic extent. The benefits of sea lamprey control for lake fishes accrue lake-wide, while non-target effects occur in the tributaries where control actions are implemented (McLaughlin et al., 2003). As of 2004, barriers basin wide were preventing spawning-phase sea lamprey from accessing approximately 15% of the best larval rearing habitat from tributaries that previously had been treated with lampricide (Burkett et al., 2004). Demographic analyses modeling the effectiveness of barriers across each Great Lake have also been completed.

Fig. 7. Proportional annual decreases in the production of each non-target fish in relation to proportional annual decreases in production of sea lamprey under different levels of blocking when young-of-the-year (YOY) survival is assumed to be density dependent. Descriptions of the thick black line, thin gray lines, closed circles, and panel labels are the same as in Fig. 6.

Fig. 8. Frequency distribution of values of fecundity elasticity for 48 migratory, non-jumping Great Lakes fishes. Dark shading denotes values for the non-target fishes used this study.
Third, our treatment of the population dynamics for sea lamprey and the non-target fishes does not consider variation in vital rates among populations. These sources of variation could become important if our framework is adapted to project the efficacy of barrier design and operation for a specific tributary (e.g., Furlong et al., 2006). For sea lamprey, we expect our findings to be robust to inter-lake and stochastic variation in vital rates, based on similarities in projections from the various models compared by Vélez-Espino et al. (2008). For non-target fishes, we expect our findings to be robust because the effects of blocking were similar across species from four taxonomic families differing in life history, and, in freshwater fishes, variation in life history traits related to fecundity tends to be greater among species than among populations within species (Blanch and Lamouroux, 2007).

Fourth, our analysis does not consider how changes in sea lamprey abundances might affect predation on non-target fishes. The outcome of barrier-mediated effects on predator–prey interactions is complex and may even be small, given that sea lamprey feed on many host fishes, including some that do not make spawning migrations from a Great Lake into tributaries (e.g., lake trout, Salvelinus namaycush) and some that jump over low-head barriers (e.g., stocked Pacific salmonids, Oncorhynchus spp.).

Fifth, for non-target fishes, we have not considered possible reductions in production that could arise if a seasonal barrier passes fish arriving at the beginning and end of the migratory run and those fish experience lower reproductive success than fish arriving at the peak of the run, e.g., due to a mismatch between timing of hatch and environmental conditions favorable for juvenile growth and survival (Cushing, 1990). Reduced reproductive success of early or late migrants, relative to migrants in the middle of the run, would exacerbate the projected reductions of non-target fishes.

Sixth, our model does not consider the possible benefits that sea lamprey barriers can have for blocking other invasive fishes, e.g., white perch (Morone americana) in the Fox River, WI (Lyons et al., 2000). Our framework can accommodate additional invasive species by incorporating their migration phenology into the blocking model. Blocking additional invasive fishes will likely extend the period of barrier operation and exacerbate the reductions of non-target fishes, unless the migration phenology of any additional invasive species is subsumed within the sea lamprey phenology or any extended time of barrier operation coincides with a period when non-target fishes are not migrating.

Lastly, our analysis does not compare the demographic effects of seasonal barriers on non-target fishes in relation to the effects of other environmental factors affecting riverine fishes. For example, Cumming’s (2004) analysis of first-order streams in Wisconsin indicated that small dams affected the species richness of fishes, but the magnitude of this effect was small relative to the effects of changes in water quality and temperature.

There is a growing need to explicitly quantify trade-offs between different human and ecosystem services in ways that help resource managers balance multiple environmental concerns (Kareiva et al., 2007). We provide an example of how such needs can be quantified. Our application is specific enough to aid fishery managers in the Great Lakes with efforts to deliver a sea lamprey management program that is ecologically and economically sound and socially acceptable (Great Lakes Fishery Commission, 2001). It is general enough to apply to aquatic and terrestrial systems beyond the Great Lakes basin where managers are facing a trade-off between restricting movements of invasive species and facilitating movements of native species (Fausch et al., 2009; Proches et al., 2005).

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