

Estimation of lake-scale stock-recruitment models for Great Lakes sea lampreys

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ABSTRACT

Understanding recruitment dynamics is an essential part of effective fisheries management, whether the focus is on conservation, harvest policy development, or invasive species control. We developed a model that estimates lake-wide Ricker stock-recruitment relations for invasive sea lampreys (*Petromyzon marinus*) in each of the five Laurentian Great Lakes to inform future control efforts. We fit adult-to-adult models, taking advantage of a long time series of lake-wide, adult, sea lamprey abundance estimates. We incorporated proportional contributions at age for the stock as well as additional explanatory variables sea lamprey weight, as a surrogate for fecundity, and lampricide quantity applied, as a surrogate for anthropogenic mortality, to explain residual recruitment variability. The best model incorporated equal cohort contributions from the adult stock (that matured 5, 6, and 7 years prior to recruitment), a single productivity parameter (α) common to all five lakes, lake-specific carrying capacity parameters (β_j), and coefficients for sea lamprey weight and lampricide quantity applied. The precision of the estimated Ricker parameters compared favorably to those estimated by adult-to-larva models, a promising development in the pursuit of sea lamprey recruitment prediction. The model should be useful to fisheries managers in the Great Lakes wishing to consider various recruitment overfishing strategies in the control of invasive sea lampreys, reaffirming that even models built on a single life stage can inform our understanding of ecological interactions and explorative management scenarios.

1. Introduction

To manage fisheries effectively, some understanding of recruitment dynamics and their dependence on stock size is key (Hilborn and Walters, 1992; Payne et al., 2017). Understanding the relation between stock and recruitment provides an ideal system to test ecological theory (Foss-Grant, Zipkin, Thorson, Jensen, and Fagan, 2016). Spawning recruitment (the number of individuals surviving to enter the reproductive population) is critical to maintain fish populations and sustainable harvests (Zhao, Kocovsky, and Madenjian, 2013).

Knowledge of recruitment dynamics of a nonindigenous species can inform the identification and prediction of future invasions (Jerde, Bampfylde, and Lewis, 2009) and their control (e.g., Dux et al., 2019; Weber, Hennen, and Brown, 2011). Modeling stochastic demography has helped predict invasion potential in the Chinese mitten crab (*Eriocheir sinensis*) and the apple snail (*Pomacea canaliculata*) (Jerde et al., 2009). Modeling population recovery rates of the brushtail possum (*Trichosurus vulpecula*) has helped fine-tune the use of toxic bait

(Veltman and Pinder, 2001). Modeling host-parasite interactions has yielded insights into the expected success of biological control where parasitoids are introduced to eliminate a pest (Singh and Emerick, 2021).

Integrated control programs for invasive fish species require knowledge of their life history and stock-recruitment relations (Sorensen and Stacey, 2004). Changes to recruitment of a pest species as the population is driven to low levels will determine whether the rate of control is sufficient to achieve lasting benefits (Dawson and Jones, 2009).

Sufficient data on invasive species population dynamics are often lacking, and empiric stock-recruitment relations have been developed for only a few invasive fish species. A stock-recruit relation was developed for the common carp (*Cyprinus carpio*), an important pest species in Australasia and North America, using replication in space, because years of data were not available (Koehn, Brumley, and Gehrke, 2000). The resulting relation was used to investigate management scenarios including fishing the spawning stock, fishing the whole stock, spawning

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or recruitment sabotage, and driving the population sex ratio towards male dominance (Brown and Walker, 2004). A stock-recruit relation was derived for the eastern mosquitofish (*Gambusia holbrooki*), a major pest species of Australia and Europe, from controlled laboratory experiments to test the sensitivity of genetically based pest control options based on sex ratio distortions (Thresher, Canning, and Bax, 2013). Several stock-recruitment relations have been derived for the sea lamprey (*Petromyzon marinus*), an invasive species in the Laurentian Great Lakes and the focus of this study (Haeseker, Jones, and Bence, 2003; Jones et al., 2003, 2015, 2015; Robinson, Wilberg, Adams, and Jones, 2013; Young, 2005).

The sea lamprey is a semelparous, anadromous fish native to the North Atlantic Ocean. It spends most of its life as a filter-feeding larva burrowed in stream sediment before migrating to the ocean to feed parasitically on other fish as a juvenile. In the Great Lakes, the land-locked invasive sea lamprey maintains its migratory behavior entirely in freshwater (Moser, Almeida, Kemp, and Sorensen, 2015). In the spring, a single cohort of adults of mixed age migrates up streams to spawn, lay eggs, and die. The eggs hatch, and the larvae live in the stream for 3–5 years, before metamorphosing and migrating to the lake to feed parasitically on host fish (Dawson, Quintella, Almeida, Treble, and Jolley, 2015). Sea lampreys feed on host fish for 12–20 months as juveniles, before maturing and migrating up streams to spawn and die (Applegate, 1950). Unlike most anadromous fishes, sea lampreys do not return to their natal rivers to spawn (Waldman, Grunwald, and Wirgin, 2008).

Recruitment and its variation require further study to understand general patterns of sea lamprey population dynamics better (Hansen et al., 2016; Jones et al., 2003). Invasive sea lampreys have been the target of control measures in the Great Lakes since the formation of the Great Lakes Fishery Commission in 1955 (Fetterolf Jr., 1980; Gaden, Brant, and Lambe, 2021). Two primary methods of control have reduced Great Lakes sea lamprey populations to a fraction of their post-invasion peaks (Heinrich et al., 2003; Lawrie, 1970; Robinson, Miehl, and Siefkes, 2021): (1) lampricides that kill larvae during their first years of life burrowed in stream sediments and (2) barriers that block upstream spawning migration of adults (Marsden and Siefkes, 2019). Great Lakes tributaries that regularly produce sea lampreys are typically treated with lampricide every 3–5 years such that every larval cohort is subjected to treatment prior to outmigration (Bregue et al., 2003). Knowledge of stock-recruitment relations would be particularly helpful in exploring control options that target adult sea lampreys (Jones, 2007; Jones and Adams, 2021; Jones et al., 2003). For example, if population densities are suppressed to levels where recruitment is only weakly density-dependent, removal of adults from the population becomes a feasible control option (Sorensen and Stacey, 2004).

In this paper, we develop adult-to-adult stock-recruitment relations for Great Lakes sea lamprey populations and determine how useful those relations might be in future modeling endeavors. We strove to answer the following questions: (1) How precise are estimated stock-recruitment parameters from an adult-to-adult model compared to an adult-to-larva model? (2) Can the stock-recruitment relations provide information on the contributions of different ages of stock to sea lamprey spawning recruitment? (3) Does the inclusion of explanatory variable surrogates for sea lamprey fecundity and anthropogenic mortality improve the model fit?

2. Historical models

Previous investigations into sea lamprey stock-recruitment relations used Ricker models because of an observed decline in larval recruitment at large stock sizes (Dawson and Jones, 2009; Haeseker et al., 2003; Jones and Adams, 2021; Jones et al., 2003, 2015; Robinson et al., 2013; Young, 2005). These studies have been used by others to project population effects of pheromone-baited sea lamprey traps (Dawson et al., 2016), barrier removals (Jensen and Jones, 2018), sea lamprey carcass nutrients (Weaver, Coghlan, and Zydlewski, 2018), genetic sea lamprey

control options (Thresher, Jones, and Drake, 2019), and levels of control needed to eradicate sea lampreys (Jones and Adams, 2021). Three of these stock-recruitment studies focused on the population in a single tributary to Lake Huron, the St. Marys River, with larval abundance (either age-0 or age-1) as the recruits, adult female abundance as the stock, and no other explanatory variables (Haeseker et al., 2003; Jones et al., 2015; Robinson et al., 2013). This approach is likely the best for investigating larval recruitment in a single stream, where information on larval and adult abundance is available. Two other studies carried out meta analyses across several Great Lakes tributaries with age-1 larval abundance per hectare of larval habitat as the recruits, adult female abundance per hectare of larval habitat as the stock, and two explanatory variables (stream temperature and alkalinity), neither of which significantly affected recruitment (Dawson and Jones, 2009; Jones et al., 2003). Standardizing the stock and larval recruits by the area of larval habitat was a clever way to combine stream-specific stock-recruitment relations in a single model. The only shortcoming is that it requires both larval and adult abundance estimates in all the streams. Variability in the relation was likely kept to a minimum in all five of these studies by using paired stock and recruit data that are fewer than two years apart in time, a fraction of the generation length. A sixth study fit an adult-to-adult relation to Lake Huron sea lampreys, with adult abundance as the recruits, adult female abundance six years earlier as the stock, and two explanatory variables (area of larval habitat treated 2–5 years prior to recruitment and mass of adults), in which mass significantly affected spawning recruitment (Young, 2005). A seventh study also fit an adult-to-adult relation across all five Great lakes, with adult abundance as the recruits, adult abundance 5–7 years earlier as the recruits (with assumed known proportional contributions), and one explanatory variable (amount of lampricide applied 2 years prior to recruitment), which significantly affected spawning recruitment (Jones and Adams, 2021). The advantage of the adult-to-adult approach for sea lamprey stock-recruit relations is its ability to inform other metrics measured on the lake-wide scale, e.g., host fish populations. The disadvantage is the introduction of variability from the inclusion of several more years of mortality between the stock and spawning recruit estimates.

Unlike larval abundance, lake-wide indices of adult sea lamprey abundance are estimated on an annual basis in the Great Lakes (Adams, Barber, Bravener, and Lewandoski, 2021-a). If adult-to-adult stock-recruitment models proved informative about sea lamprey population dynamics, they would be more broadly useful to sea lamprey researchers and decision makers. Accounting for different ages at maturation is one challenge of fitting stock-recruit models to sea lamprey populations. Sea lampreys are indeterminate semelparous, meaning they spawn once in their life at a variable age (Botsford and Brittnacher, 1998). Age at maturity is thought to be influenced by the duration of the sedentary larval stage (Purvis, 1979) and the timing (spring or autumn) of metamorphosis to the parasitic juvenile stage. Juvenile sea lampreys actively attack and feed off of other fish for approximately 12 months (if they metamorphosed in the spring) or 18 months (if they metamorphosed in the autumn) prior to spawning (Applegate, 1950). Lamprey ages are widely known to be difficult to measure, since structures typically used to age fish (scales, spines, and otoliths) are absent, and statoliths (primitive otoliths) have been found to be both imprecise and inaccurate (Barker, Morrison, Wicks, and Beamish, 1997; Dawson, Jones, Scribner, and Gilmore, 2009; Potts, Dawson, and Jones, 2015). Estimates of sea lamprey ages typically depend on the analysis of larval length frequency distributions (Haeseker et al., 2003; Potter, 1980). Two previously derived models of adult-to-adult stock-recruitment for sea lampreys have relied on deterministic inputs of stock age composition. Young (2005) fit a model to Lake Huron sea lampreys to evaluate the use of non-chemical control options in meeting fish community objectives, assuming an age at maturation of 6 years. Jones and Adams (2021) fit models to all five Great Lakes to calculate the extinction exploitation rate, with assumed values for the proportion of mature sea lampreys at

age. Explicit incorporation of sea lamprey stock from different spawning cohorts in the model could improve the fit and provide information on the typical age at maturation.

Additional factors that have been shown to contribute to sea lamprey spawning recruitment variability at the lake-wide level include adult sea lamprey mass (Young, 2005) and mortality from lampricide applications (Jones and Adams, 2021; Young, 2005). Dawson and Jones (2009) found no evidence of a common pattern of variation among years, where year could be interpreted as a surrogate for biotic and abiotic factors at the lake-scale. Stream-level factors, e.g., quality of spawning and larval habitat (Dawson and Jones, 2009; Jones et al., 2003), cannot be incorporated in stock-recruitment models at the lake scale.

3. Methods

We developed lake-wide stock-recruitment curves for Great Lakes sea lampreys, using the number of spawning adults from one generation to the next as both stock and recruits (Myers, Bowen, and Barrowman, 1999). We incorporated proportional contributions from different cohorts of stock and included two additional explanatory variables to explain some of the variability in spawning recruitment.

Several sea lamprey stock-recruitment relations were estimated, each represented by a single model fit to all five Great Lakes at once, using numbers of adults as both stock and recruits. Numbers in each lake were based on an annual index of adult abundance, obtained as the sum of mark-recapture population estimates from a subset of index streams (Adams et al., 2021-a). Each index was scaled up to a lake-wide population estimate by an expansion factor, the median of the ratio of lake-wide population estimates from the Mullett model (Mullett et al., 2003) to the adult index (Table 1, Supplemental Table S1). A Ricker stock-recruitment curve was fit (Ricker, 1975),

$$R_{ij} = \alpha_j \sum_{k=5}^7 (\pi_{kj} S_{i-k,j} e^{-\beta_j \pi_{kj} S_{i-k,j}}) \epsilon_{ij}, \quad (1)$$

where R_{ij} is the number of adults in year i and lake j (representing recruits) and $S_{i-k,j}$ is the number of adults in year $i - k$ and lake j (representing stock from three different cohorts, $k = 5, 6$, and 7 years prior to recruitment). We used Ricker stock-recruitment relations, because compensation has been observed by others in Great Lakes sea lamprey populations (Haeseker et al., 2003; Jones et al., 2003, 2015). The 21 estimated parameters included α_j , β_j , π_{5j} and π_{6j} (the proportional contribution from stock 5 and 6 years prior to recruitment), and σ^2 , the variance of the lognormally distributed error ϵ with mean zero on the natural log scale (Table 2). The error was assumed independent across years and lakes. This parameterization allows for contributions from mixed age classes while limiting the number of parameters estimated. The selected stock cohorts reflect the current presumed generation length of sea lampreys in the Great Lakes, corresponding to sea lamprey larval metamorphosis at age 3.5–5.5 years (Beamish and Medland, 1988; Young, 2005). Compensation was assumed to occur in the early stages of life (Jones et al., 2003, 2015); hence, the incorporation of β_j

Table 1

Conversion factors used to expand indices of adult sea lamprey abundance (Adams et al., 2021-a) to lake-wide population estimates (Mullett et al., 2003). Great Lakes listed in hydrologic order from most upstream (Superior) to most downstream (Ontario).

Lake	Factor
Superior	4.6
Michigan	1.9
Huron	2.9
Erie	1.2
Ontario	2.2

Table 2

Definitions of variables used to describe stock-recruit models.

Variables
R = number of adults, representing recruits
S = number of adults, representing stock
M = standardized adult sea lamprey mass
E = standardized lampricide quantity applied 2–4 years prior to recruitment
Indices
i = year
j = lake
k = stock cohort (years to maturation)
Estimated parameters
α = maximum annual reproductive rate
β = population carrying capacity
π = proportional contribution from stock cohort
δ = effect of mass on recruitment, relative to the mean mass
γ = effect of lampricide quantity applied on recruitment, relative to the mean quantity
σ^2 = variance of lognormally distributed error, ϵ
Constraining parameters
$a = \log_e(\alpha)$
$b = \log_e(\beta)$
$c = \log_e[\pi_5 / (1 - \pi_5)]$
$d = \log_e[\pi_6 / (1 - \pi_5 - \pi_6)]$

with each contribution of the three stock cohorts to recruits.

Two additional explanatory variables were considered for inclusion in the model: adult sea lamprey weight and lampricide applied. Fecundity was represented by adult sea lamprey weight measured as the median individual mass (in g) of a subset of recaptured adults in each lake and each year. Sea lamprey fecundity is linearly correlated with sea lamprey mass (Applegate, 1950; Manion, 1972; Vladykov, 1951). Lampricide quantity applied served as surrogate for anthropogenic mortality and was measured as the three-year average of TFM (3-trifluoromethyl-4-nitrophenol, Applegate, Howell, Moffett, Johnson, and Smith, 1961) applied to larvae 2–4 years prior to recruitment to the adult life stage (in kg of active ingredient).

Standardization of the explanatory variables was required so that a single coefficient could describe the relation for each across all five Great Lakes. Adult sea lamprey weight and lampricide applied were both centered and scaled by first subtracting their lake-specific means and then dividing by their lake-specific means (Fig. 1). With these effects thus on a common unitless scale, a single stock-recruitment relation was fit to all five populations at once. The resulting coefficients correspond to the expected effect of a change relative to the mean.

Model (2) incorporates fecundity as an additional effect on the productivity of individual stock cohorts (Fig. 2),

$$R_{ij} = \alpha_j \sum_{k=5}^7 (\pi_{kj} S_{i-k,j} e^{-\beta_j \pi_{kj} S_{i-k,j} + \delta M_{i-k,j}}) \epsilon_{ij}, \quad (2)$$

where M_{ij} is the standardized adult sea lamprey mass for year i and lake j , and δ is the corresponding parameter to be estimated. This is the commonly recommended approach for incorporating environmental factors in a Ricker stock-recruitment relation (Hilborn and Walters, 1992; Young, 2005; Zhao et al., 2013). This parameterization allows individual eggs and larvae produced by mothers from different cohorts to have different traits that affect mortality rates (Shelton, Munch, Keith, and Mangel, 2012).

Model (3) incorporates anthropogenic mortality as a density-independent effect on the mixed cohorts,

$$R_{ij} = \alpha_j e^{\gamma E_{ij}} \sum_{k=5}^7 (\pi_{kj} S_{i-k,j} e^{-\beta_j \pi_{kj} S_{i-k,j}}) \epsilon_{ij}, \quad (3)$$

where E_{ij} is the standardized lampricide quantity applied for years $i-2$, $i-3$, and $i-4$ and lake j , and γ is the corresponding parameter to be estimated.

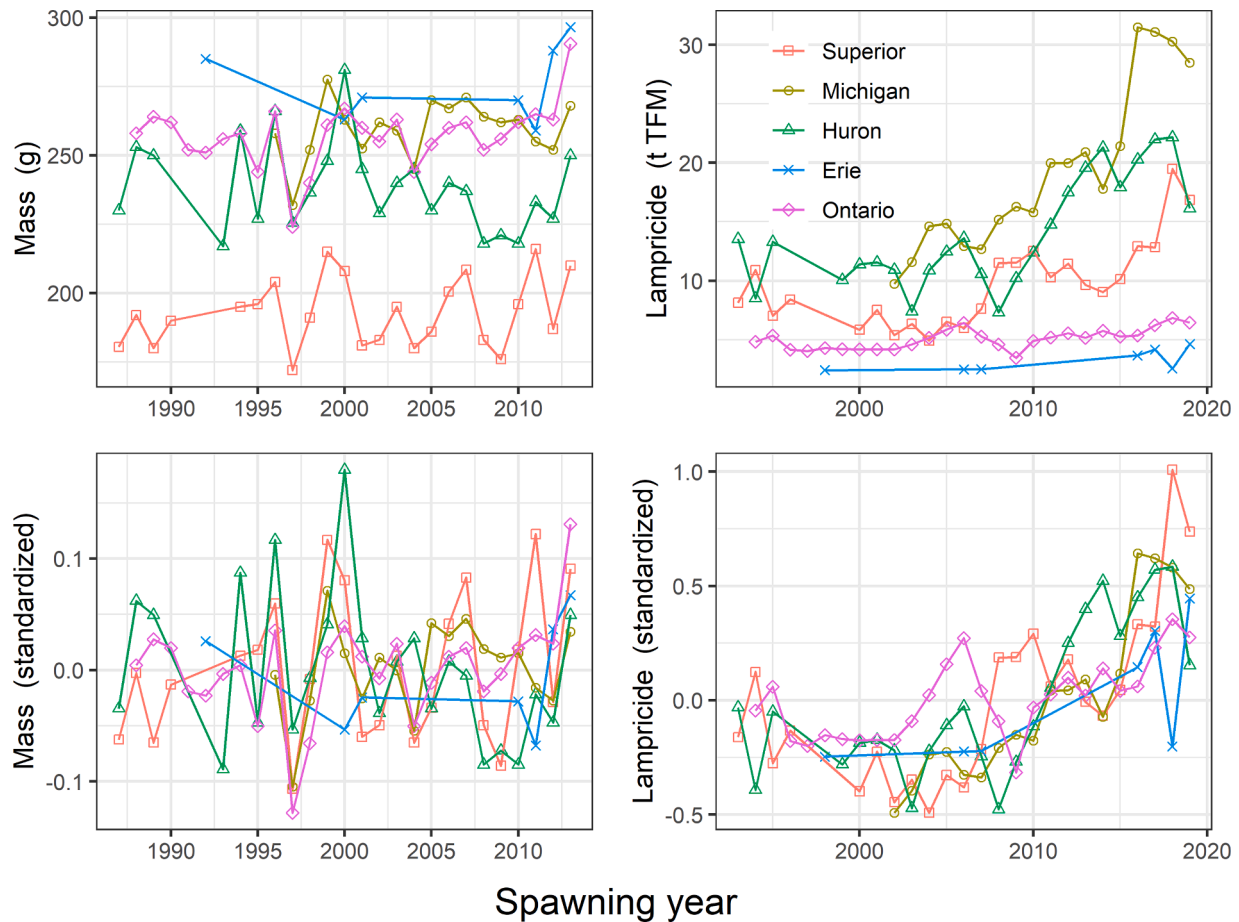


Fig. 1. Median weight of individual adult sea lampreys recaptured in traps and mean lampricide quantity applied 2–4 years prior to recruitment (t of TFM active ingredient) 1993–2019. Top row is unscaled; bottom row is centered and scaled by the mean. Great Lakes listed in hydrologic order from most upstream (Superior) to most downstream (Ontario).

mated. This parameterization allows quantification of lampricide treatment effects on mixed age larvae prior to recruitment to the adult stage (Fig. 2).

Model (4) incorporates both fecundity and anthropogenic mortality,

$$R_{ij} = \alpha_j e^{\gamma E_{ij}} \sum_{k=5}^7 (\pi_{kj} S_{i-k,j} e^{-\beta_j \pi_{kj} S_{i-k,j} + \delta M_{i-k,j}}) \epsilon_{ij}, \quad (4)$$

and has the most estimated parameters (24) of any model we fit.

Other model parameters (α_j , π_{kj} , and β_j) are characteristic of the stock-recruitment model for adult sea lampreys of an average weight and lampricide quantity applied at an average level, because when adult sea lamprey weight is at the average for a given lake, the additive $\delta M_{ij} = 0$ term drops out of the model, and when lampricide applied is at the average for a given lake, the $e^{\gamma E_{ij}} = 1$ multiplicative term drops out of the model.

Additional simplified versions of these four models were also considered. First, Great Lakes-wide (rather than lake-specific) proportions of stock cohorts were fit, leading to Models 5–8 with two (rather than 10) estimated proportions (Table 3). Second, stock was assumed to be composed of all three cohorts in equal proportions, leading to Models 9–12. Third, Great Lakes-wide α parameters were fit, leading to models 13–24.

Models were fit via maximum likelihood using the ‘optim’ function of R (R Core Team, 2018), and results were collected using the ‘tidyverse’ (Wickham et al., 2019) and ‘rlist’ (Ren, 2016) packages (Supplemental Text S2). Starting values for the α_j s (2) and β_j s (0.08) were selected as the median of the estimated coefficients (rounded to one

significant digit) from 15 separate regressions fit to each lake and stock cohort using the linearized form of the Ricker stock-recruitment relation. Small changes ($\pm 10\%$) were made to these starting values to ensure solutions were not the result of convergence at local minima. Starting values for the stock cohort contributions, π_5 and π_6 were set to 1/3, assuming equal contributions from all three stock cohorts. Starting values for the fecundity parameter, δ , and the anthropogenic mortality parameter, γ , were set to zero, assuming no effect on recruitment relative to their means. Transformations were used to constrain parameters: $\alpha > 0$, $\beta > 0$, $0 < \pi_{5j} < 1$, and $0 < (\pi_{5j} + \pi_{6j}) < 1$ (Table 2). Asymptotic standard errors of parameter estimates were generated from the Hessian matrix.

Models were compared using Akaike’s Information Criterion (AIC). Among those considered to have substantial support, $\Delta AIC \leq 2$ (Burnham and Anderson, 2002), the best model was defined as the one with the fewest parameters that met the assumption of stationarity with no evidence of time series bias. We visually inspected residual plots for evidence of non-stationarity (trends over time) and unexplained patterns related to combined stock or predicted recruitment (Walters, 1986). Such visual inspections are widely recommended for validation of model assumptions, because they are more informative than hypothesis tests (Belsley, Kuh, and Welsch, 2004; Campbell, Thompson, Guy, McIntosh, and Glaz, 2015; Hadi and Chatterjee, 2012; Kozak and Piepho, 2018). We estimated serial autocorrelations with 95% confidence intervals, lagged across a time span of 1–7 years. Autocorrelation of residuals separated by 5–7 years could indicate the presence of time series bias (Myers and Barrowman, 1995).

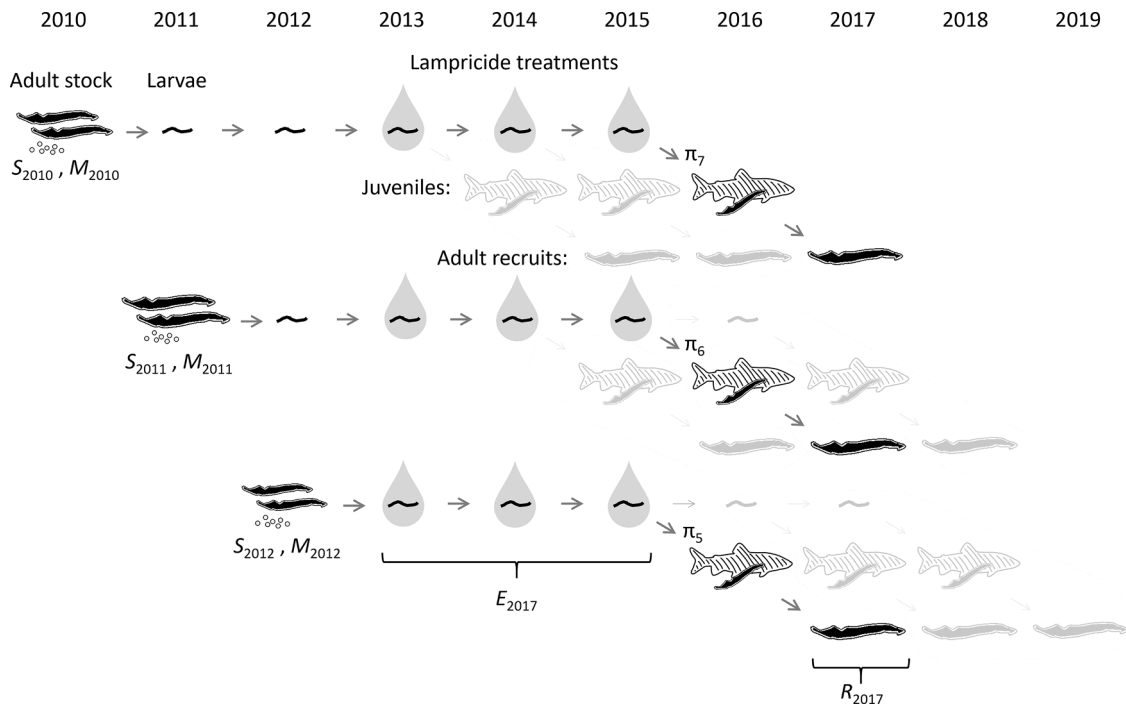


Fig. 2. Conceptual diagram of the modeled sea lamprey stock-recruitment relation for all tributaries in a single lake (j subscripts not shown for clarity) and a single recruitment year ($i = 2017$). Adult recruits (R) are modeled as a function of adult stock 5–7 years earlier (S), standardized adult stock mass (M), the proportional contribution of each stock (π), and the standardized amount of lampricide applied 2–4 years earlier (E). Over the course of a three-year period, lampricide treatments would typically be applied to most of the sea lamprey-producing streams, with each stream receiving a single treatment (i.e., the diagram covers multiple streams and is not intended to imply treatments are applied three years in a row on a single stream).

Table 3

Number of parameters included in 20 Ricker stock-recruitment models for sea lampreys in the Great Lakes, and support for each model based on Akaike's information criterion (AIC). Note that the sample size of data for each model was 99. For a given parameter, '5' indicates five lake-specific coefficients were estimated, '1' indicates a single common coefficient was estimated for all lakes, and '0' indicates no coefficients were estimated. Ricker stock-recruitment parameters are denoted by α and β . Proportional contribution from stock cohorts 5 and 6 years prior to recruitment are denoted by π_5 and π_6 . The δ and γ parameters represent coefficients for sea lamprey mass and lampricide quantity applied, respectively. The total number of parameters also includes σ^2 . Level of empirical support based on ΔAIC : three asterisks for substantial support $\Delta AIC \leq 2$, one asterisk for considerably less support $2 < \Delta AIC \leq 7$, and no asterisks for essentially no support $\Delta AIC > 7$ (Burnham and Anderson, 2002).

Group	Model	α	β	π_5	π_6	δ	γ	No. Par.	ΔAIC	Support
Lake-spec. α ,	1	5	5	5	5	0	0	21	20.0	
lake-spec. π	2	5	5	5	5	1	0	22	17.8	
	3	5	5	5	5	0	1	22	19.1	
	4	5	5	5	5	1	1	23	19.8	
Lake-spec. α ,	5	5	5	1	1	0	0	13	4.9	*
common π	6	5	5	1	1	1	0	14	5.2	*
	7	5	5	1	1	0	1	14	0.0	***
	8	5	5	1	1	1	1	15	0.4	***
Lake-spec. α ,	9	5	5	0	0	0	0	11	11.7	
$\pi = 1/3$	10	5	5	0	0	1	0	12	12.6	
	11	5	5	0	0	0	1	12	4.1	*
	12	5	5	0	0	1	1	13	5.7	*
Common α ,	13	1	5	5	5	0	0	17	25.5	
lake-spec. π	14	1	5	5	5	1	0	18	21.2	
	15	1	5	5	5	0	1	18	14.1	
	16	1	5	5	5	1	1	19	16.1	
Common α ,	17	1	5	1	1	0	0	9	12.6	
common π	18	1	5	1	1	1	0	10	12.2	
	19	1	5	1	1	0	1	10	1.3	***
	20	1	5	1	1	1	1	11	3.3	*
Common α ,	21	1	5	0	0	0	0	7	11.8	
$\pi = 1/3$	22	1	5	0	0	1	0	8	11.1	
	23	1	5	0	0	0	1	8	0.8	***
	24	1	5	0	0	1	1	9	1.5	***

4. Results

Lakes Superior, Michigan, and Huron had time series of at least 18

years and ranges of stock sizes ≥ 0.7 orders of magnitude, i.e., the common logarithm (base 10) of the ratio of the maximum to minimum observed values (Table 4). Lake Erie had a much shorter time series

Table 4

Summary of data available for fitting adult-to-adult stock-recruitment models to Great Lakes sea lampreys, including range and number of years, mean and range of independent variables expressed as orders of magnitude (OOM, $\log_{10}(\text{Max}/\text{Min})$). Stock is the number of adult sea lampreys 5, 6, and 7 years prior to recruitment (in thousands), weight is the median annual mass of subsampled sea lampreys 5, 6, and 7 years prior to recruitment (in g), and lampricide is the mean lampricide quantity applied 2–4 years prior to recruitment (in t of TFM active ingredient). Great Lakes listed in hydrologic order from most upstream (Superior) to most downstream (Ontario).

Lake	Year Min	Max	No.	Stock Avg	OOM	Weight Avg	OOM	Lampricide Avg	OOM
Superior	1993	2019	24	109	0.92	193	0.10	9.70	0.60
Michigan	2002	2019	18	128	1.04	259	0.08	19.17	0.51
Huron	1993	2019	24	228	0.70	238	0.11	13.99	0.48
Erie	1998	2019	7	17	1.13	278	0.10	3.20	0.28
Ontario	1994	2019	26	45	0.58	257	0.11	5.06	0.30

(only 7 years), and Lake Ontario had a narrower range of stock sizes. The total sample size of data from all five Great Lakes fit to each model was 99. The ranges of sea lamprey weights were ≤ 0.113 orders of magnitude for all lakes; the ranges of lampricide quantities applied were ≤ 0.6 orders of magnitude.

All five models with substantial support included a parameter for lampricide quantity applied and excluded lake-specific age composition, but varied with respect to inclusion of lake-specific α_j , a common age composition of adults for all lakes, and a parameter for sea lamprey weight (Table 3). Among these, Model 23 with the fewest parameters (8) was initially defined as best, but evidence of temporal trends in its residuals indicated apparent non-stationarity. Thus, Model 24 with the

next fewest parameters (9) was defined as the best model. The residuals from Model 24 exhibited no significant trends over time or patterns related to combined stock or predicted recruitment, supporting our assumption of stationarity. The residuals also showed no evidence of autocorrelation that would have suggested the presence of time series bias. Model 24 included parameters for weight and lampricide, a common α parameter for all lakes, and assumed contributions of 1/3 each from stock 5, 6, and 7 years prior to recruitment (Fig. 3). All eight models with lake-specific age composition parameters had essentially no support.

Stock-recruitment parameters from Model 24 were well estimated for all lakes, with confidence interval widths ranging between 0.9 and

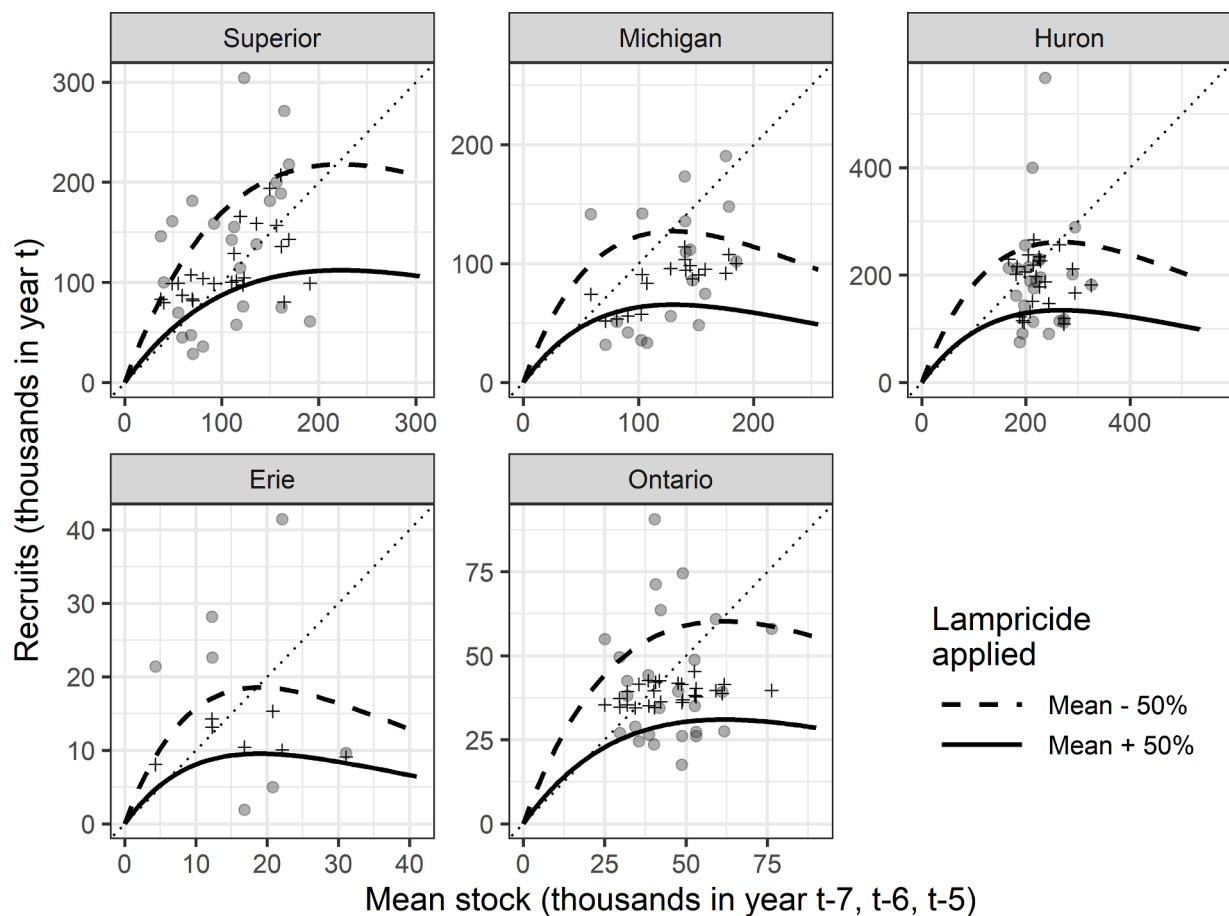


Fig. 3. Adult-to-adult sea lamprey stock-recruitment relations in the Great Lakes. Symbols represent annual observations (circles) and predictions (plus signs). Symbols are plotted at the mean stock 5, 6, and 7 years prior to recruitment, but predictions (from Model 24) incorporate stock from each cohort separately. Curved lines represent the stock-recruitment relation of Model 24 with lampricide quantity applied 50% below ($E = -0.5$) and above ($E = 0.5$) average. Curves were drawn assuming equal contribution from each stock cohort. Model 24 uses a common α parameter for all lakes, lake-specific β_j , a common δ for all lakes for the sea lamprey weight parameter, and a common γ for all lakes for the lampricide parameter. The diagonal dashed line represents the replacement line, above which recruits exceed stock. Great Lakes listed in hydrologic order from most upstream (Superior) to most downstream (Ontario).

2.0 times the estimates (Table 5, Fig. 4). Estimated β_j parameters were similar for Lakes Superior, Michigan, and Ontario. Lake Erie had a significantly greater β_j than the three upper lakes and Lake Ontario had a significantly greater β_j than Lake Huron, indicating peak recruitment at lower numbers of combined stock (Fig. 3).

The coefficient for sea lamprey weight was poorly estimated, with a confidence interval that contained zero and a confidence interval width 3.4 times the estimate (Table 5). However, its inclusion in the model was necessary to meet the assumption of stationarity. The δ parameter was positive, indicating an increase in recruitment with an increase in sea lamprey weight. The coefficient for sea lamprey weight was the only one sensitive to changes in the starting values for the Ricker parameters. The estimate for δ varied by $\pm 15\%$. Estimates of other parameters varied by less than $\pm 0.1\%$ when different starting values were used.

The coefficient for lampricide quantity applied was well estimated, with a confidence interval width 1.1 times the absolute value of the estimate (Table 5). The γ parameter was negative, indicating a reduction in recruitment with an increase in lampricide quantity applied. For example, doubling the mean lampricide quantity applied ($E = 1$) results in about a 50% reduction in predicted recruitment ($e^{\gamma E} = e^{-0.7 \cdot 1} = 0.5$) with a 95% confidence interval of 34% to 72% (Table 5, Fig. 3).

Other models with substantial support included parameters that were not included in the most parsimonious and stationary model. Models 7 and 8 included lake-specific α_j terms. Lake Erie had the highest estimated α_j (7.2 and 7.1 for Models 7 and 8, respectively), Lake Michigan the lowest (0.8 and 0.9), and the other lakes had middling estimates (ranging from 1.6 to 2.2). Models 7, 8, and 19 included terms for the proportional contribution of stock cohorts 5 and 6 years prior to recruitment. Estimates from these three models ranged from 0.35 to 0.89 for π_5 and 0.11 to 0.65 for π_6 , consistently estimating the contribution from stock 7 years prior to recruitment ($1 - \pi_5 - \pi_6$) as < 0.01 .

5. Discussion

We successfully developed adult-to-adult stock-recruitment relations for Great Lakes sea lampreys, with relatively precise parameter estimates. The best model included a single productivity parameter common to all five lakes, a lake-specific carrying capacity parameter, and parameters for fecundity and anthropogenic mortality. The modeling exercise provided some insight on the age composition of mature sea lampreys, but proportional contributions of stock at age were not included in the most parsimonious stationary model. The stock-recruit relations for the Great Lakes could help inform decision-making regarding sea lamprey control efforts.

The best model, Model 24, supported a common productivity rate (α). Two models with substantial support included lake-specific α_j terms, suggesting that there may be underlying differences in the maximum annual reproductive rate of lake populations or the relative lampricide quantity applied to them, though not enough to overcome variability in the data. The estimated α from Model 24 was within the range of typical values (1–7) estimated from adult-to-adult stock-recruitment models for 30 different fish species by Myers et al. (1999). The maximum annual

reproductive rate at average lampricide levels (1.91 with 95% confidence interval 1.23 to 2.95) was similar to those estimated by Jones and Adams (2021) (2.43 with 95% credible interval 1.56 to 4.09) for all Great Lakes and Young (2005) for Lake Huron (3.95 with 95% confidence interval 2.90 to 6.64). The estimated β_j parameters reflect the carrying capacity of the population, which is expected to vary among stocks (Hilborn and Walters, 1992). Carrying capacity tended to reflect overall lake productivity as measured by chlorophyll, with the highest estimate for Lake Erie, followed by Lakes Ontario and Michigan (Burakova et al., 2018). The positive β_j indicated density dependent survival in all five lakes, consistent with previous work (Haeseker et al., 2003; Jones et al., 2003; Young, 2005).

The most parsimonious model included fixed, equal contributions of 1/3 from each of three cohorts of stock. Three models with substantial support included estimated proportions, suggesting that there may be underlying differences in the recruitment-at-age contributions, though not enough to overcome variability in the data. Knowledge of age at maturation could be used to infer the duration of the larval life stage and thus how many years sea lampreys are susceptible to chemical control in Great Lakes streams. This would aid decision makers in efficiently planning for lampricide applications and improve models that inform those decisions (Howe, Marsden, Donovan, and Lamberson, 2012; Jones et al., 2009; Robinson et al., 2013; Treble, Jones, and Steeves, 2008). A younger age at maturation means increased productivity (Weaver et al., 2018) leading to more lake trout wounding and more frequent lampricide treatments of rivers for invasive Great Lakes populations. Better understanding of the age structure of mature sea lampreys could also influence the likelihood of their eradication (Adams et al., 2021-b; Jones and Adams, 2021). Variation in age at maturity conveys similar benefits to a population as iteroparity, i.e., repeat breeding (Einum and Fleming, 2007; Murphy, 1968). Botsford and Brittnacher (1998) found that probability of extinction for an indeterminate semelparous species was highly negatively correlated with the standard deviation of age at maturity (recasting their Fig. 4). Aging sea lampreys is difficult using statoliths or length-frequency distributions (Dawson et al., 2015), though recent genetic pedigree analysis of larval sea lampreys (Sard et al., 2020; Weise et al., 2019, *In press*) may be extensible to adults if sequencing costs decline enough to allow for lake-wide sampling (Scott Miehl, US Geological Survey, personal communication).

The best model included a parameter for sea lamprey weight, similar to the findings of Young (2005) for Lake Huron. Young (2005) included weight information dating back to 1959, with a range about three times that of this study, which may have given him more power to detect an effect. Increased recruitment from heavier females suggests that sea lamprey production in the Great Lakes will continue to increase (all other things being equal) as a result of global warming, because sea lamprey weight is positively correlated with water temperature (Cline et al., 2014). Lampricide quantity applied had a significant effect on sea lamprey recruitment in the Great Lakes, further testimony to the effectiveness of chemical control. A coefficient for lampricide quantity was included in all five models with substantial support. Our model suggests that decreasing lampricide from 50% above to 50% below the mean level of TFM applied approximately doubles ($e^{-\gamma} = e^{0.7} = 2$) the number of sea lampreys that recruit to the adult stage (Fig. 3).

The precision of the sea lamprey stock-recruitment parameters estimated from this adult-to-adult model compared favorably to those previously estimated from adult-to-larva models. This is a promising development in the pursuit of sea lamprey recruitment prediction, providing an opportunity to link recruitment to other lake-wide metrics and processes. The confidence interval width relative to the mean for Model 24's α (0.9) was greater than those of Haeseker et al. (2003) (0.4) and Robinson et al. (2013) (0.8) and less than that of Jones et al. (2015) (1.9). The confidence interval widths relative to the means for Model 24's β_j s (1.0 to 2.0) were greater than that of Dawson and Jones (2009) (0.6), similar to that of Robinson et al. (2013) (1.1), and less than that of

Table 5

Parameter estimates for stock-recruitment Model 24, with 95% confidence intervals based on asymptotic standard errors. Great Lakes listed in hydrologic order from most upstream (Superior) to most downstream (Ontario).

Parameter	Lake	Estimate	Lower	Upper
α	All	1.9068	1.23448	2.9452
β_1	Superior	0.0135	0.00558	0.0326
β_2	Michigan	0.0231	0.01421	0.0375
β_3	Huron	0.0112	0.00626	0.0201
β_4	Erie	0.1582	0.08670	0.2885
β_5	Ontario	0.0487	0.02604	0.0911
γ	All	-0.6648	-1.04042	-0.2892
δ	All	2.2551	-1.62091	6.1311

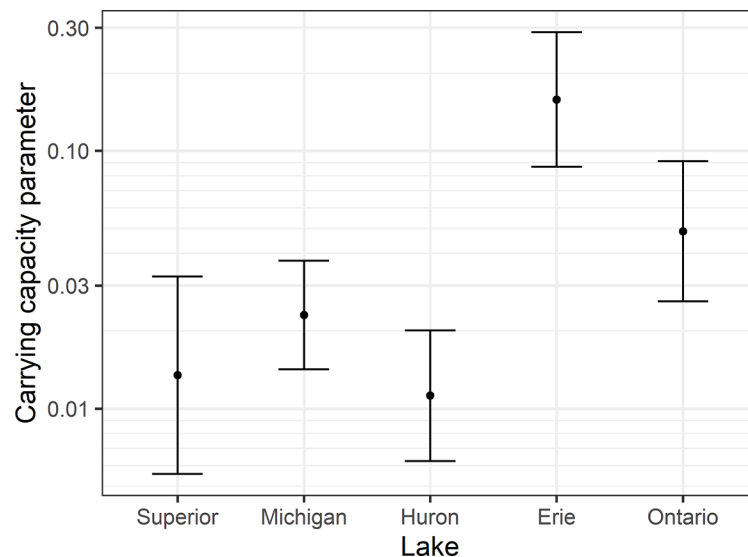


Fig. 4. Estimated Ricker stock-recruitment β_1 parameters for Great Lakes sea lampreys, plotted on a logarithmic scale with 95% confidence intervals based on asymptotic standard errors. Independent variables include stock from 5–7 years prior to recruitment and lampricide quantity applied 2–4 years prior to recruitment. Great Lakes listed in hydrologic order from most upstream (Superior) to most downstream (Ontario).

Haeseker et al. (2003) (3.5).

Ideally, we would have used only adult females as our stock, but information on the sex of captured adults was not recorded consistently. In many years, sex was only recorded for adult sea lampreys that were recaptured, and in some years, equal numbers of males and females were selected for mark and release. Rather than rely on recorded sex ratios, we used the total estimated population (males and females) as stock in our models.

Stock-recruitment relations are susceptible to bias as a result of measurement error in the stock (Walters and Ludwig, 1981). If errors are large enough, recruitment may appear to be independent of stock. Although that did not occur in this study, further investigations into the potential effects of measurement error on adult-to-adult stock recruitment models would be informative. While stream mark-recapture estimates that go into stock estimates are relatively precise (Adams, Jones, and Bence, 2020), there is unknown error associated with the factor used to scale up stream estimates to lake-wide populations. If the range of stocks is less than 0.6 orders of magnitude, as they are for Lake Ontario sea lampreys in this study, biases can be quite severe (Hilborn and Walters, 1992). Such bias tends to underestimate the response of recruitment to changes in stock.

Our stock-recruitment models did not incorporate any depensation or Allee effects (Allee, 1941; Berec, Angulo, and Courchamp, 2007; Liebhold and Bascompte, 2003). Although all sexually reproducing organisms exhibit some decline in per capita growth at low densities, because finding a mate becomes more difficult (Liebhold and Bascompte, 2003), depensation is less pronounced in sea lampreys, because their pheromone communication system enables them to locate mates over long distances (Johnson, Yun, Thompson, Brant, and Li, 2009; Miehl, Sullivan, Twohey, and Barber, 2020). A stock-recruitment relation that underestimated recruitment at low stock sizes would be evidence of depensation (Myers and Barrowman, 1995). However, we have few observations of stock sizes less than 10% of the maximum observed (one each in Lakes Superior and Erie) and none less than the 5% recommended to detect depensation (Perälä and Kuparinen, 2017). Observed recruitment at the lowest observed stock size in Lakes Superior and Erie was above that predicted by the model (Fig. 3).

Pulses in the prevalence of small and large adult sea lampreys appeared to be synchronized across the Great Lakes, with the exception of Lake Erie (Fig. 1). Excluding Erie, between lake correlations of sea lamprey weight ranged from 0.27 (Superior and Huron) to 0.83

(Superior and Ontario). This apparent synchrony suggests that broader environmental or climatic changes that span the Great Lakes influence sea lamprey weight. Similar conclusions have been found for recruitment dynamics in Great Lakes fishes, varying with water temperature, wind speed, and the North Atlantic Oscillation (Bunnell et al., 2017; Myers et al., 2015). Other studies of fish species outside of the Great Lakes have shown synchronicity in fish growth (Black, 2009; Jensen et al., 2011; Tao, Kennard, Jia, and Chen, 2018).

We believe this sea lamprey stock-recruitment model could be useful to fisheries managers in the Laurentian Great Lakes and possibly to other systems with invasive sea lampreys, e.g., Lake Champlain (in New York, Vermont, and Quebec). It may enable data-driven modeling to help advance sea lamprey trapping operations from an assessment tool to a control method (Miehl et al., 2020). Jones and Adams (2021) have already used such a relation to investigate the possibility of sea lamprey eradication from the Great Lakes, by calculating the extinction exploitation rate, i.e., the lowest exploitation rate that will eventually result in the population declining to zero. It could be used to inform various recruitment overfishing strategies in the control of invasive sea lampreys. Adult-to-adult stock-recruitment relations are particularly advantageous to the sea lamprey control program on the Great Lakes because of readily available annual estimates of lake-wide adult abundance.

Attempts to model the population dynamics of invasive species are often met with challenges of data sparsity. Estimates of abundance may be limited temporally, spatially, as well as ontogenically. Models built on a single life stage provide a direct empirical estimate of the carrying capacity, but they require the assumption that no bias is introduced by not quantifying the survival at each transitional life stage (Mueller, 1986). This study reaffirms that even population growth models built on a single life stage can inform our understanding of ecological interactions and explorative management scenarios.

CRedit authorship contribution statement

Jean V. Adams: Conceptualization, Methodology, Software, Validation, Formal analysis, Writing – original draft, Visualization, Supervision, Project administration. **Michael L. Jones:** Methodology, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at [doi:10.1016/j.ecolmodel.2022.109916](https://doi.org/10.1016/j.ecolmodel.2022.109916).

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