ADVANCING THE SCIENCE OF INVASIVE SEA LAMPREY INTEGRATED PEST MANAGEMENT USING POPULATION DYNAMICS MODELING AND DECISION ANALYSIS

By

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ABSTRACT

Chapter 1 Resource managers frequently are tasked with mitigating or reversing adverse effects of invasive species through management policies and actions. In Lake Superior, of the Laurentian Great Lakes, invasive sea lamprey populations are suppressed to protect valuable fish stocks. However, the relationship between choice of long-term control strategy and the future chance of achieving the suppression target is unclear. Using a 60+ year time-series of suppression effort and monitoring data from 50 assessment sites located on Lake Superior tributaries, we developed a Bayesian state-space model to forecast the probability of suppressing lamprey below the suppression target. With annual application of lampricide (i.e., lamprey-specific pesticide) at historical mean levels, we forecasted a 15% chance of achieving the Lake Superior sea lamprey suppression target in 2040. Increasing lampricide effort and/or supplementing lampricide control with age-1 recruitment reduction increased suppression chance. Annual application of the maximum historical lampricide effort resulted in a 50% predicted chance of achieving the target, annual application of the mean historic lampricide effort plus a 40% reduction in recruitment resulted in a 54% chance, and the maximum amount of effort considered (maximum historic lampricide and 60% reduction in recruitment) resulted in a 94% chance. We developed a simulation model from a robust, long-term monitoring dataset that improves understanding of why long-term sea lamprey suppression objectives have been difficult to achieve in Lake Superior. Furthermore, the model provides a means to gauge efficacy of sea lamprey control policy and action scenarios based on forecasted chance of achieving the suppression target. Creating processes for iteratively refining our forecasting model with stakeholder and technical-expert input and integration with a decision analysis framework could strengthen the link between ecological knowledge obtained from long-term monitoring and invasive sea lamprey management.

Chapter 2 Quantifying fish spatial recruitment dynamics at the sibling group offers a powerful methodology for understanding density-dependent and environmental drivers of recruitment. We propose a continuous-time multistate modeling framework that combines sibship and abundance estimation datasets to estimate mean sibling group size, sibling group size process error, environmental and density-dependent effects on sibling group size, dispersal, and mortality rate. Geographic states in the model consist of discrete habitat patches connected through dispersal. Simulations were used to investigate the influence of sampling processes and

mean sibling group size on parameter estimation accuracy and precision for our proposed modeling framework. Mean sibling-group size, environmental effects on recruitment, and dispersal rate among habitat patches could be estimated with high accuracy under a wide range of sampling conditions, including imprecise out-of-model estimates of capture probability, subsampling within habitat patches (extrapolating density estimates to habitat abundance using area expansion), and subsampling among habitat patches. Density-dependent effects on recruitment and process error tended to be estimated with lower accuracy than other model parameters, though accuracy improved as sibling group size increased and sampling intensity increased. The main contribution of this work is a flexible quantitative modeling framework for conducting power analyses and parameterizing mechanistic models of recruitment dynamics in spatially structured fish populations with empirical sibship data.

Chapter 3 A major aim of invasive species management is to enact Integrated Pest Management (IPM) principles. However, operationalizing IPM can be challenging due to ecological and values-driven uncertainties. We applied decision analysis to develop a collaborative adaptive management framework that enables effective consideration of the societal and environmental consequences of control tactic selection and use decisions for invasive sea lamprey (*Petromyzon marinus*) in North America's Laurentian Great Lakes. We developed a multi-level objective hierarchy that included both localized management and multi-stream coordination fundamental objectives, conducted a feasibility analysis that constrained alternatives to those with high probability of social acceptance and technical success, and quantified expected outcomes of alternatives in terms of multi-stream coordination objectives (minimize costs and maximize learning about efficacy of novel sea lamprey control strategies). Optimal deployment configurations for scenarios that favored maximize learning over minimize costs consisted of a more diverse portfolio of control tactics compared to scenarios that favored cost effectiveness, which demonstrates the sensitivity of sea lamprey control tactic selection and use decisions to values-driven uncertainty. Iterative application of our collaborative adaptive management framework could support social learning and cross-scale linkages if ideas about multi-stream coordination and internal validity of invasive sea lamprey management practices can be exchanged in a trusting environment. Collaborative adaptive management frameworks capable of enabling such social learning may be broadly useful for operationalizing IPM in heterogeneous social-ecological landscape.

PREFACE

The chapters in this dissertation were drafted as stand-alone manuscripts that have been/will be submitted for publication in peer-reviewed journals. First-person plural pronouns are used within the body of the chapters because multiple co-authors will be credited in publication.

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INTRODUCTION

Invasive species are one of the largest direct drivers of ecosystem change and can negatively affect human well-being (Pyšek and Richardson, 2010). While preventative measures that limit establishment and spread of invasive species are crucial for grappling with this global problem, suppression or eradication can help reverse or alleviate societal and ecological damage caused by established invasive populations (Baker and Bode, 2021; Lambin et al., 2020). Achievement of these desired effects through invasive species management is usually not straightforward; management decisions involving invasive species are often challenged by multiple sources of uncertainty (e.g., abundance levels, population dynamics, spatial locations) and are made in pursuit of multiple objectives, requiring appraisal of collateral damage and opportunity-cost tradeoffs (Dobiesz et al., 2018; Fenichel and Hansen, 2010). Mathematical models of population dynamics and control offer a value-added tool for invasive species management by providing probabilistic measures of predicted suppression or eradication success that can be weighed against tradeoffs associated with a particular management action and can be continually updated as new information becomes available (Tiberti et al., 2021; van Poorten et al., 2019). However, population dynamics modeling by itself offers little guidance for evaluating tradeoffs among multiple invasive species management objectives. Decision analysis helps practitioners decompose problems into key components, account for multiple objectives, foster group deliberation, and identify desirable action alternatives (Hemming et al., 2022). Combined applications of population dynamics modeling and decision analysis may build capacity to engage with complex invasive species management challenges and opportunities.

The construction of navigable canals in the late 1900s that bypassed natural barriers between the Atlantic Ocean and the Great Lakes basin allowed sea lamprey (*Petromyzon marinus*) to invade the Great Lakes and become established by 1938 (Docker et al., 2021). Sea lamprey live primarily burrowed in sediment for 2 or more years, undergo metamorphosis, then outmigrate into the Great Lakes (Applegate, 1950; Bergstedt and Swink, 1995). Semelparous adults return to tributaries to spawn but, lacking natal philopatry, redistribute widely among Great Lakes tributaries. These life history traits lead to widespread production of parasitic juvenile sea lamprey, each capable of damaging valuable fishes by consuming approximately a kilogram of host-fish blood during their lifespan (Jorgensen and Kitchell, 2005; Madenjian et al., 2003). Prior to efforts to control their densities in the Great Lakes, sea lamprey parasitism

contributed to significant abundance declines of native lake trout (*Salvelinus namaycush*) populations and limited efficacy of fish stocking for lake trout conservation and development of recreational salmonid fisheries (Dann and Schroeder, 2003; Muir et al., 2012).

Success in controlling invasive sea lamprey in the Great Lakes traces back to the 1954 Convention on Great Lakes Fisheries and the formation of the Great Lakes Fishery Commission (GLFC). The 1954 bi-national treaty and the GLFC mobilize funding from the United States and Canada for sea lamprey control in the Great Lakes. By 1980, integrated pest management (IPM) principles began to influence sea lamprey control practices and a strategic vision for allocating these funds (Sawyer, 1980). Sea lamprey control decisions often have high degrees of uncertainty, require consideration of conflicting values systems, and necessitate tradeoffs among multiple objectives. IPM provides clarity on how to address these complexities through "… a decision support system for the selection and use of pest control tactics, singly or harmoniously coordinated into a management strategy, based on cost/benefit analyses that take into account the interests of and impacts on producers, society, and the environment" (Kogan, 1998). However, applying IPM to sea lamprey control is challenging. Implementing IPM requires both an understanding of the target species' life history and ecology and fine-tuned institutional structures and communication pathways for effective consideration of the societal and environmental consequences of control tactic selection and use decisions (Arora and Dhawan, 2012). Scientists, practitioners, and policy makers have confronted these challenges for decades and, in doing so, have updated and refined the science and practice of applying IPM to invasive sea lamprey control in the Great Lakes (Christie and Goddard, 2003; Sawyer, 1980). Forward-looking analyses and institutional reviews from the 3rd Sea Lamprey International Symposium (2019) suggest that continued success in delivering sea lamprey control in the complex and ever-changing Great Lakes social-ecological system may depend on continued effort to better understand and overcome barriers to applying IPM (McLaughlin et al., 2021).

The objective of my dissertation was to advance the science of applying IPM to sea lamprey control in the Great Lakes using population dynamics modeling and decision analysis. In *Chapter 1*, Lake Superior adult sea lamprey trapping data and control effort records (1953-2019) and a Bayesian state-space population dynamics model provide the basis for generating probabilistic forecasts of sea lamprey control outcomes under alternate hypothetical control effort scenarios. In *Chapter 2*, I develop an analytical framework for using combined genetic

pedigree analysis (a method that uses genetic markers for relationship estimation) and abundance estimation datasets to resolve demographics of spatially structured fish populations. The sea lamprey control program launched an integrated genetic pedigree analysis and conventional fisheries survey monitoring program in 2020 that spans 13 tributaries in the Upper Great Lakes (Lewandoski et al., 2021). My analytical framework combined with this novel dataset offers a promising avenue for learning about the cryptic early-life history of sea lamprey. These innovations in sea lamprey population dynamics modeling advance the science of applying IPM to sea lamprey control by providing quantitative tools capable of using ecological monitoring data to make probabilistic predictions of sea lamprey control outcomes.

In *Chapter 3*, I synthesize a collaborative application of decision analysis that was motivated by the decision support needs for an ongoing management-scale experiment (the Sea Lamprey Supplemental Control Initiative http://www.glfc.org/supplemental-controls.php). This work culminated in an adaptive management framework that enables overlapping decision-making processes occurring at the localized and multi-system coordination levels. This work advanced the science of applying IPM to sea lamprey control by developing a decision support framework that can be iteratively applied to refine how achievement of multiple objectives related to environmental and societal consequences of sea lamprey control (maximizing sea lamprey control, minimizing non-target effects, minimizing collateral damage, minimizing cost, and maximizing learning) are considered in sea lamprey control decisions.

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CHAPTER 1. FORECASTING SUPPRESSION OF INVASIVE SEA LAMPREY IN LAKE SUPERIOR

Abstract

Resource managers frequently are tasked with mitigating or reversing adverse effects of invasive species through management policies and actions. In Lake Superior, of the Laurentian Great Lakes, invasive sea lamprey populations are suppressed to protect valuable fish stocks. However, the relationship between choice of long-term control strategy and the future chance of achieving the suppression target is unclear. Using a 60+ year time-series of suppression effort and monitoring data from 50 assessment sites located on Lake Superior tributaries, we developed a Bayesian state-space model to forecast the probability of suppressing lamprey below the suppression target. With annual application of lampricide (i.e., lamprey-specific pesticide) at historical mean levels, we forecasted a 15% chance of achieving the Lake Superior sea lamprey suppression target in 2040. Increasing lampricide effort and/or supplementing lampricide control with age-1 recruitment reduction increased suppression chance. Annual application of the maximum historical lampricide effort resulted in a 50% predicted chance of achieving the target, annual application of the mean historic lampricide effort plus a 40% reduction in recruitment resulted in a 54% chance, and the maximum amount of effort considered (maximum historic lampricide and 60% reduction in recruitment) resulted in a 94% chance. We developed a simulation model from a robust, long-term monitoring dataset that improves understanding of why long-term sea lamprey suppression objectives have been difficult to achieve in Lake Superior. Furthermore, the model provides a means to gauge efficacy of sea lamprey control policy and action scenarios based on forecasted chance of achieving the suppression target. Creating processes for iteratively refining our forecasting model with stakeholder and technical-expert input and integration with a decision analysis framework could strengthen the link between ecological knowledge obtained from long-term monitoring and invasive sea lamprey management.

Introduction

Invasive species are one of the largest direct drivers of ecosystem change and can negatively affect human well-being (Pyšek and Richardson, 2010). While preventative measures that limit establishment and spread of invasive species are crucial for grappling with this global problem, suppression or eradication can help reverse or alleviate societal and ecological damage

caused by established invasive populations (Baker and Bode, 2021; Lambin et al., 2020). Achievement of these desired effects through invasive species management is usually not straightforward; management decisions involving invasive species are often challenged by uncertainty and necessitate appraisal of collateral damage and opportunity cost tradeoffs (Dobiesz et al., 2018; Fenichel and Hansen, 2010). Mathematical models of population dynamics and control offer a value-added tool for invasive species management by providing probabilistic measures of predicted suppression or eradication success that can be weighed against tradeoffs associated with a particular management action (Tiberti et al., 2021; van Poorten et al., 2019). Time-series analytic techniques provide the foundation for building population management forecasting models from long-term monitoring datasets (Shea et al., 1998). Additional information on vital rates from short-term studies of the population of interest (Shea and Kelly, 1998), studies of other representative populations (Jensen et al., 2009), expert elicitation (Johnson et al., 2017), or a combination of these sources (Govindarajulu et al., 2005) provide the means to develop forecasting models with stage or age structure and control tactics targeting multiple life stages (Shea and Kelly, 1998; Vélez-Espino et al., 2008). Bayesian approaches can combine multiple sources of information into a common statistical framework and allow for seamless building of forecasting models (with robust consideration of uncertainty) from the posterior distribution of process-based model elements. Hobbs et al. (2015) suggested that Bayesian forecasting approaches are versatile for evaluating population management challenges, including management of invasive species, and noted that the probabilistic output from these approaches is well suited to evaluations of alternate management actions within decision analysis frameworks. Indeed, applications of Bayesian forecasting approaches range from consideration of how management actions influence *Brucellosis* prevalence in Yellowstone National Park bison (*Bison bison*) (Hobbs et al., 2015), feasibility of sterilization as a management tool for reducing white-tailed deer (*Odocoileus virginianus*) density (Raiho et al., 2015), to the influence of harvest policy on Eurasian lynx (*Lynx lynx*) abundance (Andrén et al., 2020).

Lake Superior, of the North American Great Lakes, supports valuable populations of lake trout (*Salvelinus namaycush*) that have been the target of extensive conservation and management efforts undertaken to mitigate anthropogenic threats, including depredation by invasive sea lamprey (*Petromyzon marinus*). Lake Superior is the largest freshwater lake by surface area in the world. It is a glacial lake formed during the Pleistocene; the earliest

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zoogeographically significant lake in the current Lake Superior basin was formed roughly 12000 years ago (Bailey and Smith, 1981). Lake trout inhabiting Lake Superior differentiated into multiple morphotypes, each with specialized habitat preferences, diet, and physiology that, presumably, are the result of divergence and adaptation to habitat niches present in large lakes with abundant deep-water habitat (>100 m) (Muir et al., 2014). After European colonization of the region, unsustainable fishing practices, habitat degradation, and the establishment of invasive sea lamprey caused the collapse of Lake Superior lake trout fisheries. Sea lamprey consume blood and other body fluids during their parasitic juvenile lifestage. Lake trout are killed directly by sea lamprey parasitism (Madenjian et al., 2008) and sub-lethal effects can be energetically costly (Firkus et al., 2022). Multi-jurisdictional, cooperative efforts that have been undertaken to reestablish and sustain lake trout fisheries include stocking hatchery-reared lake trout to supplement wild stocks, fishery regulation and assessment, and sea lamprey suppression (Hansen and Bronte, 2019). These ongoing efforts have since helped to reverse abundance declines of lake trout and enabled development of co-managed lake trout fisheries (Hansen and Bronte, 2019; Mattes, 2020). However, invasive sea lamprey remain the single largest threat to lake trout fisheries in Lake Superior (Muir et al., 2012). Lake Superior fisheries managers determined that this threat was acceptably low during 1993-1997, based on lake trout wounding metrics (sea lamprey wounds per 100 lake trout captured in standardized surveys), and set the sea lamprey suppression target to mean sea lamprey abundance during this time period (Treska et al., 2021). Despite this long-standing management objective, sea lamprey abundance has often been above the suppression target in Lake Superior and the quality and amount of effort required to consistently suppress abundance below the target is unclear. Forecasts of sea lamprey suppression given a suite of hypothetical sea lamprey control policy and action alternatives could address this knowledge gap.

Our objective was to develop a Bayesian forecast model of sea lamprey dynamics and control in Lake Superior that makes use of information from long-term population abundance trend monitoring and apply this model towards the evaluation of alternate sea lamprey suppression scenarios. Sea lamprey are anadromous and do not exhibit natal philopatry, rather they are guided into tributaries by river plumes containing pheromones emitted by stream-resident lamprey larvae (Buchinger et al., 2015). As part of our modeling effort, it was necessary to consider the intricacy of relating observations (catch of adult sea lamprey in individual

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tributaries) to the population-level process of interest (change in lake wide sea lamprey abundance over time). We accomplished this through multivariate autoregressive state-space modeling (Holmes et al., 2012; Tolimieri et al., 2017) to represent the geographically dispersed long-term monitoring dataset with patchy temporal coverage and concerns regarding heterogeneous observation variability among monitoring sites. A further intricacy of the observation process, the possibility of reduced pheromone signal in the years following application of lamprey-specific pesticides (hereafter lampricides) causing reduced catch of adult sea lamprey (Mullett et al., 2003), was addressed by modeling the relationship between lampricide application history and expected catch at each monitoring site.

Materials and Methods

Catch Data

Catch data have been collected in Lake Superior tributaries since 1953 to monitor adult sea lamprey population trends. We grouped these catch data into assessment units based on location and gear type. From 1953 to 1979, catch data were obtained from traps operated in conjunction with electric weirs deployed to halt upstream spawning migration of sea lamprey. Since 1980, catch data have come primarily from traps operated immediately downstream of dams, weirs, or natural stream features. Daily catches were summed by year to generate annual catch time series for each assessment unit. To be included in analyses, assessment units needed at least 10 years of catch data to ensure there was sufficient information to estimate assessment unit-specific scaling parameters, observation covariate effects, and observation variance parameters. With this criterion, the Lake Superior adult sea lamprey catch dataset contained 50 assessment units. In any given year, between 9 and 31 units had sea lamprey catch data available. Most assessment units were associated with tributaries located in the southeast region of Lake Superior (35), with 12 units associated with southwest shore tributaries and 3 units associated with north shore tributaries (Figure 1). The imbalanced north-south geographic distribution of assessment units follows the distribution of sea lamprey producing tributaries in Lake Superior, as much of the north shore coastline does not contain sea lamprey producing tributaries (Heinrich et al., 2003). Our research did not involve activities requiring approval by Michigan State University Institutional Animal Care & Use Committee (IACUC). Adult sea lamprey catch records used in our research were obtained from Fisheries and Oceans Canada and US Fish and Wildlife Service databases.
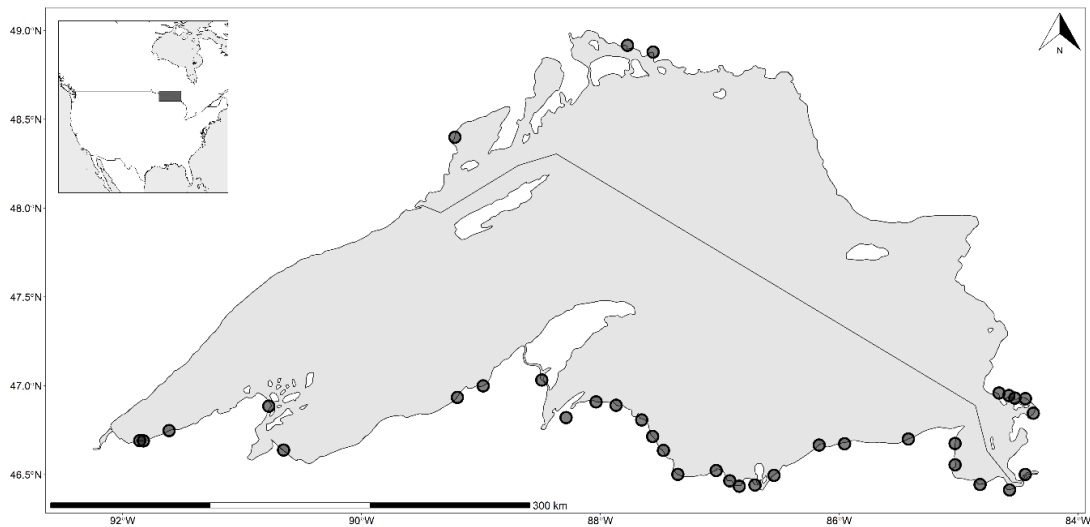
Figure 1.1. Map of Lake Superior of the North American Great Lakes with the locations of long-term monitoring sites included in the analysis. Points are located at the mouth of the corresponding tributary.

Control Effort Indices

Multiple control tactics have been used on Lake Superior to suppress invasive sea lamprey populations (Figure 1.2). As previously indicated, traps in conjunction with electric weirs were heavily relied upon prior to the 1980s in an attempt to reduce spawning sea lamprey abundance in Lake Superior tributaries (Hunn and Youngs, 1980). Electric weir control effort peaked in 1957 (n=73) and declined incrementally over the next two decades as the objective of electric weir operation switched from suppression to assessment of adult sea lamprey population trends. Two lampricides have been used to kill sea lamprey larvae. Treatment of lotic habitats within Lake Superior tributaries with TFM (3-trifluoromethyl-4'-nitrophenol) began in 1958 and has been a heavily relied upon control tactic ever since, though effort has been variable with peaks early and late in the time series. Slow moving tributaries of Lake Superior and associated lakes, large connecting waterways, and estuaries off the mouths of tributaries (lentic habitats) have been treated with granular Bayluscide (2', 5-dichloro-4'-nitrosalicylanilide) since 1960, although application was temporarily halted from 1989 to 1999 due to registration issues with the lampricide. Bayluscide effort increased within the last decade, as lentic areas within the US waters of Lake Superior began being treated in addition to infested lentic areas in Canadian

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waters. From 1991 to 1996, large scale trials of a control tactic referred to as the sterile-male-release-technique (SMRT) were conducted (Twohey et al., 2003). This tactic was implemented by sterilizing captured male sea lamprey with bisazir, and then releasing sterilized males back into Lake Superior tributaries where they would compete with fertile males for spawning females. Construction of permanent weirs has been another sea lamprey control tactic implemented in tributaries to Lake Superior. The distribution of sea lamprey larvae within Lake Superior tributaries was concentrated by the construction or modification of 18 permanent weirs between 1967 and 2014 (Hrodey et al., 2021). Cumulatively, these barriers blocked spawning sea lamprey from approximately 2,100 river km. Annual indices of these control tactics (km of stream treated with TFM, kg of Bayluscide applied, number of electric weirs operated, SMRT applied (Y/N), and km of stream blocked by permanent weirs) were amalgamated from control program records and incorporated in our population dynamics and control model as time-varying covariates associated with control-induced mortality parameters. Control effort also varied spatially from year-to-year, but our population and control dynamics model was not spatially explicit and did not account for this variability.
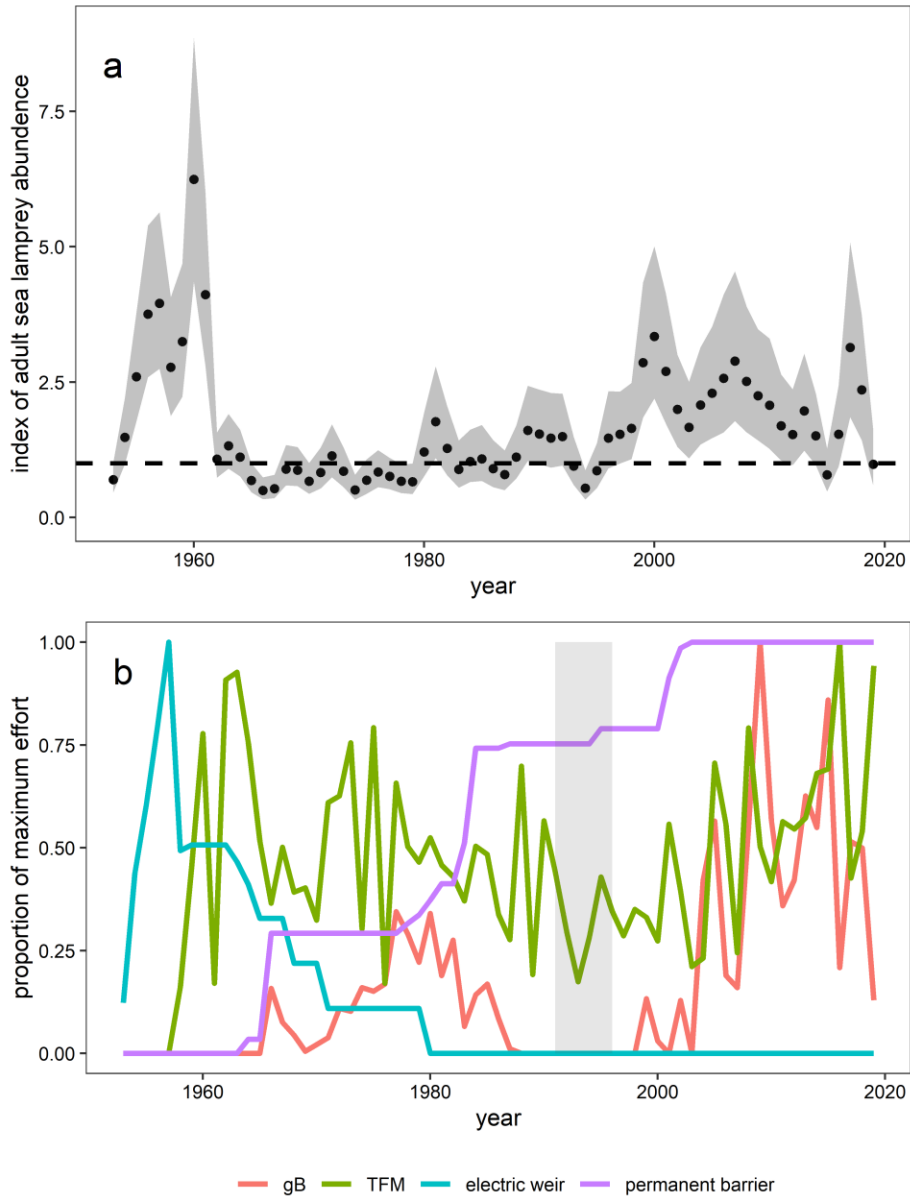
Figure 1.2. Estimated index of adult sea lamprey abundance in Lake Superior 1953-2019 with 95% credible intervals indicated by the shaded ribbon (a) and time-series of sea lamprey control effort indices (b). The adult index is scaled by the suppression target (indicated by the broken horizontal line). Control effort indices are plotted as proportion of maximum effort (granular Bayluscide (gB)= 1032 kg of active ingredient; TFM= 1114 km of stream treated; electric weir= 74 weirs deployed; permanent barrier= 2100 km of stream blocked). The shaded region in panel (b) indicates the duration of the large-scale trial of the sterile-male-release-technique.

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Population dynamics and control model

We developed a combined stage- and age-structured model for the Lake Superior sea lamprey population that included multiple life stages (larval, juvenile, adult), age-classes, and larval habitat types (see Appendix A and Appendix B for detail on model development). Changes in abundance in each state (stage or age class) were affected by multiple processes, including recruitment, mortality, and juvenile and adult transformation rates (Figure 1.3). The number of age-1 larvae produced each year (age-1 recruitment) was based on the number of age-1 larvae produced per adult (recruitment rate) and abundance of adults the previous year. Recruitment rate was parameterized by a long-term average recruitment rate, annual deviation from the long term average, control-induced effects, and abundance of adults the previous year (inverse density-dependence). Age-1 larvae were assumed to be distributed among three habitat types: lentic, lotic, and areas invulnerable to lampricides. Larval survival was influenced by natural mortality and treatment mortality stemming from application of either granular Bayluscide or TFM, depending on the habitat occupied. Age-5, age-6, and age-7+ larvae transform into parastic juveniles. Finally, individuals remained in the juvenile life stage for one or two years before they transitioned to the adult (i.e., spawning) lifestage. Sea lamprey are semelparous; adult abundence in any given year was equal to the number of juveniles that transitioned into the adult life stage that year.
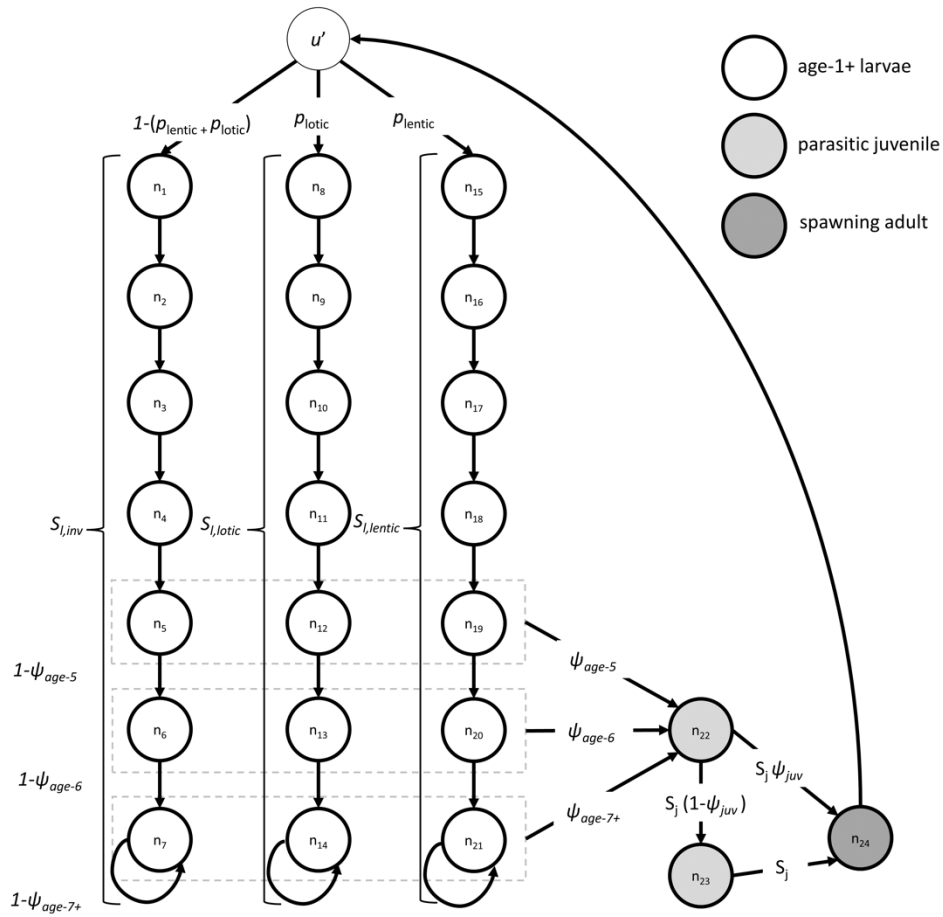
Figure 1.3. Lifecycle graph showing states included in the Lake Superior sea lamprey population model and proceses affecting transition between states. States include larvae inhabitating invulernable to lampricde habitat (n_1-n_7), larvae inhabitating lotic habitat vulnerable to TFM application (n_8-n_{14}), larvae inhabiating lentic habitat vulnerable to Bayluside application (n_{15}-n_{21}), juveniles (n_{22}-n_{23}), and adults (n_{24}). Processes influencing state transitions include recruitment of age-1 larvae (u'), probablity of age-1 larvae recruiting to lotic habitat (p_{lotic}), probability of age-larvae recruiting to lentic habitat (p_{lentic}), annual larval survival in lampricide invulnerable habitat ($S_{l,Inv}$), annual larval survival in lotic habitat ($S_{l,lotic}$), annual larval survival in lentic habitat ($S_{l,lentic}$), metamorphasis probability of ages 5-7+ larvae (φ_{age-5}, φ_{age-6}, and φ_{age-7+}), probability of juveniles becoming spawning adults after one year (φ_{juv}), and annual juvenile and adult survival (S_j).

Observation model

The observation model relating annual catches of adult sea lamprey at each assessment

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unit to the population-level index of adult abundance took the form of

$$y_{t,k} \sim Normal\left(\log_e[n_t^{adult}] + s_k + \beta_{treat,s} \cdot X_{t,s}, \sigma_k\right)$$

where *y* was the $\log_e$ catch of adult sea lamprey at site *k* during year *t*, n_t^{adult} was lake-wide expected adult abundance index at year *t* (a derived parameter obtained from parameters of the stage-age population model), s_k was a scaling parameter for site *k*, $\beta_{treat,s}$ was the stream-specific effect of number of years after treatment on the observation process, $X_{t,s}$ was an ordered categorical covariate for stream *s* at year *t* with three levels (0,1,2) corresponding to 0, 1, or 2+ years after TFM treatment, and σ_k was site-specific observation variance. The s_k parameters allowed for multiple observations of the same state process with potentially different scalings to be included in the analysis (Holmes et al., 2012). An arbitrary assessment unit was selected as the reference scale for the adult abundance index and had its scaling parameter fixed at zero.

Parameter estimation

Posterior distributions of model parameters were generated through Markov Chain Monte Carlo (MCMC) sampling implemented in Stan (Carpenter et al., 2017) using the *rstan* package (Stan Development Team, 2020) and R version 4.0.2 (R Core Team, 2020). Four MCMC chains were run for 28000 iterations with a warmup of 8000 iterations. Visual inspection of trace plots and computation of R-hat statistics indicated that saved iterations after the burn-in period were sampling from the posterior distribution and had achieved stationarity.

We generated a posterior distribution for long-term deterministic population growth rate of sea lamprey in Lake Superior in the absence of control (λ) from the posterior distributions of population dynamics parameters. We calculated this derived parameter (for each MCMC iteration) as the dominant eigenvector of the stage-age matrix population dynamics model using the *popbio* package (Stubben and Milligan, 2007).

Post posterior checking

We simulated replicated datasets of adult sea lamprey catch from the posterior distribution of our fitted model and compared the observed data to the predicted range of values (full post-posterior checking results are presented in Appendix C). Plotting observed values against the range of predicted values for each assessment unit allowed us to examine for evidence of systematic lack-of-fit in the model. We also calculated the percentage of observations that fell within the corresponding estimated 95% credible interval. Finally, we calculated residuals for each observed data point and summarized them by year to assess for

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temporal patterns in model over or under prediction. We did not observe strong evidence of systematic lack-of-fit or autocorrelation in annual observation-level residuals.

Forecasting suppression strategies

We forecasted future sea lamprey population abundance for a suite of long-term lampricide suppression strategies with consistent annual effort. We considered lampricide effort levels encompassing the historic range of annual granular Bayluscide (0 – 1,032 kg of active ingredient) and TFM (0 – 1,113 km of stream treated) application crossed with different levels of management-induced reduction in age-1 recruitment rate (0, 0.20, 0.40, 0.60). Reductions in age-1 recruitment were modeled, rather than annual effort of historically applied control tactics, because the current suppression program would ostensibly adopt recruitment-reducing tactics that differ from historically applied approaches. We generated approximate posterior distributions for projected adult sea lamprey abundance in 2040 for each strategy using the posterior distribution of our 2019 abundance index derived parameters (for each stage-age class) and population dynamics and control process model parameters. In this fashion, our forecasts accounted for uncertainty in sea lamprey population dynamics, uncertainty in the relationship between lampricide effort and control-induced mortality, correlation among estimated parameters, and stochastic age-1 recruitment. We assumed that management actions were implemented annually and that there was no implementation uncertainty associated with any of the control measures.

Target suppression abundance index was calculated based on the methodology used to set the sea lamprey suppression target for Lake Superior, which is the average sea lamprey abundance during 1993-1997 (Treska et al., 2021). We present our forecast results as the probability of projected 2040 adult sea lamprey abundance being less than this target.

Results

Sea lamprey population dynamics in the absence of control comprise expected long-term annual population growth rate (λ) and year-to-year variability in λ (modeled as stochastic variability in age-1 recruitment rate). At target suppression abundance, mean λ was estimated at 1.19 (95% credible interval: 1.06-1.43). Year-to-year variability in age-1 recruitment rate was substantial, the ratio of the standard deviation of year-to-year variability in recruitment rate to mean age-1 recruitment rate was 0.14 (0.08-0.22). This translated to high year-to-year variability in realized λ. With recruitment rate set at one standard deviation below the mean, λ was 1.07

(0.93-1.30); at one standard deviation above the mean, λ was 1.33 (1.18-1.58). Though we included inverse-density dependent recruitment in our model, the posterior distribution for *b* was nearly identical to the prior distribution (*see* Appendix B for detail on posterior and prior distributions for *b* and other model parameters), which indicates that our prior assumption of weak inverse density dependent recruitment rate was neither supported nor refuted by our data analysis.

Sea lamprey suppression tactics either targeted recruitment of age-1 larvae (electric weir operation and sterile-male-release technique), larvae inhabiting lotic habitat (application of TFM), or larvae inhabiting lentic habitat (application of granular Bayluscide). Estimated amount of management-induced mortality and associated 95% credible intervals are reported for each suppression tactic at the mean effort level (calculated only from years in which the tactic was implemented). Electric weir operation (mean effort of 24 operational weirs) reduced age-1 recruitment rate by 29% (12 - 44%). The effect of implementing SMRT in Lake Superior on recruitment rate was less clear. There was a 74% chance that recruitment rate declined during years SMRT was implemented. The mean estimated effect was an 11% decrease in recruitment rate, although based on the 95% credible interval, recruitment may have decreased by as much as 44% or increased by as much as 33%.

Population-level effects of lampricide application depended upon two modeled processes, the percentage of age-1 recruits distributed to each habitat type (lentic, lotic, or habitat invulnerable to lampricides) and mortality caused by lampricide application. Of all recruited age-1 larvae, 21% (2% – 63%) recruited to habitat invulnerable to lampricide application, 16% (0%-70%) recruited to lentic habitat and were vulnerable to granular Bayluscide application, and 63% (6%-96%) recruited to lotic habitat and were vulnerable to TFM application. Granular Bayluscide application (mean effort of 279 kg of active ingredient applied) resulted in a finite management-induced larval mortality rate of 0.18 (0.02-0.65). The relationship between TFM application and larval mortality depended upon the amount of river kilometers blocked by permanent barriers to migration. At the amount of river blocked by permanent barriers to migration by 2019, TFM application (mean effort of 542 km of river treated) resulted in a finite larval mortality rate of 0.23 (0.02-0.74). At the amount of river blocked by permanent barriers to migration by 1963 (2100 km less than was blocked by 2019), TFM application resulted in a finite larval mortality rate of 0.18 (0.01-0.58).

Observation processes associated with TFM application history in tributaries containing assessment sites influenced expected catch. However, this effect was variable among tributaries; expected number of sea lamprey captured was positively associated with years-after-treatment in 20 of the 34 tributaries. There was strong evidence (>0.90 probability of an effect) of a positive effect in 8 tributaries and of a negative effect in 1 tributary.

The historic mean scenario with no age-1 recruitment reduction had a 15% chance of achieving the suppression target in 2040. Decreasing age-1 recruitment by 20, 40, and 60% combined with historical mean lampricide application increased the probability of achieving suppression target to 30%, 54%, and 84%, respectively (Figure 1.4). At the highest level of effort considered for lampricide control, but without age-1 recruitment reduction, the chance of achieving suppression target was 50%. At 60% reduction in age-1 recruitment but in the absence of lampricide application, there was a 24% chance of achieving the suppression target.

The scenario consisting of annually applying the historical mean TFM and granular Bayluscide effort had a wide 2040 forecasted posterior distribution (90% quantile interval: 5.95-0.64) compared with the scenarios with maximum annual lampricide application (90% quantile interval: 3.88-0.14) and mean lampricide integrated with 40% recruitment reduction (90% quantile interval: 3.02-0.27) (Figure 1.5). The scenario composed of maximum annual lampricide application and 60% recruitment reduction had a narrow posterior distribution centered well below the suppression target (90% quantile interval: 1.01-0.02). Individual simulated adult abundance trajectories were autocorrelated and displayed periodicity (Figure 1.5).
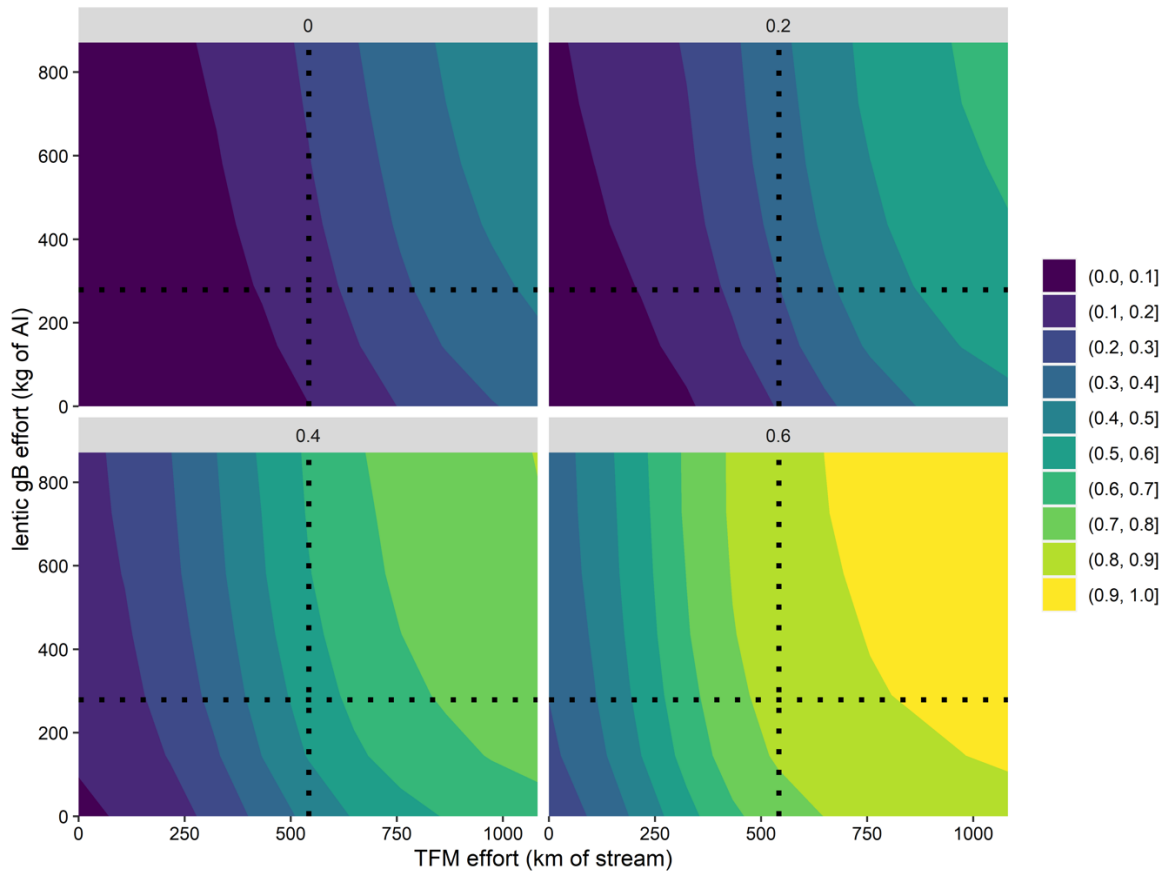
Figure 1.4. Forecasts of the probability of achieving sea lamprey suppression target in Lake Superior in 2040 for a suite of long-term sea lamprey suppression strategies. Facets show level of control-induced reduction in age-1 recruitment rate (status quo reduction in age-1 recruitment is 0). The probability gradient is represented by color gradient, with warmer colors indicating higher probability (0 to 1 scale). Dotted lines are the mean historic annual lampricide application effort.
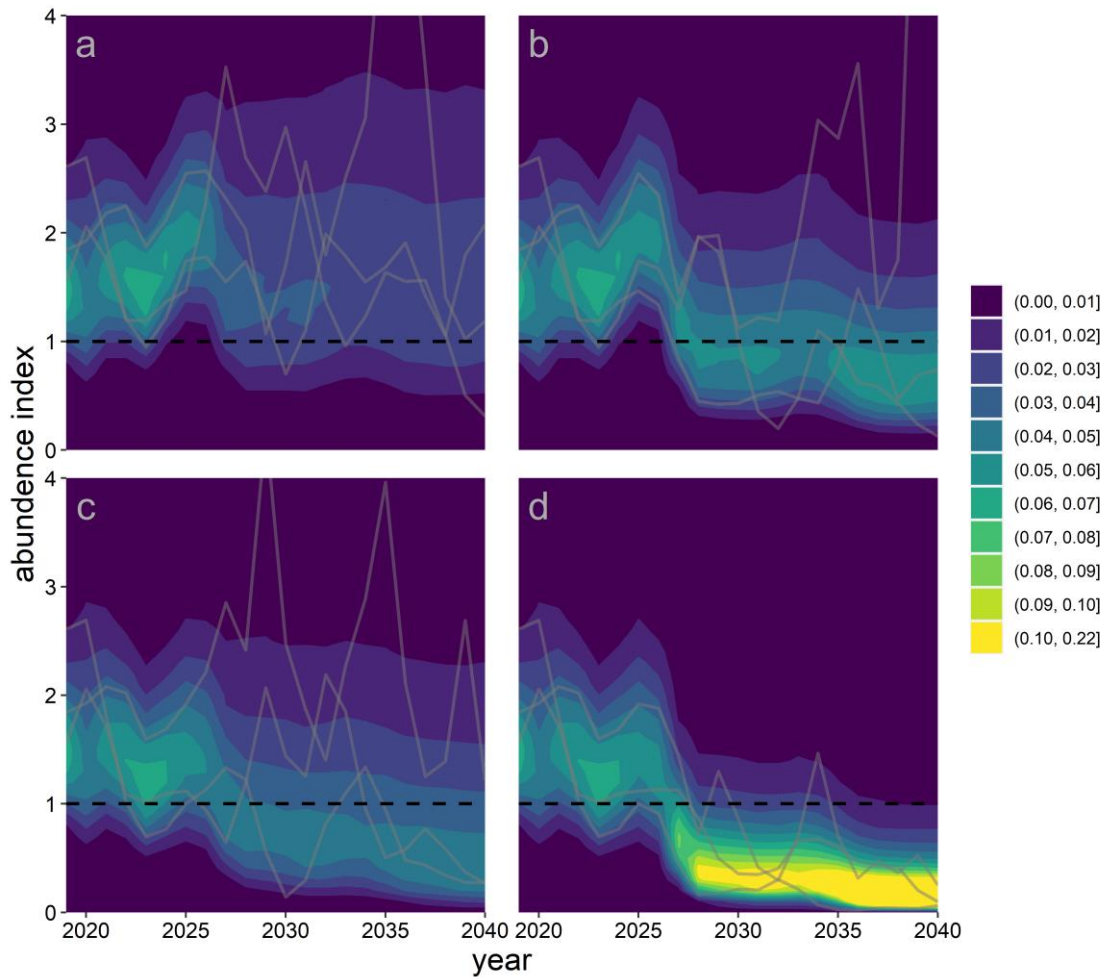
Figure 1.5. Forecast of adult sea lamprey abundance index (2020-2040) for long-term strategies consisting of (a) annual application of the historic mean amount of lampricide and no control-induced reduction in age-1 recruitment, (b) annual application of the historic mean amount of lampricide combined with 0.40 reduction in age-1 recruitment, (c) annual application of the historic maximum amount of lampricide, and (d) annual application of the historic maximum amount of lampricide combined with 0.60 reduction in age-1 recruitment. Warmer colors show higher density regions of the approximate posterior distribution of forecasted abundance. Grey lines show three randomly selected trajectories to demonstrate model behavior. The broken horizontal line is placed at the suppression target.

Discussion

Forecasts of lamprey suppression were regulated by the amount of control-induced mortality required to suppress sea lamprey (i.e., shift population growth from positive to negative) and the relationship between management-induced mortality and lampricide effort.

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Based on our empirical estimates of these phenomena, applying the historic average amount of lampricide effort annually, without supplemental management-induced reduction in age-1 recruitment, is unlikely to result in consistent achievement of the sea lamprey suppression target in Lake Superior. We identified two divergent strategic directions (representing end points of a continuum of possible strategies) that could be implemented to boost probability of achieving the suppression target to approximately 0.50: 1) annually apply lampricide effort equal to the maximum levels that have been historically applied or 2) annually apply mean lampricide levels in combination with deployment of management tactics that cause 40% reduction in age-1 recruitment. This level of reduction in age-1 recruitment may have historic precedent. Based on our modeled estimates, the extensive network of electric weirs deployed in Lake Superior from 1956-1962 probably reached 40% management-induced reduction in age-1 recruitment at its peak operation.

Both the strategic directions considered here would require substantial capacity building in the sea lamprey control program to fully implement as long-term strategy. Lampricide application is a pillar of current sea lamprey suppression strategy (Sullivan et al., 2021), but applying the annual historical maximum lampricide effort on an annual basis over a two-decade period would represent a massive increase from status-quo control effort because recent peaks in effort occurred as part of an intermittent targeted treatment strategy, not a sustained annual effort (Symbal et al., 2021). The electric weir program was discontinued because electric weir technology circa the 1960s had issues related to perceived effectiveness as a sea lamprey control tool and persistent non-target fish mortality (Hunn and Youngs, 1980). Modern electric weirs can be highly effective at reducing sea lamprey recruitment with much less non-target fish mortality (Johnson et al., 2021); application of the sterile-male-release-technique has effectively reduced larval recruitment in scenarios when a high ratio of sterile to non-sterile males (>40:1) can be achieved (Johnson et al., 2020). Other approaches to reducing age-1 recruitment, such as enhanced sea lamprey trapping techniques involving attractive and/or repellent semiochemicals, have been developed (Hume et al., 2020; Johnson et al., 2016). However, there currently is not capacity to implement management actions capable of achieving large-scale reduction of age-1 recruitment rate in Lake Superior using modern, socially acceptable tactics (Siefkes et al., 2021). Furthermore, it is not clear how much effort would be required to cause large-scale reduction of age-1 recruitment rate, though resource managers are seeking to learn about this relationship by

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using an adaptive management framework to investigate alternative control policies on some target streams in the Great Lakes basin (Lewandoski et al., 2021).

Contextualizing our sea lamprey suppression forecasts within ecosystem-based fisheries management could clarify potential tradeoffs between sea lamprey control policies that prioritize augmentation of either lampricide application or age-1 recruitment reduction capacities. Ecosystem-based fisheries management situates invasive species control outcomes within the larger goal of achieving conservation objectives (Brodziak and Link, 2002; Prior et al., 2018). Ecosystem-based management is implemented in Lake Superior with multiple management levers hypothesized to protect and sustain fisheries resources (Melius et al., 2011), including fish stocking (Hansen et al., 1995; Hansen and Bronte, 2019), fishery regulation and assessment (Nieland et al., 2008), habitat restoration (Bouvier et al., 2009; Host et al., 2011; Mitsch and Wang, 2000), and invasive sea lamprey suppression. Within this management framework, neither over- nor under-investment in sea lamprey suppression is desirable. At some point, over-investment will result in diminishing returns possibly at the expense of applying other management levers; conversely, under-investment in an effective sea lamprey suppression strategy would be a missed opportunity to realize conservation objectives and perhaps lead to unacceptable damage on valuable fisheries. Furthermore, decision makers must consider non-target outcomes of sea lamprey control actions that may work against achievement of other resource management objectives and vice versa. For example, dam removal decisions that increase connectivity between lake and tributary habitat in the Great Lakes basin involves consideration of tradeoffs among multiple resource management objectives (Walter et al., 2021) and deferred lampricide application costs (Hrodey et al., 2021). Thus, while our forecast model sheds light on the linkage between achievement of sea lamprey suppression goals and choice of control strategy, it represents only a piece of the decision-making capacity needed to holistically consider tradeoffs among alternative long-term sea lamprey control strategies. Combining probabilistic predictions of management outcomes with values-based models elicited from stakeholders in a multi-objective decision analysis framework offers a rigorous approach to invasive species management using both defensible science and stakeholder values (Maguire, 2004; Robinson et al., 2021; van Poorten et al., 2019). This could be an effective methodology for bolstering the effectiveness of sea lamprey suppression as a tool for achieving ecosystem-based Lake Superior fishery management conservation objectives.

Model-generated probabilistic forecasts of management alternatives can add value to decision making processes when there is buy-in from those involved in the decision and sensible alignment between the model and system characteristics expected to influence the outcomes of management alternatives. Thus, for the task of developing a sea lamprey suppression forecast model capable of improving conservation outcomes in Lake Superior, the challenge remains in creating an iterative model refinement process that enables decision-makers, stakeholders, and technical experts to identify key elements of model uncertainty, identify technical issues with the forecast model, and implement solutions. Designing processes that follow best-practice recommendations for evaluating fisheries stock assessment models and management procedures, including stakeholder involvement in model development and identification of optimization targets, explicit delineation of what constitutes unacceptable model behavior, external peer review, a holistic approach to model evaluation, and standardized sensitivity tests, may be advantageous (Goethel et al., 2019; Punt et al., 2020, 2016; Smith, 1999).

Communicating a model's strengths and weaknesses can help maintain sensible alignment between a forecast model and its intended management application. The strengths of our forecast model are that it makes use of a robust long-term monitoring dataset in Lake Superior spanning 60+ years to inform estimates of sea lamprey population and control dynamics and directly relates implementation of a given long-term suppression strategy to probability of achieving a politically-agreed-upon sea lamprey suppression target. A limitation of our forecast model is that it does not use information from available larval survey data – perhaps the most relevant dataset for conducting short-term forecasts of adult sea lamprey abundance. In contrast, established approaches for ranking streams for lampricide application rely heavily on the most recently available larval survey data (Jubar et al., 2021). Furthermore, our model assumes larvae inhabiting a given habitat type (lotic, lentic, or invulnerable to lampricide) constitute a single population. Thus, our model is not appropriate for evaluating management approaches leveraging among-stream heterogeneity to improve lake-wide control effectiveness or decisions related to a specific river system. However, a management strategy evaluation model developed to simulate the full sea lamprey control management process that generates basin-wide population dynamics from estimates of stream-level stock and recruitment relationships has provided useful insight in these types of scenarios (Dawson and Jones, 2009; Jensen and Jones, 2017; Jones et al., 2009; Miehls et al., 2020). Finally, we model the Lake Superior sea lamprey

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population as a single stock and consider each assessment site a valid (but possibly imprecise) index of lake wide abundance. While lack of homing behavior and long-distance movement of juvenile sea lamprey indicate that widespread mixing probably occurs within Lake Superior, complete panmixia is unlikely (Docker et al., 2021). Robust parasitic juvenile dispersal datasets would facilitate development of sea lamprey population dynamics models with sub-basin stock structure.

A further aspect of our forecast model that warrants evaluation through an iterative refinement process is our assumption of stationary population and control dynamics from 1953-2019 and during the forecasted time period (2020-2040). Climate change could influence future sea lamprey population and control dynamics in the Great Lakes (Lennox et al., 2020), such that empirical estimates of these dynamics from time-series data assuming stationarity may generate unreliable predictions of mid-century control outcomes. Analyses investigating sensitivity of sea lamprey control forecasts to different model formulations and climate change scenarios, including alternate non-stationary population and control dynamics assumptions, would build on our work herein and provide a more in-depth treatment of the uncertainty associated with forecasting sea lamprey control outcomes.

Globally, resource managers are faced with the challenge of developing effective management solutions to mitigate or reverse adverse effects of established invasive populations. The modeling approach we demonstrated can provide insight into the effectiveness of potential management solutions by forecasting suppression of invasive populations. Furthermore, intricacies we encountered associated with relating observation data to population-level processes of interest (that we expect are common to many long-term monitoring datasets collected by invasive species management institutions) were addressed by applying elements of a previously-developed, flexible statistical framework (Holmes et al., 2012; Tolimieri et al., 2017). Incorporating long-term monitoring data into actionable forecasts of invasion dynamics, as we do here, can help bring ecological knowledge to the forefront of invasive species management decision making.

The crux of transforming a forecast model into a useful conservation tool may be in creating effective processes within invasive species management institutions that enable iterative refinement, with the aim of building technical proficiency and buy-in from end users regarding the role of the model in decision processes. In a recent review of published invasive species

management case studies, half of the case studies reported positive responses after invader removal or suppression, with the rest reporting mixed results, no change, or negative impacts (Prior et al., 2018). Because many invasive species management actions do not generate expected, positive outcomes, data-driven forecast model development should become a higher priority within invasive species management institutions. For example, emerging strategies for controlling invasive carps in North America include forecast model development through population dynamics modeling and decision analysis (Cupp et al., 2021; Robinson et al., 2021). Given the overlap of fisheries science and invasive species management objectives from a population ecology perspective (Shea et al., 1998), lessons learnt by fisheries scientists could provide guidance on how to more fully integrate forecast model development with invasive species control practice.

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Data Availability Statement

Data and model code available via the Dryad Digital Repository https://doi:10.5061/dryad.69p8cz946 (Lewandoski and Brenden, 2022).

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CHAPTER 2. A MODELING FRAMEWORK FOR QUANTIFYING SPATIAL RECRUITMENT DYNAMICS USING ABUNDANCE ESTIMATION AND SIBSHIP ANALYSIS

Abstract

Quantifying fish spatial recruitment dynamics at the sibling group offers a power methodology for understanding density-dependent and environmental drivers of recruitment. We propose a continuous-time multistate modeling framework that combines sibship and abundance estimation datasets to estimate mean sibling group size, sibling group size process error, environmental and density-dependent effects on sibling group size, dispersal, and mortality rate. Geographic states in the model consist of discrete habitat patches connected through dispersal. Simulations were used to investigate the influence of sampling processes and mean sibling group size on parameter estimation accuracy and precision for our proposed modeling framework. Mean sibling-group size, environmental effects on recruitment, and dispersal rate among habitat patches could be estimated with high accuracy under a wide range of sampling conditions, including imprecise out-of-model estimates of capture probability, subsampling within habitat patches (extrapolating density estimates to habitat abundance using area expansion), and subsampling among habitat patches. Density-dependent effects on recruitment and process error tended to be estimated with lower accuracy than other model parameters, though accuracy improved as sibling group size increased and sampling intensity increased. The main contribution of this work is a flexible quantitative modeling framework for conducting power analyses and parameterizing mechanistic models of recruitment dynamics in spatially structured fish populations with empirical sibship data.

Introduction

Effective fisheries management depends on a good understanding of recruitment dynamics. Expected efficacy of harvest regulations, habitat enhancement actions, and changes in stocking rates are strongly affected by the underlying recruitment rate of the targeted fish population (Arlinghaus et al., 2015). Quantitative models of fish population dynamics that include recruitment processes provide guidance on sustainable harvest of exploited populations, conservation status of threatened or endangered populations, and the amount of control effort needed to reduce densities of invasive species (Boyce, 1992; Jones et al., 2015; Quinn and Deriso, 1999; Syslo et al., 2020). However, unambiguously explaining the mechanisms driving

recruitment with the goal of improving forecasts of fisheries management outcomes is challenging. Recruitment is a complex process that seems at odds with the relatively simple concept of young fish produced from mature adults (mathematically formulated as a linear stock-recruitment relationship with recruitment proportional to spawning stock size). Density-dependent processes can lead to reductions in per capita recruitment at high population densities, which ultimately gives rise to non-linear stock-recruitment relationships (Rose et al., 2001). For some fish populations, environmental factors that are independent of population density may be the dominant driver of recruitment and impart a high degree of variability in observed data. Indeed, a meta-analysis of stock-recruitment data from commercially exploited marine fish stocks found that recruitment was not positively related to spawning stock size in 61% of stocks analyzed and that environmental factors possibly played a dominant role in recruitment for these stocks (Szuwalski et al., 2015). Density-independent environmental factors can also be consequential for recruitment in freshwater fish populations. Habitat enhancement (deliberate manipulation of environmental factors) can increase recruitment rates (Radinger et al., 2023), while anthropogenic degradation of habitats cause recruitment declines and failures (Dudgeon et al., 2006). Finally, successful implementation of management actions intended to build or sustain climate-resilient fish populations, such as development of harvest control rules robust to environmentally-driven recruitment uncertainty and variability (Plagányi et al., 2019), identification and management of climate refugia (Ebersole et al., 2020), and conservation aquaculture (Overton et al., 2023), require at least a basic understanding of how environmental factors influence recruitment processes in fish populations. Given both the importance of understanding recruitment to fisheries management and its complexity, untangling how spawning stock size, density-dependent compensation, and environmental factors influence recruitment remains a fundamental challenge of fisheries science.

Spatially-explicit study design and data analysis offers more power to resolve recruitment mechanisms compared to non-spatial approaches. Evaluating data at spatial scales conducive to biological realism, rather than aggregating across broad spatial scales for pragmatic purposes, may improve efforts to quantify and make predictions about relationships between environmental factors and fish population dynamics (Rose, 2000). Indeed, a common limitation in studies of physical habitat–fish population productivity relationships in freshwater habitats has been scale mismatch between expected functional relationships and study design (Smokorowski

and Pratt, 2007). However, even with appropriate scale considerations, a challenge arises when analyzing and interpreting spatial data: are population fluctuations in spatial subsets related to demographic connectivity or environmental factors (Liebhold et al., 2004)?

Metapopulation models, in which species occurrences are conceptualized as idealized, well-mixed populations inhabiting discrete habitat patches connected by migration (Hanski, 1998), provide a framework for simultaneous consideration of demographic connectivity and environmental heterogeneity. While foundational metapopulation theory focused on colonization and extinction (Levins, 1969), applications of metapopulation concepts to fisheries science and management describe a broad range of population characteristics (abundance, size/age structure, and genetic structure) (Kritzer and Sale, 2004). Metapopulation concepts are formative in domains such as the theory and use of marine protected areas and habitat manipulation for conservation and fisheries management (Baine and Side, 2003; Cowen and Sponaugle, 2009), configuration of spatial-stock assessment methods (Cadrin and Secor, 2009), habitat fragmentation and connectivity in dendritic river networks and connected river-lake systems (Fagan, 2002; Jones, 2010), dispersal and establishment of invasive fish populations (Docker et al., 2021), and the effects of climate change on recruitment processes in marine and freshwater habitats (Cowen and Sponaugle, 2009; Kaeding and Mogen, 2023; Munday et al., 2009; Troia et al., 2019).

Genetic identification of parent-offspring pairs and/or sibling groups (Blouin, 2003) has been used to advance understanding of spatial recruitment dynamics in fish metapopulations. Sibling group identification (sibship analysis) is particularly effective because it is not limited by sampling constraints on the parental population (Schunter et al., 2014). Understanding recruitment processes related to local retention and planktonic dispersal of reef fishes during their larval stage is crucial for management of exploited and threatened marine fishes (Botsford et al., 2009). Sibship analysis has advanced understanding in this domain by providing empirical measures of recruitment dispersal among open-coastline rocky reefs (Schunter et al., 2014) and among neighboring (Baetscher et al., 2019) and regional marine protected areas separated by >500 km (Stockwell et al., 2016). Alternative larval dispersal hypotheses have been investigated with sibship analysis. Observations of collocated siblings on small reefs despite life history strategies with long pelagic drift duration have been interpreted as support for the cohesive larval dispersal hypothesis (i.e., that larvae use behavioral and sensory adaptations to maintain group

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cohesiveness during dispersal) (Bernardi et al., 2012; Robitzch et al., 2020). Spatial patterning of siblings across a 41-km reef transect was parsimoniously explained by the distance-limited dispersal model (declining number of collocated siblings as the distance between them increases) and did not lend support for cohesive dispersal (D'Aloia et al., 2018). In freshwater systems, sibship analysis has also been used to look for distance-limited dispersal patterns as predicted by the restricted movement paradigm (Rodriguez, 2002). Distance-limited dispersal was observed in studies of juvenile brown trout (*Salmo trutta*) (Vøllestad et al., 2012), age-1 sea lamprey (*Petromyzon marinus*) larvae (Derosier et al., 2007), and brook charr (*Salvelinus fontinalis*) alevin (Morrissey and Ferguson, 2011). Conversely, there was little evidence of distance-limited dispersal for young-of-year largemouth bass (*Micropterus salmoides*) siblings in a 126 ha lake (Hessenauer et al., 2012) and juvenile Roanoke log (*Percina rex*) perch siblings at scales ≤15 km, though distance-limited dispersal was detected at greater spatial distances (Roberts et al., 2016). Sibship analysis has also been used in freshwater systems to evaluate the effects of potential barriers (e.g., natural falls, perched culverts, and dams) on dispersal (Bowersox et al., 2016; Neville and Peterson, 2014; Weinstein et al., 2019; Zhai et al., 2019). Simulation research revealed that an analytic approach *sib-split* based on detections of full-siblings on opposite sides of potential barriers could accurately estimate dispersal across a barrier, and this method has been applied to resolve fisheries management questions related to dispersal across barriers and road crossing culvert remediation efforts (Neville and Peterson, 2014; Whiteley et al., 2014). Finally, in addition to advancing ecological theory and practical understanding of dispersal, sibship analysis applications have revealed novel insight into mating systems and levels of reproductive skew in wild fish populations (Liu and Ely, 2009; Sard et al., 2020; Serbezov et al., 2010; Shen et al., 2020).

While inferences from sibship analysis are typically made from a sample of individuals rather than an exhaustively sampled population (but see Serbezov et al., 2010), there has been little research into how sampling processes could mediate the effectiveness of sibship analysis as a tool for learning about recruitment dynamics at the sibling group scale. Spatially varying capture probability could lead to inaccurate inferences about dispersal and/or recruitment variability. For example, Morrissey and Ferguson (2011) noted that capture probability was expected to vary throughout the sampled stream reach so they accounted for spatially varying capture probability in their analysis of dispersal rate from sibship data. However, while methods

for quantifying abundance and demographic parameters for the parental sample of genetic parent-offspring pair datasets are well studied (i.e. close-kin mark recapture) (Bravington et al., 2016), quantitative methods for integrating inferences from sibship analysis with the range of survey methodologies and abundance estimation approaches used by fisheries managers and scientists are underrepresented in the literature. Methodological advances in this area may be broadly useful for predictive modeling in support of fisheries management and conservation because it would provide a novel approach to empiric estimation of recruitment and dispersal in metapopulations.

Herein, we propose a continuous-time multistate modeling framework that combines sibship and abundance estimation datasets to improve fine-scale understanding of the recruitment process. In essence, the aim of the framework is to quantify sibling-group-scale recruitment dynamics in spatially-structured populations given that habitat patch abundance is usually not directly observed and requires estimation. We conducted simulations to evaluate how sampling processes associated with abundance estimation influenced estimation of dispersal, mortality rate, and recruitment dynamics parameters (mean sibling group abundance, environmental effects, density dependent effects and variability in sibling group abundance). Specifically, we examined how parameter estimation was influenced by imprecise out-of-model estimates of capture probability, application of area expansion to estimate habitat patch abundance from localized density estimates, and the number of habitat patches sampled. The main contribution of the work is a flexible modeling framework that can be used to parameterize mechanistic models of recruitment and survival with demographic connectivity among habitat patches and guide field sampling efforts for future sibship analysis applications investigating recruitment dynamics in spatially structured populations.

Methods

Data Generating Processes

Our modeling framework and simulation study were based on a continuous-time multistate model of fish metapopulation dynamics (Miller and Andersen, 2008). We extend this modeling framework to accommodate applications that track genetically tagged sibling groups, rather than physically tagged individual fish. This extension introduces further complexity. The number of individuals being tracked (the number of individuals in a sibling group) and their initial location (the spawning patch location) become model output rather than model input. Our

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theoretical contribution is to accommodate this added complexity within the continuous-time multistate modeling framework.

Sibling group recruitment events are defined by a spatial component (the spawning habitat patch situated within a larger metapopulation) and the number of individuals in the sibling group at the time of initial sampling (t_1). We define sibling group generically here, but a sibling group could be alternatively defined (based on sibship data limitations, analytical constraints, and learning objectives of the model application) as full siblings, full and half siblings, or all individuals that share at least one parent. The number of individuals in a sibling group can be influenced by environmental effects, density-dependent compensation, and a sibling-group-specific deviation from mean recruitment rate (Eq. 1; Figure 2.1). Sibling-group-specific deviations follow a normal distribution with a variance parameter representing the magnitude of among-sibling group variation in recruitment rate (Eq. 2).

$$log_e(a_{g,h}) = log_e(a + X_h \cdot a_{env} + D_h \cdot a_{dd} + e_a) \ (1)$$

$$e_a \sim Normal(0, \sigma_a) \ (2)$$

Recruitment rate of sibling group g spawned in habitat patch h ($a_{g,h}$) on a log_e scale equals the sum of the mean recruitment rate a and deviations from the mean stemming from environmental effects, density-dependent compensation (product of spawning density in habitat patch h D_h and the per unit change in recruitment due to compensation a_{dd}), and random error e_a. Index g ranges from 1 to the number of sibling groups detected in the dataset N_{obs}, whereas h ranges from 1 to the number of habitat patches in the metapopulation.
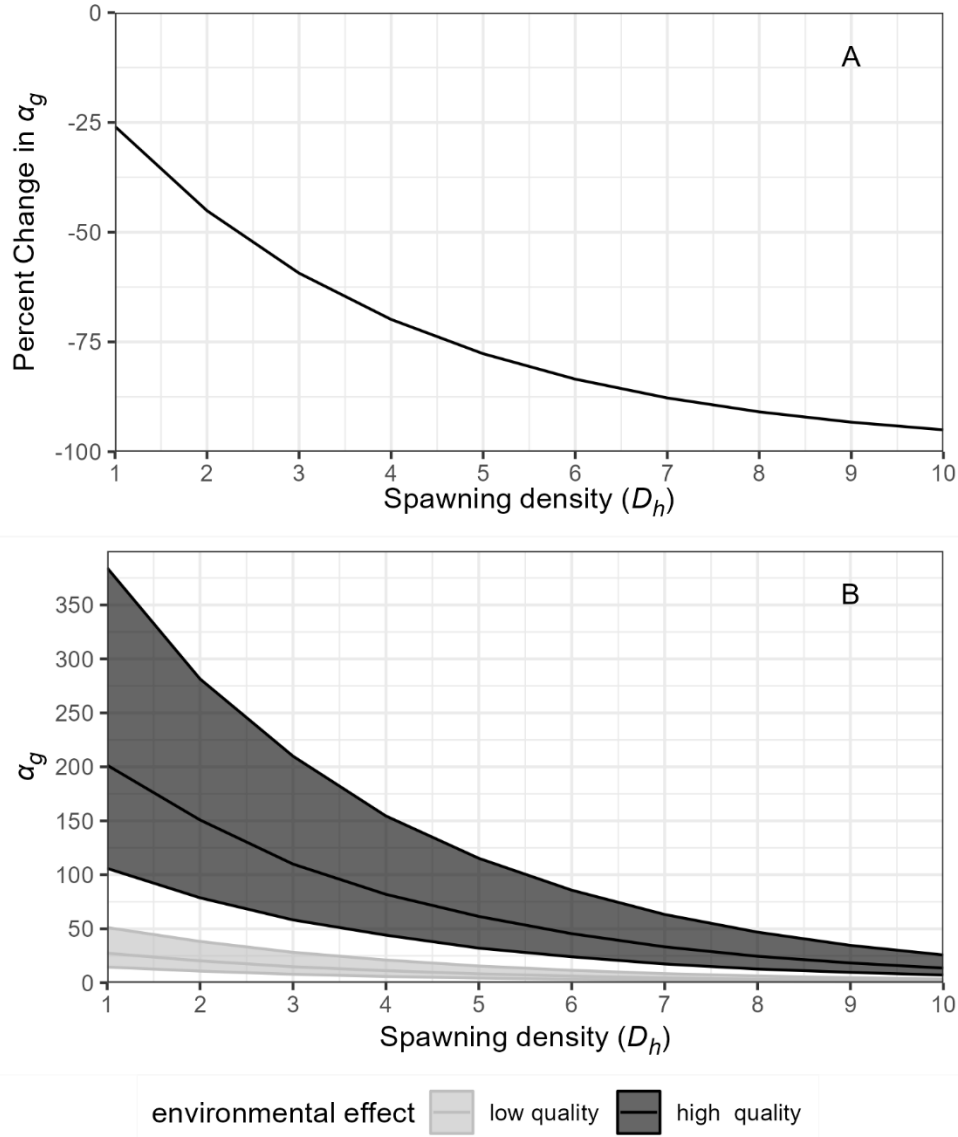
Figure 2.1. Schematic of mechanisms influencing sibling group size (a_g). As spawning density (D_h) increases, density dependent compensation results in declining sibling group size (panel A; curve depicted a_{dd}=-0.3). In addition to density dependent compensation, sibling group size depends upon average sibling group size, environmental conditions in the spawning patch and process error (panel B; median, 10th quantile, and 90th quantile of a_g depicted for exp(a)=100, σ_a=0.5, a_{env}=1, $X_{h=low\ quality}$=-1, and $X_{h=high\ quality}$=1).

We assume that spawning and recruitment occur spatially over a set of discrete, non-overlapping habitat patches. We represent the spatial aspect of recruitment through a multinomial probability distribution where the probability of sibling group g spawning in patch h $s_{g,h}$ is bounded between 0 and 1 and the sum of $s_{g,h}$ values across all habitat patches equals one.

Expected spawning density is solely based on the number of sibling groups observed and will tend to underestimate the true spawning density when sibling groups present in the metapopulation are not sampled. Expected spawning density in habitat patch h (D_h) with area A_h is equal to the sum of $s_{g,h}$ values across all sibling groups multiplied by a constant C_g related to how spawner density is characterized (Eq. 3). Two approaches are considered for characterizing the constant in the spawning density numerator: 1) the number of unique parental parings in a habitat patch, or 2) the number of unique parents that contribute to recruitment in a habitat patch. In applications where sibling groups are defined as full siblings, this constant will be the same for every sibling group and can be dropped from the equation.

$$E(D_h) = \frac{\sum_g s_{g,h} \cdot C_g}{A_h} \quad (3)$$

Metapopulation spatial network structure can be seamlessly represented within the continuous-time multistate modeling framework. Habitat patches are discrete states in the model and instantaneous transition rates q represent movement among connected habitat patches. Survival dynamics are modeled as one-way transitions from geographic states into absorbing mortality states. Survival can be represented as homogenous throughout the metapopulation or allowed to vary spatially among habitat patches. Multiple absorbing mortality states can be included to represent multiple mortality sources and/or life-stage transitions resulting in emigration from the sampled metapopulation (e.g., smolting). Movement and survival dynamics are represented mathematically as a matrix of transition rates among states (both geographic and mortality states). The transition intensity matrix Q includes all allowable state transitions, with the diagonal elements of Q equal to the negative sum of all transitions out of a given state, such that each row of the matrix sums to one. Instantaneous transition intensities can vary spatially, temporally, and with age. Covariates on transition intensities (hazards) can be modeled using proportional intensities (Jackson, 2011). Using this approach, baseline rate q is replaced with $q(z)$, the baseline line rate multiplied by vectors of explanatory variables z and covariates X (Eq. 4).

$$q_{j,k}(z) = q_{j,k} \cdot \exp\left(\sum X_i \cdot z_i\right) \quad (4)$$

Assuming constant state transition rates, the exponential of a matrix containing all possible state transitions provides a generalizable method to calculate the probability of movement among states after a given timestep. Time- and age-varying state transition rates can

be accommodated by relaxing the constant transition rate assumption to piece-wise constant and recursively modeling each timestep (Jackson and others, 2011). The transition probability matrix for timestep Δt_i is calculated as $\mathbf{P_i} = \exp(\mathbf{Q}\,\Delta t_i)$. Elements of $\mathbf{P_i}$ $p_{j,k}$ correspond to the probability of moving from j to state k during time interval i. These state transitions include all geographic state transitions and transitions into absorbing mortality states. Mortality that occurs between hatch (t_0) and the initial sampling time (t_1) is confounded with abundance at t_0. Accordingly, the transition matrix for the initial timestep from t_0 to t_1 (Δt_1) in our baseline model only includes dispersal, but mortality could be included if auxiliary information on survival during Δt_1 is available (resulting in sibling-group recruitment a being defined as abundance at hatch rather than abundance at the time of the first sample).

The expected distribution and abundance of individuals from a sibling group can be calculated from the transition probability matrix and recruitment model. These dynamics can be written as a discrete-time difference equation (Eq. 5).

$$
n_{t,g,h'} = \begin{cases} \displaystyle\sum_h a_g \cdot p_{h,h'} \cdot s_{g,h} & if\ t = 1 \\ \displaystyle\sum_h n_{t-1,g,h} \cdot p_{h,h'} & if\ t > 1 \end{cases} \tag{5}
$$

At the initial sampling time, the number of individuals from sibling group g in habitat patch h is calculated from the sum of a vector of products that combines elements from the recruitment model and transition probability matrix. Elements of the vector are equal to the product of the sibling group abundance a_g, the probability of moving from habitat patch h to h' (h' indexes all habitat patches in the same fashion as h), and the probability of spawning in habitat patch h. In cases where all spawning occurs in a single habitat patch, this collapses to a_g multiplied by the probability of moving from the spawning habitat patch to habitat patch h'. For subsequent timesteps, the process is similar except the abundance multiplier is the number of individuals in habitat patch h at $t\text{-}1$ rather than the number of age-t recruits.

The discrete-time difference equation (Eq. 5) takes into account losses due to mortality as sibling groups age. The sum of transition probabilities among geographic states $\sum_{h'} p_{h,h'}$ is equal to the discrete-time survival probability over timestep i. Exponential mortality is modeled with a single instantaneous transition rate (M) linking each habitat patch to an absorbing mortality state such that $exp(-M) = \sum_h p_{h,h'}$. For the general case, allowing for spatially heterogenous transitions into one or more absorbing mortality or permanent emigration states, expected

number of individuals entering a given absorbing state can be tracked in a similar fashion as in Equation 5 by replacing movement probabilities among geographic states with the set of probabilities representing transition probabilities from each geographic state to the absorbing state of interest.

Equation 5 relates the expected number of siblings in a given habitat patch to a recruitment event. For wild fish populations, abundance estimation methods are applied to estimate habitat patch abundance because the number of individuals in a habitat patch is not directly observed. Two commonly used methods of abundance estimation are 1) convert the number of individuals captured within a targeted sampling area to a density estimate by accounting for imperfect detection probability; and 2) use area expansion methods to extrapolate habitat patch abundance from localized density. Imperfect detection probability can be accounted for by estimating capture probabilities directly (e.g., mark-recapture methods, multi-pass depletion sampling) or applying standardized single-pass survey methods with prior information on the expected capture efficiency. Additionally, given that the expected detection probability p_{int} is an estimated quantity it will deviate from the true value by an unknown amount p_{dev} (Eq. 6). We modeled p_{dev} explicitly to account for how the expected deviation from the out-of-model estimate of detection probability for a given sample is expected to influence the capture probability of each sibling group present in the sampled habitat patch in the same fashion.

$$p_i = logit(p_{int} + p_{dev,i})^{-1} \quad (6.1)$$

$$p_{dev} \sim Normal(0, \sigma_p) \quad (6.2)$$

Area expansion methods rely on the assumption of a well-mixed population within each habitat patch. A simple approach to estimating habitat patch abundance n_h using area expansion is to divide the localized abundance estimate for the sampled area n_s by the proportion of the habitat patch that was sampled v_s (Eq. 7).

$$n_h = \frac{n_s}{v_s} \quad (7)$$

An observation model (Eq. 8) for the expected number of individuals from a given sibling group captured in a given sample ties together the metapopulation dynamics model Eq.5 and the abundance estimation methodologies adopted to relate catch survey data to habitat patch abundance.

$$\widehat{n_{t,g,h,i}} \sim Poisson(n_{t,g,h} \cdot p_i \cdot v_s) \quad (8)$$

Catch of age t individuals from family group g in habitat patch h in sample i is a Poisson distributed random variable with λ equal to the product of the expected number of individuals in the habitat patch ($n_{t,g,h}$), the detection probability of sample i (p_i), and the proportion of the habitat patch h sampled by sample i (v_s).

A derived parameter of interest is the expected probability of observing a sibling group (p_g). This derived parameter estimate can be used to approximate the total number of sibling groups present in the metapopulation. The probability of observing a sibling group p_g is equal to the inverse of the probability of observing a zero catch in every sample targeting the sibling group, given the expected catch rate (Eq. 9).

$$p_g = 1 - \prod dpois(0|n_{t,g,h} \cdot p_i \cdot v_s) \quad (9)$$

An observation of an individual sibling group can be adjusted to an estimate of available sibling groups as $\frac{1}{p_g}$ and the total number of sibling groups in the metapopulation $\widetilde{N_g}$ can be estimated as

$$\widetilde{N_g} = \sum_{N_{obs}} \frac{1}{p_g} \quad (10)$$

We expect the proposed modeling framework to provide accurate estimates of the total number of sibling groups in the metapopulation when 1) the recruitment model and transition probability matrix are well estimated such that Eq. 9 provides an accurate estimate of the detectability of each observed sibling group, 2) discrepancies between estimated and actual sibling group detectability caused by differences in the observed and actual spawning density are negligible, and 3) average spatial spawning distribution of the observed sibling groups is representative of the unobserved sibling groups.

Parameter Estimation

Parameter estimation in a Bayesian framework consists of capture data (observed catch by sibling group and associated indices for sample, habitat, patch, and age) and environmental covariates hypothesized to influence metapopulation dynamics or sampling processes (static or time varying, measured at the habitat patch scale), the model likelihood (Eq. 8), prior distributions on metapopulation dynamics and observation process parameters, and a Markov Chain Monte Carlo (MCMC) sampler. Capture data can be formatted as a table with columns for sample identification, age, sibling group identification, and the number of individuals captured, with rows corresponding to the aggregated catch of a sibling group in a given sample. Sample

metadata can be formatted as a table with columns for sample identification, habitat patch identification, date of sample, proportion of habitat patch sampled, and estimated detection probability. A data processing step is required to add zero-catch rows to the capture data table to reflect no catch of a sibling group in a survey (for analyses tracking multiple cohorts, zero catches for a given family group are only added for samples that occur after the family group reaches recruitment age).

Simulations to Evaluate Accuracy and Precision

We simulated recruitment dynamics for a hypothetical metapopulation with ten habitat patches arranged in a circular pattern with bidirectional dispersal between adjacent habitat patches (Figure 2.2, Panel A). Heterogeneous environmental conditions were included by randomly assigning an environmental covariate to each habitat patch. For each simulation, environmental covariates were sampled from a uniform distribution then scaled and centered to maintain a similar environmental gradient among simulations. Sibling group abundances (on a $\log_e$ scale) were randomly sampled from a normal distribution a_g~Normal(a, a_{sd}). We note that by simulating from a lognormal distribution centered on a with standard deviation a_{sd} the expected mean sibling group size on the natural scale becomes $exp(a - 0.5a_{sd}^2)$. Spawning habitat patch locations were simulated as a multinoulli random draw with uniform spawning probability across all habitat patches (biologically representing a scenario where each sibling group spawns in a single habitat patch). The simulated number of sibling groups spawning in a given habitat patch was used to calculate D_h. Realized sibling group abundance for sibling group g spawning in habitat patch h $a_{g,h}$ was simulated by adding density-dependent and environmental effects associated with X_h and D_h to a_g. The transition intensity matrix $\boldsymbol{Q}$ was parameterized with a single movement rate for movement among habitat patches ($q=0.3$) and exponential mortality ($M=0.2$). Dispersal from spawning patch locations was simulated as random draws from a multinomial probability distribution ($n = a_g$) consisting of the transition probabilities away from the spawning habitat patch (Eq. 5).

We simulated datasets where only sibling groups detected at age-1 were included in the analysis (sibling groups first detected at age-2 or age-3 were omitted from simulated datasets). This mimics a scenario that uses length-based ageing to assign age at age-1, but the method becomes unreliable for older age classes. Age-1 sibling groups captured at *t1* were monitored during sampling events *t1, t2* and *t3*; age-1 sibling groups detected at *t2* were monitored during

t2 and *t3*; and age-1 sibling groups captured at *t3* were only monitored once at *t3*. Dispersal and mortality after *t1* were modeled by recursively applying Eq. 5 and iterating through each habitat patch and family group. For each year of sampling, sampling processes (Figure 2.2, Panel B) included randomly selecting *H* habitat patches to sample, subsampling within habitat patches, and modeling error in the out-of-model estimate of capture probability p_{int}. The capture probability for sample *i* was simulated as a random deviation from p_{int}.
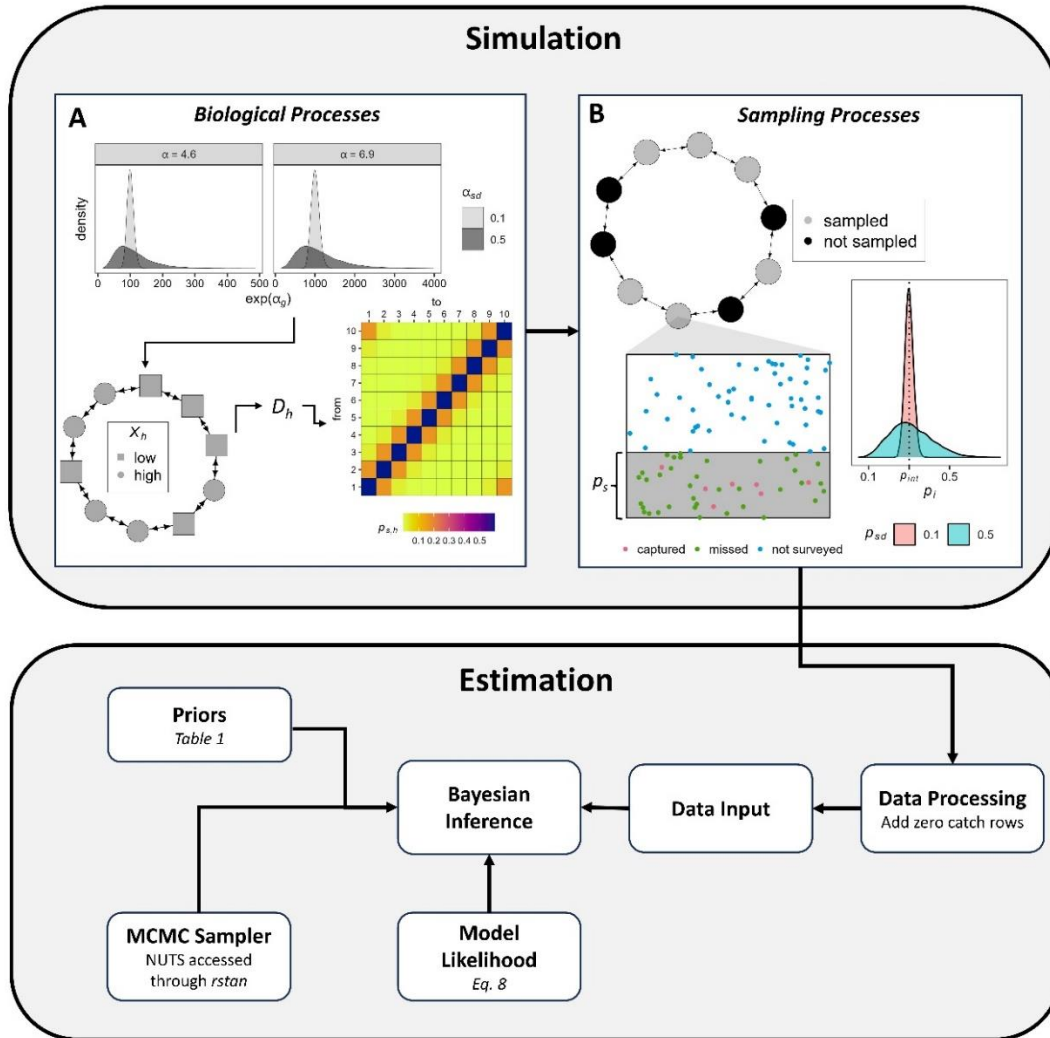
Figure 2.2. Flowchart of the simulation-estimation study. Biological processes simulated include sibling group abundance and dispersal (panel A). Sibling-group-level variation in abundance is simulated by random draws from Normal(a_g, a_{sd}). Realized sibling group abundance also depends upon environmental characteristics X_h and the sibling group density of the spawning habitat patch D_h. Dispersal during the time between hatch and sampling is modeled as a

Figure 2.2 (cont'd)

multinomial with probabilities taken from the corresponding row of $\boldsymbol{P_1}$ (the to-from matrix). Sampling processes simulated include random selection of habitat patches to sample, subsampling within habitat patches (with the proportion of the habitat patch sampled $= p_s$), and error in the out-of-model estimate of capture probability p_{int} (B). The capture probability for sample i was simulated as a random deviation from p_{int}. Simulated datasets are processed by adding zero catch rows to reflect that every observed sibling group could have been captured in each sample. Bayesian inference proceeds using the simulated data input, the model likelihood derived in the *Data Generating Processes* section and summarized by Equation 5, the NUTS sampler implemented in Stan, and prior distributions specified in Table 2.1.

Table 2.1. Symbols and descriptions of simulation-estimation study simulation specifications and model parameters. Prior distributions are provided for estimation model parameters. Multiple model values are included for the sampling processes (number of samples, capture probability estimation error, and proportion of habitat sampled) and biological processes (mean recruitment rate) that were evaluated at multiple values in the simulation-estimation study.

Symbol	Description	Simulation model values	Estimation model priors/fixed values
	Simulation Specifications		
-	The number of habitat patches in the metapopulation	10	-
-	Number of years sampled	3	
N_g	The number of sibling groups present in the metapopulation during sample years	120 (40 per year)	-
H	The number of habitat patches randomly sampled (without replacement).	5, 10	-
A	Habitat patch area (all patches set to the same value)	1	-
	Metapopulation Processes		
$s_{g,h}$	The probability of sibling group g spawning in habitat patch h. The set of spawning probability parameters for each sibling group is transformed to a multinomial by dividing each value of $s_{g,h}$ by $\sum_{i=1}^{n_{patch}} s_{g,i}$. The number of estimated parameters equals $n_g*(1-n_h)$	0.1	$\log_e(s_{h,g}) \sim \text{Normal}(0, 10)$
q	Annual instantaneous among-patch dispersal rate.	0.3	$q \sim \text{Uniform}(0,10)$
a	Average number of age-t_1 individuals produced per sibling group.	100	$\log_e(a) \sim \text{Normal}(\log_e(100), 5)$
		500	$\log_e(a) \sim \text{Normal}(\log_e(500), 5)$
e_a	Deviation from the average recruitment rate for family group g	$e_a \sim \text{Normal}(0, \sigma_a)$	$e_a \sim \text{Normal}(0, \widehat{\sigma_a})$
σ_a	Variance term for the distribution of e_a	0.5	$\sigma_a \sim \text{Half-Normal}(0.5, 2)$
a_{env}	Effect of habitat covariate X_h on a	0.5	$a_{env} \sim \text{Normal}(0.5, 2)$
a_{dd}	Effect of sibling group spawning density (number of sibling-groups spawning per habitat patch, D_h) on a	-0.3	$a_{dd} \sim \text{Normal}(-0.3, 2)$
M	Annual instantaneous mortality rate	0.2	$M \sim \text{Uniform}(0,5)$
	Sampling Processes		
p_{int}	Estimated capture probability from out-of-model estimate	0.3	Fixed at the true value
p_{dev}	Deviation from p_{int} on the logit scale	$\text{logit}(p_{dev}) \sim \text{Normal}(0, \sigma_p)$	$\text{logit}(p_{dev}) \sim \text{Normal}(0, \widehat{\sigma_p}))$
σ_p	Variance term for the distribution of p_{dev}	0.1	$\sigma_p \sim \text{Half-Normal}(0.1, 1.0)$
		0.5	$\sigma_p \sim \text{Half-Normal}(0.5, 1.0)$
v	Percentage of habitat patch area sampled	0.50, 1.0	Fixed at the true value
N_{obs}	Detected number of sibling groups in the metapopulation	Outcome of sampling process simulation	-
$\tilde{N}_g$	Estimated number of sibling groups in the metapopulation	Derived parameter	-

We were interested in determining how sampling processes influenced estimation of recruitment dynamics and if the relationship depended upon the average sibling group size of the sampled fish metapopulation. For this objective, we evaluated 12 scenarios with varying levels of sampling intensity (H=5 or H=10), proportion of habitat patch sampled (v=0.50 or v=1.0), level of out-of-model capture probability estimation error (p_{sd}=0.1 or p_{sd}=0.5), and average sibling group size (a=100 or a=500). Additionally, we investigated the performance of the estimator for $\tilde{N}_g$ (Eq. 10). We simulated single-year datasets with low sampling effort (5 habitat patches and v=0.5) at a range of mean sibling group sizes (a_g=50, 100, 150, 200, 250, 300).

Lower sampling effort and sibling group sizes were simulated because we were interested in measuring the relative error in $\tilde{N}_g$ as the proportion of family groups observed N_{obs} declined. All other parameters were kept the same as in the main simulation-estimation study.

We used a low information prior for spawning probability location $s_{g,h}$, representing a scenario with no prior information on spawning location. In practice, informative priors could be placed on $s_{g,h}$ if the spawning requirements of the modeled species were well-understood (e.g., need for pea sized gravel for redd construction) and relevant habitat data were available. We applied a uniform prior on dispersal rate q and mortality rate M with a lower bound of 0 (because the exponential distribution does not support negative numbers) and an upper bound where further increases would lead to negligible changes in detectable outcomes. At $q=10$ the metapopulation is panmictic with uniform distribution among habitat patches expected after each time step and at $M=5$ annual mortality approaches 100%. All other parameters were assigned normal priors with means centered on the true simulated value and a large variance (Table 2.1).

Bayesian parameter estimation was undertaken with the MCMC sampler implemented in Stan and accessed through the *rstan* package (Stan Development Team, 2023) for R (R Core Team, 2023). Each model was run with four MCMC chains, 3000 warmup iterations, 2000 sampling iterations, adapt-delta set to 0.99, and max tree depth set to 13. We used diagnostics reported by *rstan* to designate MCMC model runs that were sampling from the posterior and had sufficient iterations to reliably characterize parameter mean and variance. We flagged MCMC estimation implementations with model parameter $\hat{R}>1.02$, effective sample sizes less than 100 per chain, and any divergent transitions or transitions in which the maximum tree depth was exceeded. MCMC implementation that passed all of these checks were considered successful model runs. Posterior distributions from the successful model runs were summarized to evaluate parameter estimation statistics.

Estimation results were evaluated based on measures of accuracy (relative error) and precision (relative 80% credible interval width).

$$Relative\ error = \frac{100[\hat{\theta} - \theta]}{\theta}$$

$$Relative\ 80\%\ CI\ width = 100\left[\sqrt{\left(\frac{\hat{\theta}_{90} - \hat{\theta}_{10}}{\hat{\theta}}\right)^2}\right]$$

where $\hat{\theta}$ is the mean of the posterior distribution, $\hat{\theta}_{10}$ and $\hat{\theta}_{90}$ are the 10th and 90th percentiles of

the posterior distribution, and θ is the true simulation parameter value used in the simulation study. We calculated metrics for each model run and graphically examined the summary statistics (mean, 10th, 25th, 50th, 75th, and 90th percentiles) to gauge the reliability of our model and characterize how the accuracy and precision of parameter estimates varied among simulation scenarios.

Results

We repeated simulations until at least 50 iterations for each evaluated scenario passed all convergence checks. Overall, 72% of the iterations passed convergence checks. Models failed checks due to $\hat{R}$ values greater than 1.02 and/or effective sample size (ESS) less than 400. In our simulated datasets, the average number of siblings detected per family group varied at different levels of mean sibling group size and as sampling intensity increased (either sampling more habitat patches or moving from 0.5 to 1.0 proportion of habitat patches sampled) (Figure 2.3). Increased variance in capture probability (σ_p) had little effect on the average number of individuals captured per sibling group.
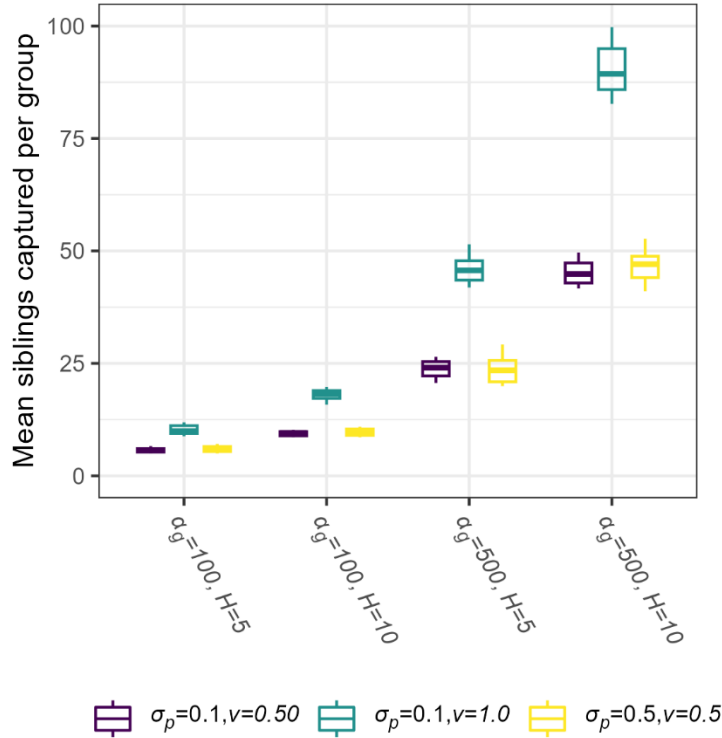
Figure 2.3. Mean number of siblings captured per family group in each simulation scenario. Simulation-estimation scenarios varied according to the number of habitat patches sampled (H=5 or H=10; x-axis), mean sibling group size (a_g=100 or a_g=500; x-axis), among-sample variability in capture probability (σ_p=0.1 or σ_p=0.5; plot legend), and proportion of habitat patch sampled (v=0.5 or v=1.0; plot legend). Boxplots show the 10th, 25th, 50th, 75th, and 90th quantiles of $\geq$50 simulation-estimation iterations per scenario.

Simulation results indicated the modeling framework reliably estimated recruitment, mortality, and dispersal parameters, though some parameters were well estimated across all scenarios tested and others were only estimated with high accuracy in scenarios with high sampling effort and/or large sibling group size (Figure 2.4). Mean relative error of mean sibling group size (a), environmental effects on sibling group size (a_{env}), and dispersal rate (q) were estimated with high accuracy across all scenarios (mean relative error less than 6%). The strength of density-dependence was underestimated in all scenarios but not by a large degree (positive relative error ranging from 6% to 13%). While increased sampling effort and larger sibling group size reduced the spread of simulation results, there was not a strong effect of these variables on mean density-dependence estimate relative error. Recruitment process error σ_a tended to be estimated as smaller than the true value (negative relative error) but scenarios with

increased sampling effort tended to have a relative error closer to zero. Sibling group size also influenced the reliability of σ_a; accuracy for low sibling group size scenarios (a_g=100) was highly dependent upon sampling effort (mean relative error of -40% with v=0.5 and H=5 versus mean relative error of -7% with v=1.0 and H=10). Accuracy was high across all scenarios with a_g=500 (largest mean relative error for all a_g scenarios was -8%). Accuracy of exponential mortality (M) estimates also varied substantially among scenarios. Estimates were reasonably unbiased (mean relative error range of 8% to -9%) in all scenarios except for the two scenarios with low sampling effort (H=5 and v=0.50) and a_g=100. Mean relative error for these two scenarios was >30%. Finally, increasing the among-sample variability in detection probability from σ_a=0.1 to σ_a=0.5 had negligible effects on parameter estimation accuracy. Each scenario with σ_a=0.5 had similar mean relative error as its corresponding scenario with lower observation error.
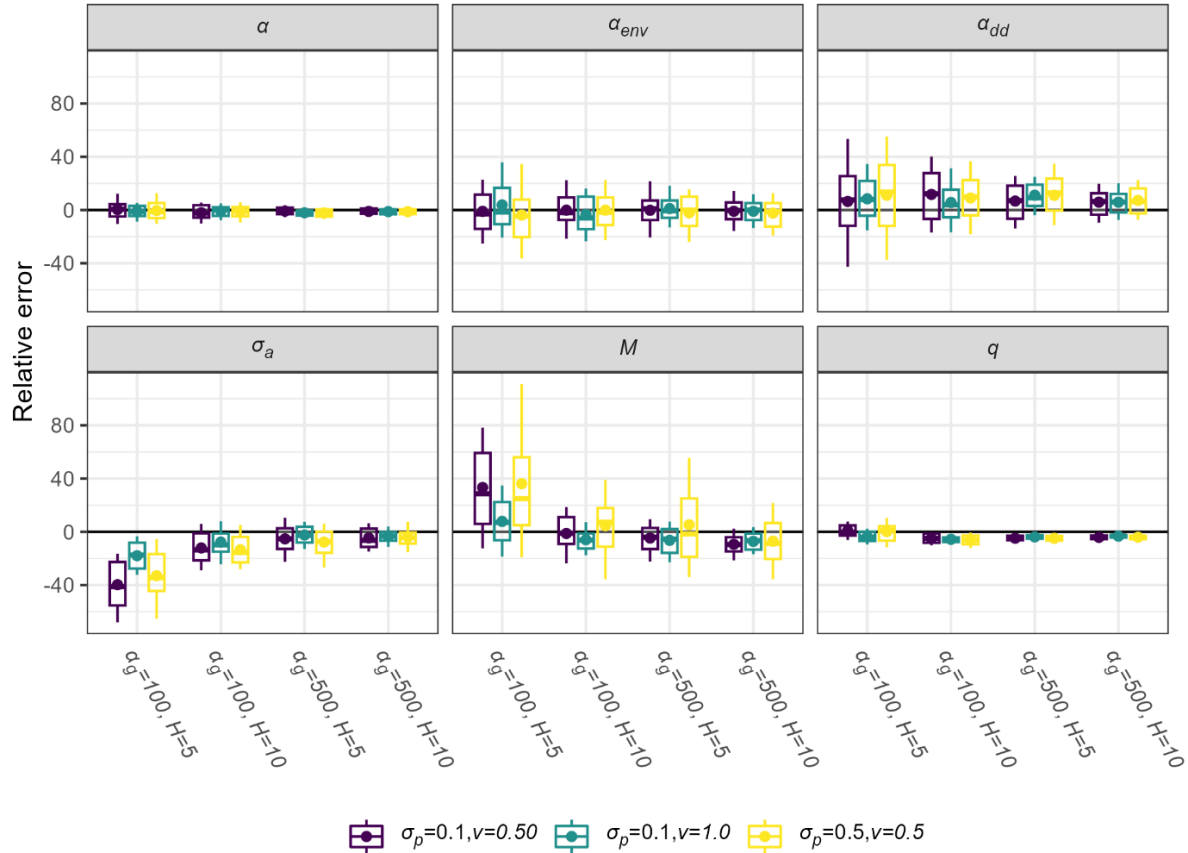
Figure 2.4. Relative error for recruitment parameters (a=mean sibling group size, a_{env}=environmental effects on sibling group size, a_{dd}=density-dependent effects on sibling group size, σ_a=process error for among sibling group size variability), exponential mortality rate (M), and dispersal rate (q). Simulation-estimation scenarios varied according to the number of habitat patches sampled (H=5 or H=10; x-axis), mean sibling group size (a_g=100 or a_g=500; x-axis), among-sample variability in capture probability variability (σ_p=0.1 or σ_p=0.5; plot legend), and proportion of habitat patch sampled (v=0.5 or v=1.0; plot legend). Points show the mean of ≥50 simulation-estimation iterations and boxplots show the 10th, 25th, 50th, 75th, and 90th quantiles.

Across all scenarios, mean sibling group size and dispersal rate tended to be estimated with higher precision than the other recruitment parameters and exponential mortality, but precision was influenced by each of the sampling variables we investigated and sibling group size (Figure 2.5). Increased sibling group size, number of habitat patches sampled, and proportion of habitat patches sampled resulted in increased precision (narrower 80% credible intervals). Increasing sampling error σ_p caused precision to decline, but this effect was negligible for some parameters (a, σ_a, and q) and most pronounced for a_{env} and M. Reduction in the

precision for M was most pronounced for the large sibling group simulation (a_g=500) with H=10; increasing σ_p from 0.1 to 0.5 resulted in a more than a doubling of the mean 80% credible interval width.
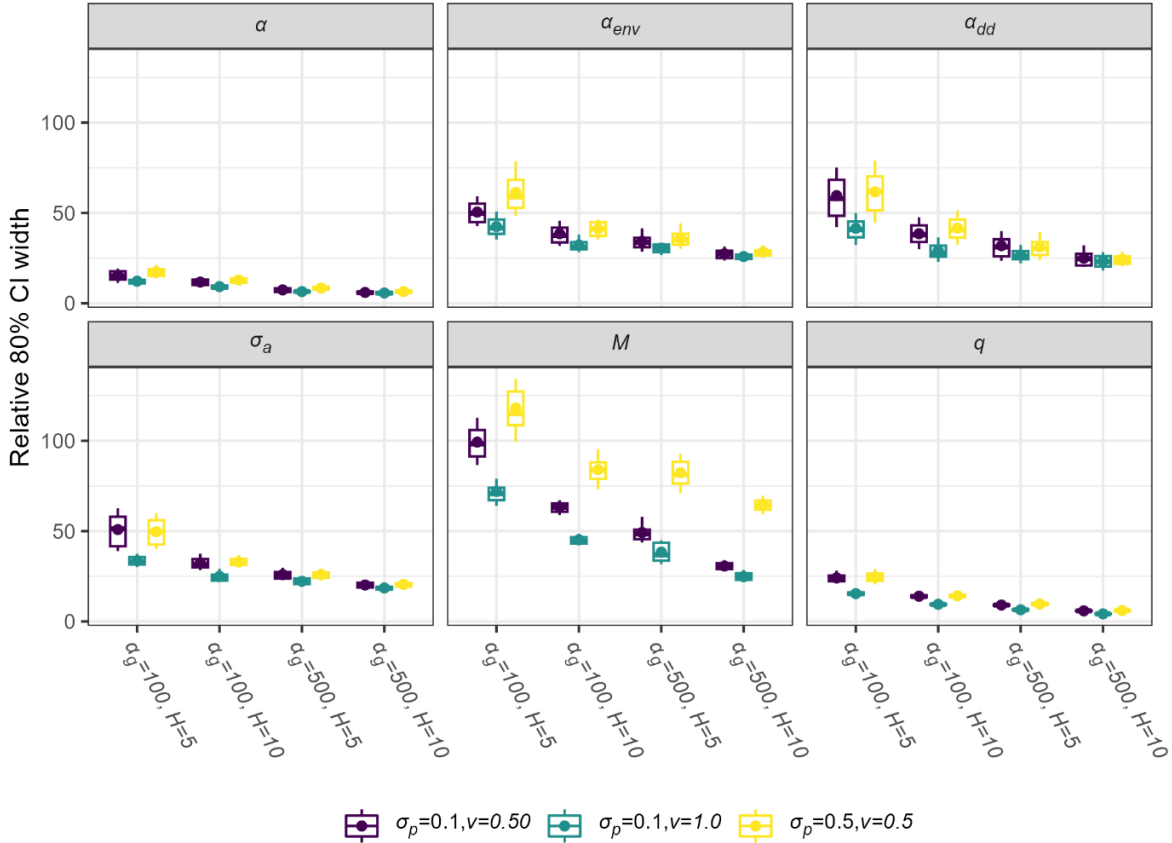
Figure 2.5. Relative 80% credible interval (CI) width for recruitment parameters (a=mean sibling group size, a_{env}=environmental effects on sibling group size, a_{dd}=density-dependent effects on sibling group size, σ_a=process error for among sibling group size variability), exponential mortality rate (M), and dispersal rate (q). Simulation-estimation scenarios varied according to the number of habitat patches sampled (H=5 or H=10; x-axis), mean sibling group size (a_g=100 or a_g=500; x-axis), among-sample variability in capture probability variability (σ_p=0.1 or σ_p=0.5; plot legend), and proportion of habitat patch sampled (v=0.5 or v=1.0; plot legend). Points show the mean of $\geq$50 simulation-estimation iterations and boxplots show the 10th, 25th, 50th, 75th, and 90th quantiles.

Mean estimated number of sibling groups $\tilde{N}_g$ in the simulated metapopulation reached an asymptote at the true value (40 sibling groups) as mean sibling group size increased beyond 100, but the estimator tended to underestimate the true value at low sibling group sizes (a_g=50 and

100) (Figure 2.6). Observed number of sibling groups in simulated datasets increased as sibling group size increased but was an underestimate of the true value at all values of a_g.
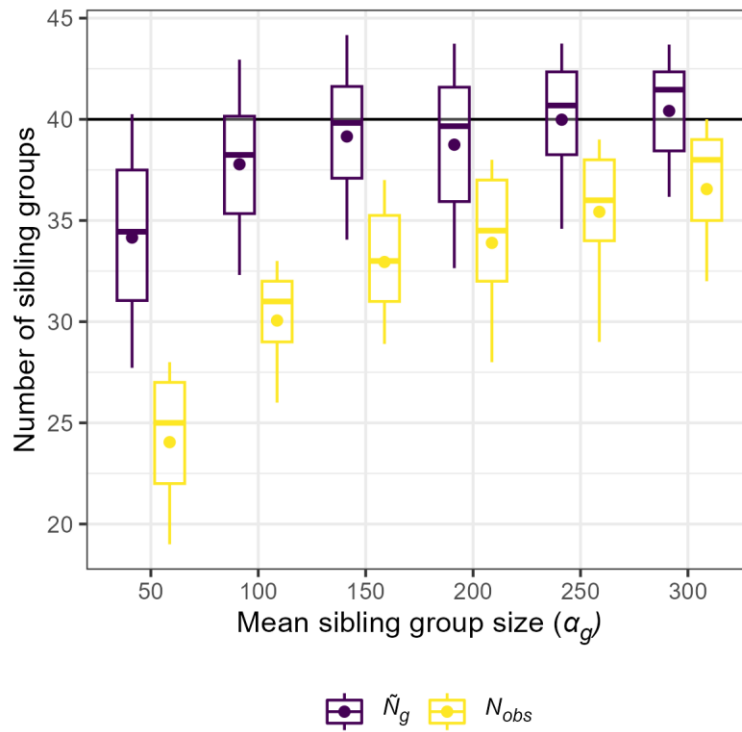
Figure 2.6. Number of sibling groups observed in simulated datasets (N_{obs}) and estimated ($\tilde{N}_g$) for simulation scenarios with variable mean sibling group size (a_g). The true number of sibling groups in each simulation was 40 (horizontal line). Points show the mean of $\geq$50 simulation-estimation iterations and boxplots show the 10th, 25th, 50th, 75th, and 90th quantiles.

Discussion

We demonstrated a novel modeling framework for quantifying recruitment dynamics at the sibling-group scale. The framework is based on metapopulation theory and formulated using continuous-time multistate modeling. Using this framework, spatial recruitment models and transition probability matrices can be developed from empirical sibship data to suit a wide range of fisheries science and management predictive modeling applications. Results of our simulation study provide some initial insight on the data requirements for reliable parameter estimation. Intuitively, parameter estimation accuracy and precision tended to increase as sampling intensity increased. However, we found that relatively accurate parameter estimates could be obtained with sampling intensity constraints (not sampling all habitat patches in a metapopulation and/or subsampling available habitat within each patch) and accurate but imprecise estimates of capture

probability. This finding suggests that with well-conceived sampling design, reliable population-level inferences related to dispersal among habitat patches, size of sibling groups, and environmental and density-dependent effects on sibling group size are possible from sibship data.

Sampling effort and sibling group size had a strong influence on the accuracy of mortality and recruitment rate processes error estimates, but were less influential on mean recruitment rate, estimates of environmental and density-dependent effect size, and dispersal rate. Estimates of mortality were relatively unbiased for all but the most challenging simulation scenarios considered (i.e., low sampling effort and low mean sibling group size). Unreliable estimates may be due to increased noise caused by demographic stochasticity at lower sampling effort and low sibling group size; inferences about sibling group size at older age classes tended to be made from observations of only a few individuals. Further investigations into the constraints of reliably estimating mortality using this model framework are needed. We observed that recruitment rate process error σ_a tended to be underestimated and the degree of underestimation was higher when simulated datasets were less informative. This occurred because of the shrinkage effect of using hierarchical modeling to estimate processes error; estimated deviations from the average recruitment rate were expected to be pulled towards zero (compared to a model that estimated these deviations as a fixed effect) and the amount of shrinkage towards zero for a particular random deviate is expected in increase as information available to resolve it decreases (Gelman et al., 2013). Recruitment deviations with substantial shrinkage towards zero then result in underestimation of recruitment deviation process error σ_a. However, we expect that the shrinkage effect of the hierarchical approach will often be desirable for empirical datasets that contain asymmetrical amounts of data on individual sibling groups (some sibling group sizes that can be well estimated by the data and others that cannot). Notwithstanding, an alternative modeling approach (for scenarios in which a and σ_a are not directly of interest but a means to an end of estimating sibling group size a_g) would be to estimate sibling group size as a fixed effect. For empirical applications where the fixed effect model is considered, model selection approaches that compare expected log predictive density, such as the hold-one-out cross validation methods implemented in the *loo* package (Vehtari et al., 2017), could be used to assess the relative performance of hierarchical and non-hierarchal model approaches to estimating among sibling group variation.

Future research is needed to assess the effects of sibling group mis-assignment or omission on spatial recruitment dynamics inferences. We assumed that sibling groups were assigned without error and that every captured individual could be genotyped and assigned to a sibling group, but in practice these conditions may not be met. The reliability of sibship assignment depends upon the information content of the suite of genetic markers used to assign sibship (Baetscher et al., 2018; Sard et al., 2020). Pedigree reconstruction methods using full-pedigree likelihood methods (Jones and Wang, 2010) and likelihood ratio tests on putative pairs of related individuals require analysts to make decisions about reliability thresholds that balance the risk of including possibly unreliable sibship assignments versus the costs of omitting good data. Simulation studies that follow the pipeline of sibship-abundance estimation dataset construction– sampling processes used to capture individuals, expected levels of sibship assignment error given a set of genetic markers, pedigree reconstruction methods, reliability filtering thresholds, and statistical estimation of population dynamics parameters from the reliable subset of sibship data and the associated sampling metadata – would clarify downstream effects of sibship assignment error and reliability threshold decisions on inferences about spatial recruitment processes.

Review of empirical sibship data could inform simulation testing of our proposed modeling framework tailored to specific decision contexts and targeted fish populations. For example, we found that average sibling group size was an important population characteristic for predicting the quality of parameter estimation. Number of siblings captured, which can be directly observed and is reported in most applications of sibship analysis to fish populations, is related to this quantity through sampling processes. Consideration of the spatial extent of habitat expected to be accessible to observed sibling groups, the proportion of this habitat surveyed, and the detection probability of the survey gear provides a roadmap for back-of-the-napkin calculations of sibling group size based on observed number of siblings. Dispersal needs to be considered in these calculations and is another key demographic process to consider. Average dispersal rate, spatially variable dispersal associated with heterogenous environment, and density-dependent mechanisms all may influence dispersal and, collectively, predict which habitat patches are expected to be accessible for a given sibling group by way of distance-limited dispersal, spatially heterogenous physical processes such as oceanic currents, discrete barriers to dispersal in river network systems, and/or behavioral habitat selection preferences.

Application of this framework requires discrete-space representation of habitat. Both the decision context and dispersal characteristics may be informative for deciding upon the appropriate scale and zoning procedure for delineating habitat patches and thereby represent dispersal processes. For example, interpreting the effects of a culvert remediation could be influenced by the scale of habitat patch delineation relative to the scale of distance-limited dispersal. While the process of interest here is the discrete effect of the culvert on movement before and after remediation, distance-limited dispersal may be important to consider when interpreting cross-barrier transition probabilities. If distance-limited dispersal is not accounted for and sibling groups are sampled at locations where they have a reduced probability to encounter the barrier, inferences from a simple two habitat patch model (above barrier and below barrier) may conclude that the remediation had limited success at removing barriers to migration, even if passage was returned to stream-like conditions. A higher resolution model with multiple spatial states above and below the barrier could capture spatial patterning due to distance-limited dispersal and the presence of a discrete barrier to migration. This second version is analogous to the concept of isolating fishway entrance and passage probabilities from attraction probability when evaluating overall fish passage at barriers (Castro-Santos et al., 2009). In general, the ability to consider both discrete and distance-limited mechanisms of spatial structuring in the same analytical model is a strength of applying the metapopulation concept to ecological dispersal questions.

Empirical support for developing predictive metapopulation models is often limited (Botsford et al., 2009; Kritzer and Sale, 2004). We posit that combined sibship-abundance estimation datasets could further advance empirical support for predictive metapopulation models because the methodology has different strengths and constraints compared to methods using individual tagging and telemetry methods. Individual tagging and telemetry methods provide a wide range of approaches for quantifying movement and survival (Lucas and Baras, 2000; Pine et al., 2003; Thorstad et al., 2013), and international collaborations (Iverson et al., 2018) and innovations in technoscience (Cooke et al., 2022) are continuously advancing the potential of these methods. However, making inferences from tagged individuals requires both a statistically robust sample from the population of interest and careful management of tagging and handling effects. These requirements limit the usefulness of this method for studying fish species and/or life stages sensitive to tagging and handling. Previous applications of sibship analysis

applications demonstrate the usefulness of the method for studying the movement of fishes at early life stages (e.g., Hessenauer et al., 2012), where individual tagging approaches would have had limited efficacy. We demonstrated that sibship analysis data can be used to estimate survival in a similar fashion as individual tagging datasets when the sampling processes and/or prior information facilitate abundance estimation. Finally, longitudinally sampling sibling groups may be particularly useful for applications where ageing approaches based on counting annuli on hard parts are costly or unreliable. Initial age of a sibling group can be assigned during an early life stage (when length can be used as a reliable indicator of age) and this age assignment can be caried on to individuals captured thereafter (when length-based age assessment would not be feasible).

The sibling group scale is an information rich and biologically realistic lens to study recruitment. As the power and feasibility of reconstructing pedigrees of wild populations from genetic markers continues to increase (Anderson and Garza, 2006; Baetscher et al., 2018), quantitative population dynamics models are needed to translate this information rich data source into empirical predictive models useful to policy makers, resource managers, and scientists. The metapopulation concept and continuous-time multistate modeling methods provide a theoretical and mathematical foundation for analysis of sibship data that encompasses both the dispersal and sibling group abundance aspects of sibship data. The utility of empirical quantitative models developed from combined sibship-abundance estimation datasets will be context specific. Simulation-based power analysis approaches (e.g., Perkins et al., 2021) may provide key insight into the expected efficacy of the method and could provide insight into best sampling practices for building integrated sibship-abundance estimation long term monitoring datasets that are well poised to reduce key uncertainties in spatial recruitment mechanisms of fish populations.

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CHAPTER 3. A COLLABORATIVE ADAPTIVE MANAGEMENT FRAMEWORK FOR SELECTION AND USE OF INVASIVE SPECIES CONTROL TACTICS

Abstract

A major aim of invasive species management is to enact Integrated Pest Management (IPM) principles. However, operationalizing IPM can be challenging due to ecological and values-driven uncertainties. We applied decision analysis to develop a collaborative adaptive management framework that enables effective consideration of the societal and environmental consequences of control tactic selection and use decisions for invasive sea lamprey (*Petromyzon marinus*) in North America's Laurentian Great Lakes. We developed a multi-level objective hierarchy that included both localized management and multi-stream coordination fundamental objectives, conducted a feasibility analysis that constrained alternatives to those with high probability of social acceptance and technical success, and quantified expected outcomes of alternatives in terms of multi-stream coordination objectives (minimize costs and maximize learning about efficacy of novel sea lamprey control strategies). Optimal deployment configurations for scenarios that favored maximize learning over minimize costs consisted of a more diverse portfolio of control tactics compared to scenarios that favored cost effectiveness, which demonstrates the sensitivity of sea lamprey control tactic selection and use decisions to values-driven uncertainty. Additionally, sensitivity analyses revealed that optimal deployment recommendations depended upon assumptions about social and technical feasibility. Iterative application of our collaborative adaptive management framework could support social learning and cross-scale linkages if ideas about multi-stream coordination and internal validity of invasive sea lamprey management practices can be exchanged in a trusting environment. Collaborative adaptive management frameworks capable of enabling such social learning may be broadly useful for operationalizing IPM in heterogeneous social-ecological landscapes.

Introduction

Adapting natural resource management practices to non-stationary, social-ecological system dynamics depends upon learning processes. Adaptive management with a plan for learning (active adaptive management) enables iterative updating of social-ecological system models through the synergistic integration of monitoring, collaboration, and deliberate management experimentation (Lee, 1993; Parma, 1998; Walters, 1986). However, implementing a deliberate management experiment is a complex, interdisciplinary endeavor (Endter-Wada et

al., 1998). Adaptive management learning plans consist of experimental replicates enacted sequentially in a particular experimental management unit (temporal replication) and/or multiple replicates enacted simultaneously (spatial replication) (Williams, 2011). Learning aims can span biological conservation, ecosystem management, and natural resource governance practices (Fabricius and Cundill, 2014), and the epistemology and values of those involved in decision processes influence learning objective development and evaluation of management practice suitability (McLain and Lee, 1996). Furthermore, dynamic tension may exist between adaptive management objectives focused on improving management practices through collaboration and social learning and those focused on enacting particular experimental designs to improve learning about system dynamics (Jacobson et al., 2009). Collaborative adaptive management frameworks can assist in navigating these complexities and tradeoffs (Scarlett, 2013). Collaborative decision-support frameworks additionally help practitioners move among decision analysis steps, decompose problems into key components, account for multiple objectives, foster group deliberation, and identify desirable action alternatives (Hemming et al., 2022). Application of collaborative adaptive management decision support frameworks may build capacity to confront complex natural resource management challenges and opportunities situated within social-ecological systems characterized by multiple, possibly conflicting, value systems and non-stationary dynamics.

Management decisions for invasive species often have high degrees of uncertainty, require consideration of conflicting values systems, and necessitate tradeoffs among multiple objectives. Integrated Pest Management (IPM), which is defined as "… a decision support system for the selection and use of pest control tactics, singly or harmoniously coordinated into a management strategy, based on cost/benefit analyses that take into account the interests of and impacts on producers, society, and the environment" (Kogan, 1998), provides conceptual clarity on how invasive and/or pest species management can operate despite these challenges and uncertainties. However, applying IPM in practice can be challenging. Basic understanding of the target populations' life history and ecology is a prerequisite to implementing IPM. Even when equipped with this understanding, however, institutional and communication constraints can limit effective consideration of the societal and environmental consequences of control tactic selection and use decisions (Arora and Dhawan, 2012).

Adaptive management has been suggested as a viable approach to overcoming barriers to

IPM implementation. Learning about how control tactic effectiveness interacts with the target species' life history dynamics and ecology can be advanced with successful execution of an adaptive management learning plan (Shea et al., 2002). Adaptive management can also build linkages among practitioners, decision makers, and resource users and enable informational feedback loops necessary for effective consideration of multi-faceted societal and environmental consequences of invasive species management decisions (Chaffin et al., 2016; DiTomaso et al., 2017). Collaborative adaptive management frameworks that mobilize Indigenous knowledge, mainstream Western science, and operational logistics may be particularly well-suited to invasive species management applications (Mason et al., 2021). Collaborative processes that allow for multiple ways of knowing to coexist and knowledge coproduction can enrich understanding of complex resource management problems or concerns (Reid et al., 2021; Tengö et al., 2014), such as how to manage invasive species (Nonkes et al., 2023).

The sea lamprey (*Petromyzon marinus*) is an invasive fish to the Laurentian Great Lakes of North America. Sea lamprey spread and establishment was facilitated by the construction of navigable canals in the late 1900s that bypassed natural barriers between the Atlantic Ocean and the Great Lakes basin (Docker et al., 2021). As larvae, sea lamprey live primarily burrowed in sediment for 2 or more years; individuals subsequently metamorphose and outmigrate to the Great Lakes where they reside as parasitic juveniles for 12 to 18 months (Applegate, 1950; Bergstedt and Swink, 1995). Semelparous adults return to tributaries to spawn but, lacking natal philopatry, redistribute widely among Great Lakes tributaries. These life history traits led to widespread production of parasitic juvenile sea lamprey in the mid 20th century, each capable of damaging valuable fishes by consuming approximately a kilogram of host-fish blood (Jorgensen and Kitchell, 2005; Madenjian et al., 2003). Prior to efforts to control their densities in the Great Lakes, sea lamprey parasitism contributed to significant abundance declines of native lake trout (*Salvelinus namaycush*) and *Coregonus* spp. populations and limited efficacy of fish stocking for native fish conservation and development of recreational salmonid fisheries (Dann and Schroeder, 2003; Muir et al., 2012).

A major aim of invasive sea lamprey management has been to enact IPM principles as part of the control program (Christie and Goddard, 2003; Sawyer, 1980). Supplementing existing sea lamprey control tactics (lampricide control and maintenance of barriers to block spawning migrations) with novel sea lamprey control tactics, including enhanced trapping, co-option or

disruption of the sea lamprey's chemosensory system, deployment of electric weirs and traps, and sterile male release technique, could increase capacity to do this (Siefkes et al., 2021). However, the effectiveness of these novel control tactics is uncertain and feedback loops linking learning about effectiveness of novel sea lamprey control tactics to management practice are not well developed. Adaptive management decision support frameworks could assist with overcoming these barriers.

We re-examined the prospects for implementing IPM principles in invasive sea lamprey management through the lens of adaptive management. Despite operationalizing IPM principles being a longstanding goal in the Great Lakes basin for sea lamprey control, existing ecological knowledge and management practices may be insufficient for effective consideration of the societal and environmental consequences of sea lamprey control tactic selection and use decisions. Notwithstanding this uncertainty, adaptive management decision support frameworks can offer a blueprint for decision making while progressing towards operationalization of IPM principles. Furthermore, adaptive management frameworks that consider both multi-system coordination and localized management objectives may be instrumental to learning about societal and environmental consequences of sea lamprey management actions throughout the Great Lakes basin, a heterogenous ecological and social landscape poorly suited to general-purpose management strategies. The multi-system coordination focal scale works to make sea lamprey control agents and partners, stakeholders, rightsholders, and decision makers aware of the possible benefits of coordinated collective action. The single-stream focal scale offers greater opportunity for mobilizing place-based and operational knowledge bases, but at the cost of supporting coordination among experimental units. Both of these functions are expected to enhance success of invasive species management; collective responses to invasive species management are enhanced when the benefits of coordinated actions are evident (Graham et al., 2019), and integrating operational knowledge systems with decision-making processes enables development of actionable invasive species management plans (Mason et al., 2021).

Our objective was to develop a collaborative adaptive management decision support framework for the selection and use of novel invasive sea lamprey control tactics. Decision analysis tools and theory were used to achieve this objective. We conclude by discussing how conceptual and practical outcomes of our decision analysis case study relates to the theory and practice of operationalizing IPM.

Methods

We applied decision analysis towards development of a collaborative adaptive management decision support framework. This decision analytic approach to adaptive management has been applied to natural resource management and conservation challenges (McFadden et al., 2011; Williams and Brown, 2016). Decision analysis breaks down complex decisions into key components (commonly represented with the PrOACT acronym): 1) collaboratively define the <u>pr</u>oblem, 2) identify <u>o</u>bjectives and ways to measure to what degree they have been met, 3) identify possible <u>a</u>lternative actions, 4) predict the <u>c</u>onsequences of each alternative action in terms of the objectives, and 5) make <u>t</u>radeoffs among objectives (Hammond et al., 2015). Our decision analysis consisted of convening multiple, collaborative workshops, developing models and quantitative tools, and synthesizing lessons learned from iterative facilitated discussions anchored around the PrOACT framework. Here, we describe key aspects of the decision context, provide detail on the methods we used to address each step in the PrOACT framework, provide the problem statement and objective hierarchy (*Methods*), and report on the outcomes of predicted consequences and evaluation of tradeoffs (*Results*).

Decision Context

A working group consisting of sea lamprey control agents and decision makers (hereafter the Core Group) was formed in 2019 to guide planning and implementation of an invasive sea lamprey management experiment. The motivation for conducting the management experiment was based in a renewed philosophy about supplemental sea lamprey control, which makes the case for integrating sea lamprey control tactics targeting adult and outmigrating juveniles with established control tools (lampricides and barriers) to build capacity for operationalizing IPM principles in sea lamprey management (Siefkes et al., 2021).

The first major decision was to select the streams in which to deploy and evaluate experimental sea lamprey management strategies. Decision theory was not explicitly referenced during the collaborative decision-making process that the Core Group used, but we apply terminology *post hoc* for clarity. Stream selection was treated as a classification problem; candidate experimental streams could be classified as *green* (definitely include), *yellow* (maybe include), or *red* (do not include). Stream characteristics were identified that would increase the chances of experimental sea lamprey management out-performing status quo lampricide management and limit chances of logistical challenges derailing effective monitoring and

experiment implementation. The identified stream characteristic objectives were 1) maximize consistency of larval sea lamprey production, 2) minimize lampricide treatment effectiveness, 3) minimize adult run size relative to larval habitat, 4) minimize distance from a sea lamprey control field station, 5) maximize opportunities for collaboration with local partners, and 6) maximize ability to effectively quantify larval densities with backpack electrofishing (Lewandoski et al., 2021). Considering these multiple objectives but without making explicit tradeoffs among them, a direct classification method was used to classify candidate streams. Candidate streams were selected for experimental deployments and evaluation (*n*=9) and the scope of the management experiment comprised these streams along with streams with existing experimental management deployments (*n*=4) (Figure 3.1).
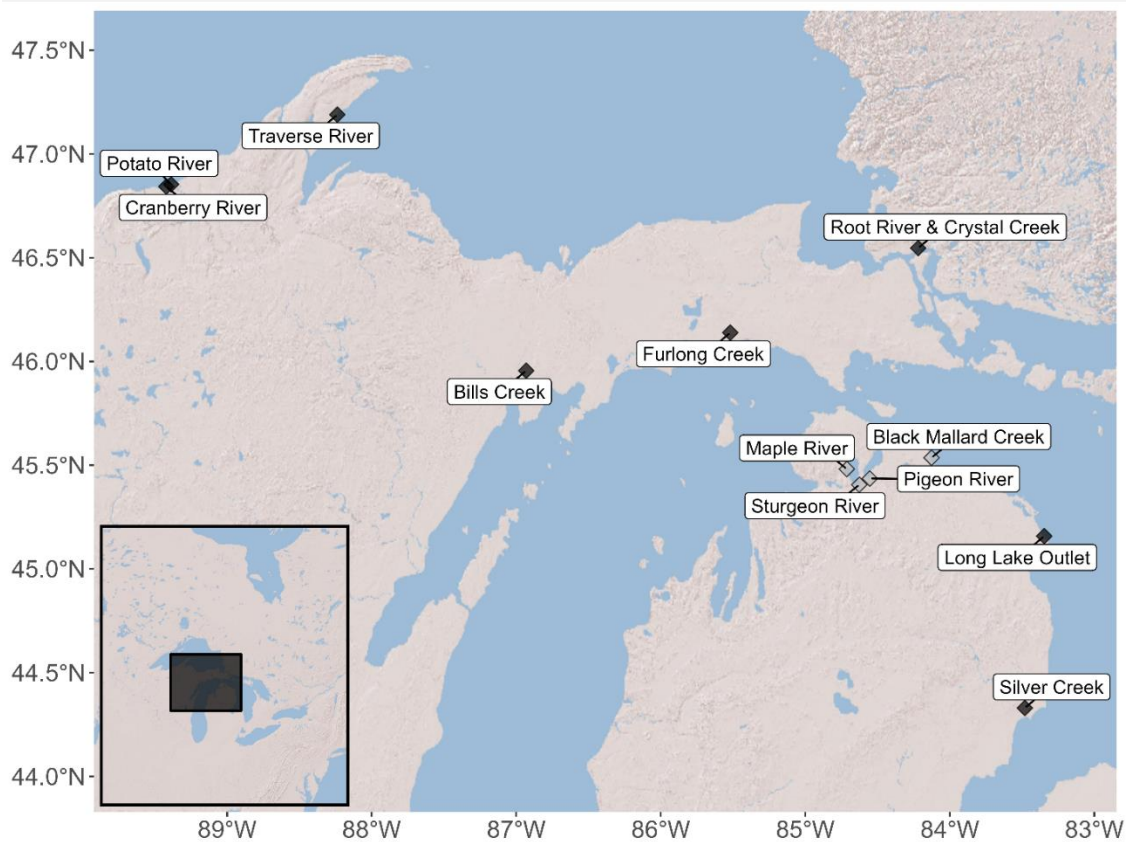
Figure 3.1. Candidate streams to deploy and evaluate experimental sea lamprey control strategies (dark shaded points) and existing experimental deployments (light shaded points).

After selection of experimental streams, a monitoring plan was developed and implemented in 2020 that consisted of monitoring multiple sea lamprey life stages before (during status quo lampricide only management) and during experimental management deployments

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(experimental management tactics targeting the adult life stage combined with lampricide). After collection of baseline data during status quo sea lamprey management, the management experiment design called for deployment of experimental supplemental sea lamprey control strategies. The Core Group identified the need to develop a decision-support framework to guide experimental deployment decisions. Which experimental sea lamprey management strategy should be tested where and why? Decision analysis was applied to contend with these questions.

The scope of the experimental sea lamprey management deployment decision was initially limited to a single experimental unit located in the Keweenaw Peninsula of Michigan, the Traverse River. A workgroup including members of the Core Group, sea lamprey management partners from the Keweenaw Bay Indian Community Natural Resources Department, decision analysis subject matter experts, and sea lamprey management researchers convened for an in-person workshop in Houghton, MI, and multiple online workshops. These workshops along with asynchronous efforts led to a decision-support framework prototype that provided a means to explicitly assess tradeoffs among sea lamprey management outcomes, learning, cost of deployment, and collateral damage when considering experimental sea lamprey deployments. However, development of this decision-support framework did not culminate in a deployment decision. Lack of robust accounting for uncertainty in sea lamprey control tactic effectiveness (both in terms of sea lamprey control outcomes and consideration of environmental and societal outcomes of management actions) and lack of a satisfactory measurable attribute for objectives associated with learning outcomes limited the usefulness of the decision-support framework prototype. Ultimately, learning from the prototype effort on the Traverse River supported development of an adaptive management framework that integrated learning across multiple streams and accommodated iterative sea lamprey control tactic selection and use decisions.

Problem Framing

The decision problem was a need to identify effective sea lamprey management strategies well-suited to the social, physical, and ecological context of targeted streams while simultaneously optimizing the benefits of coordinating experimental deployments of novel control tactics among multiple candidate experimental streams. Linked cross-scale decisions regarding the selection and use of sea lamprey control tactics underlay this decision problem. Sea lamprey control tactic selection and use decisions can be framed along localized experimental

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unit focal-scale pathways and widespread management application focal-scale pathways. Multiple knowledge systems and evidence-based approaches (Reid et al., 2021; Tengö et al., 2014) can be applied along both pathways (Figure 3.2).

A multi-scale perspective adds complexity to decision making but may benefit sea lamprey management experiment planning and implementation. From a learning standpoint, construing large-scale invasive species management applications as spatial subsets increases learning power and allows for examination of relationships between the experimental treatment and spatial habitat variables (Shea et al., 2002). Implementing experimental designs intended to increase learning power improves capacity to make inferences to other sea lamprey producing systems in the Great Lakes. However, fully realizing the increased learning power gained from spatial sub-setting also requires giving traction to large-scale management perspective to ensure proper coordination and sharing of learning outcomes among localized management units (Watts et al., 2020). Secondly, consideration of scale is needed to describe the type of collective action underpinning current invasive species management practices (externally led, community led, co-managed, and organizational coalitions *sensu* Graham et al., 2019) and the opportunities, risks, and feasibility of cultivating a type of collective action different from the status quo through implementation of the planned management experiment. Finally, invasive species management arrangements that have overlapping levels of authority occurring at multiple scales are expected to enable adaptive management learning feedback loops driven by management-scale experimentation (Chaffin et al., 2016; Folke et al., 2005). As a corollary, we expect that enabling access to the decision-making process through both the widespread management perspective and the localized experimental unit perspective is beneficial to the process of planning and implementing invasive species management experiments.
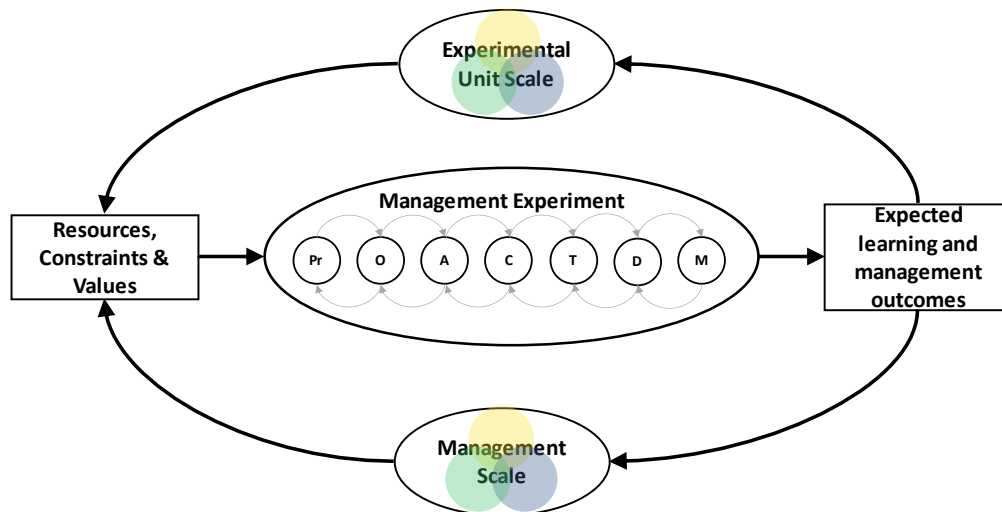
Figure 3.2. Conceptual model for framing decisions associated with invasive sea lamprey management experiments. The inner loop illustrates iteration among decision elements (define problem (Pr) and objectives (O) and measurable attributes, identify alternatives (A), evaluate consequences (C), make tradeoffs (T) among objectives, make a decision (D) and implement, and monitor (M) outcomes) (adopted from (Hemming et al., 2022) and the outer loop illustrates how framing of the decision problem can occur along multiple focal-scale pathways and that expected learning and management outcomes of the management experiment inform the values and constraints that frame the experiment and the resources mobilized for implementing it. Intersecting circles represent multiple knowledge systems and evidence-based approaches framing the decision problem along each focal-scale pathway.

Objectives

We developed a multi-level objective hierarchy that included both multi-stream coordination objectives and localized objectives to accommodate the linked cross-scale decisions that underlay our decision problem (Fig. 3). The levels were linked through a feedback loop between feasibility analyses conducted at the multi-stream coordination level and application of multi-objective decision analytic tools at the localized level. Learning objectives were present at both levels of the objective hierarchy. At the multi-stream coordination level, learning objectives support external validity; at the localized level, learning objectives support internal validity. In

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the context of adaptive management, external validity is the extent to which inferences drawn about the effectiveness of a management application can be generalized to other social-ecological systems, while internal validity describes the suitability of management practices for the system within which they are operating (Lee, 1993).

In developing the multi-level objective hierarchy, we applied the multi-criteria decision-making principle of ensuring objectives are non-redundant (Keeney, 2007) based on our expectation that if decision-making processes at both focal scales are expected to work well in concert (rather than provide redundant functionality) then this principle should be applied to the collective multi-level objective hierarchy. Practically, non-redundant objectives clarify the roles of multi-stream coordination and localized decision processes in the overall design and implementation of sea lamprey management experiments. Fundamental objectives at the multi-stream coordination level were to maximize learning for external validity and minimize costs to resources mobilized for the management experiment. At the localized level, fundamental objectives included minimize production of juvenile sea lamprey, maximize learning for internal validity, minimize collateral damage, and minimize costs mobilized for localized objectives. Means objectives for minimize juvenile sea lamprey production included minimize spawner recruitment and maximize larval mortality. Means objectives for minimize collateral damage were grouped as non-target effects of management actions (minimize lampricide application rate and minimize km of river seasonally blocked) and maximize social license for implementing sea lamprey management (minimize loss of river access by resource users and minimize aesthetic impact of management actions on the resource).

Measurable attributes were developed for the fundamental objectives at the multi-system coordination level. The measurable attribute for minimize cost was the expected annual cost of the experimental deployment and the measurable attribute for maximize learning was an index of increased predictive power.
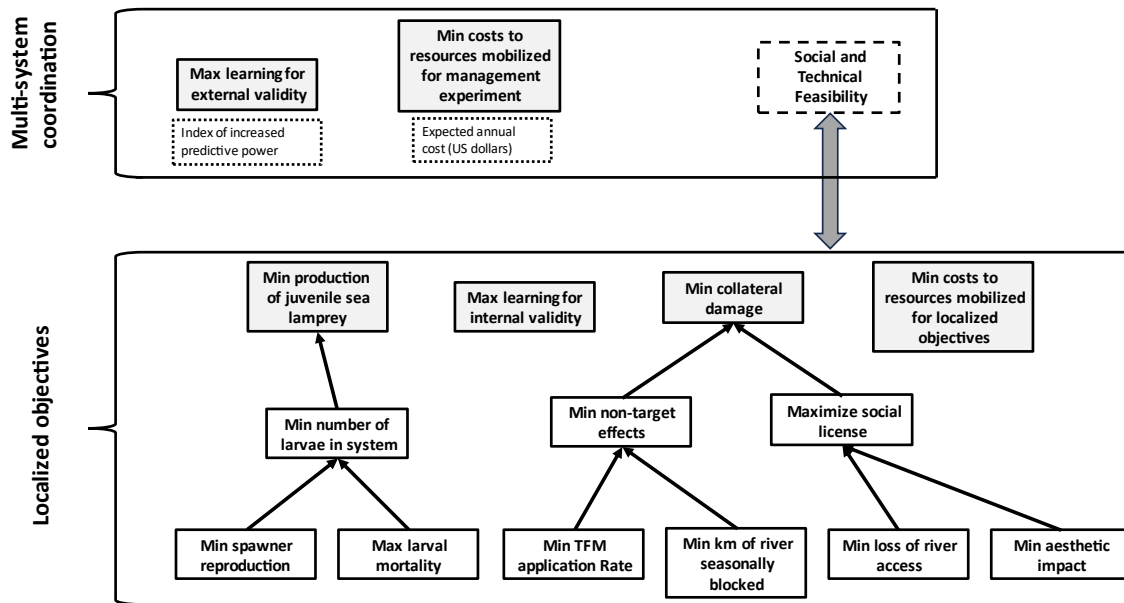
Figure 3.3. Multi-level objective hierarchy for sea lamprey management experiment decisions. The block arrow indicates a vertical linkage between multi-objective decision analyses conducted at the experimental unit (stream) scale and feasibility assessments conducted to aid with multi-stream coordination. Achievement of means objectives (unshaded boxes) enable achievement of the supported fundamental objective (shaded boxes). Measurable attributes (dotted line boxes) were developed for quantifying expected outcomes of multi-stream coordination fundamental objectives. (Min=minimize, Max=maximize, SL=sea lamprey, TFM = primary chemical control tool).

Alternatives

The set of possible experimental control tactics for adult sea lamprey comprised combinations of remove (remove adults prior to spawning), divert (divert adults away from spawning habitat), and disrupt (disrupt the spawning process to lower production of viable embryos) tactics. The removal category included traps and passage-friendly traps. The divert category consisted of a single control tactic (seasonal electric weir). The disrupt category consisted of the sterile-male-release-technique and application of pheromone antagonists (Table 3.1; see Siefkes et al., 2021 for a review of these methods). Experimental sea lamprey management strategies were combinations of these tactics (Table 3.2). The set of strategies considered included all combinations of at most one tactic from each of the remove, divert, and disrupt categories, excluding combinations that included both passage-friendly trap and diverting

tactics. Alternatives consisted of a control strategy deployment at each of the 9 candidate experimental streams. The scope of possible alternatives was constrained by conducting a feasibility analysis. Stream-strategy scenario pairings with a failed feasibility analysis were excluded from consideration. The alternative list was based on all permutations of feasible stream-strategy pairings, with an additional constraint for deployments in Crystal Creek and the Root River mainstem. We limited alternatives to those with the same strategy deployed in both tributaries to simplify communication of the deployment recommendation for the Root River system as a whole and streamline development of an operational-scale deployment plan. Finally, the alterative list was filtered by removing alternatives that called for releasing more sterile males than were expected to be available for the management experiment in total.

Table 3.1. Descriptions of experimental sea lamprey control tactics and key references/ rationale listed by category and type.

Tactic category	Tactic Type	Description	References/Rationale
Remove	Trap	Deploy one or more capture devices to remove adult sea lamprey prior to spawning	(Hume et al., 2020; Johnson et al., 2016; Miehls et al., 2020)
	Passage-friendly trap	Deploy one or more capture devices to remove adult sea lamprey prior to spawning while minimizing possible disruption of wading and boating recreation and fish passage	Passage-friendly features can be implemented through some combination of chemosensory behavioral manipulation, trap operation modifications, and restrictions on the stream-width coverage of trap leads
Divert Disrupt	Electric weir	Deploy a seasonal electric weir	(Johnson et al., 2021b)
	Sterile-male-release-technique	Release sterilized males, targeting a 40:1 sterile male to non-sterile male ratio	(Bravener and Twohey, 2016; Johnson et al., 2021a; Twohey et al., 2003)
	Pheromone antagonist	Inundate sea lamprey spawning habitat with pheromone antagonist during the 3-4 week peak spawning window	(Buchinger et al., 2020)

Table 3.2. Experimental sea lamprey control strategy scenarios. Control strategies consist of one or more control tactics, with a maximum of one tactic in each of the remove, divert, and disrupt categories. SMRT = sterile male release technique, antagonist = pheromone antagonist.

Strategy scenario	Remove	Divert	Disrupt
1 (Trap)	Trap	No	No
2 (Passage-friendly trap)	Passage-friendly trap	No	No
3 (Block)	No	Electric weir	No
4 (SMRT)	No	No	SMRT
5 (Antagonist)	No	No	Antagonist
6 (Trap + Block)	Trap	Electric weir	No
7 (Trap + SMRT)	Trap	No	SMRT
8 (Trap + Antagonist)	Trap	No	Antagonist
9 (Trap + Block + SMRT)	Trap	Electric weir	SMRT
10 (Trap + Block + Antagonist)	Trap	Electric weir	Antagonist
11 (Passage-friendly trap + SMRT)	Passage-friendly trap	No	SMRT
12 (Passage-friendly trap + Antagonist)	Passage-friendly trap	No	Antagonist
13 (Block + SMRT)	No	Electric weir	SMRT
14 (Block + Antagonist)	No	Electric weir	Antagonist

Feasibility Analysis

Feasibility of the possible control tactics was assessed qualitatively (assigning either a *High* or *Low* feasibility) in terms of whether or not a deployment would be socially accepted and technically possible. A qualitative approach to conducting these feasibility assessments appeared sensible for our application based on perceived limitations in satisfactorily accounting for uncertainty in how control tactic efficacy would vary among possible deployment locations and uncertainty in quantifying collateral damage outcomes and objective weights across all experimental units. Alternatively, a probabilistic, quantitative approach could be considered for the feasibility assessment as applied in Priority Threat Management (Carwardine et al., 2019). Social feasibility of a stream-strategy pairing was assessed through consultations with natural resource managers with jurisdictional authority for the stream in question and expert judgement of the co-authors for this work. A constructed scale and score threshold was created to assist with social feasibility assessments (Supplement A). Scores were assigned based on the degree to which collateral damage from a deployment was expected to erode trust between the Sea

Lamprey Control Program and partners, stakeholders, and rightsholders.

Technical feasibility was informed in part by whether a tactic was expected to reduce spawning potential of adult sea lamprey by 90%. This high expected efficacy benchmark was chosen to minimize the risk of experimental deployments increasing larval sea lamprey recruitment due to release from density-dependent overcompensation. We developed a simple deterministic probability tree representing the probability of migratory adults evading control in each of the remove, divert, and disrupt aspects of a given control strategy (Supplement A). Probabilities and initial spawning potential were informed by expert judgment and monitoring data, respectively. Other aspects of technical feasibility included that deployment would not exceed the number of sterilized males expected to be available and the expected annual deployment cost would not exceed $150,000 USD. Finally, all strategy-stream pairings containing pheromone antagonist were considered to have low technical feasibility except for those conducted in Silver Creek (Tawas). The rationale for this was that Silver Creek has a relatively stable stream flow, which is needed for a pheromone antagonist strategy to be effective, and is the closest stream to the pheromone antagonist experts' laboratories (Michigan State University campus, East Lansing, MI).

Consequences

We developed methods for predicting the expected outcome of each potential deployment alternative in terms of measurable attributes associated with the minimize cost and maximize learning fundamental objectives. The measurable attribute for minimize cost was the expected annual cost of the experimental deployment whereas the measurable attribute for maximize learning was an index of increased predictive power. Expected annual cost was measured as both staffing costs and annualized infrastructure/equipment costs (Figure 3.4; Supplement A). Costs were estimated through discussions with subject matter experts (sea lamprey control agents and researchers that use or develop experimental sea lamprey management tactics). The expected annual cost of each strategy was calculated as the sum of the cost of each tactic included in the strategy. The cost of disruption tactics depended on the expected number of wild males in a stream and the expected percentage that would evade remove and divert tactics. The target sterile-male to wild-male ratio was 40:1 and the target pheromone ratio was 100 3sPZS:100 PZS:1 3kPZS. 3kPZS is a naturally occurring sea lamprey pheromone that influences migratory and spawning behaviors via chemosensory communication and 3sPZS and PZS are synthesized

antagonists capable of disrupting this communication. We estimated a conversion factor for converting expected wild male abundance to expected 3kPZS concentration based on an analysis of lab measurements with a known number of males and field trials where 3kPZS concentrations were measured and number of males present in the stream estimated from trap catch data. Estimated annual costs obtained through our simple cost model were converted to relative cost to reduce possible misrepresentation of the realized cost of the experimental deployment if these deployments are implemented.
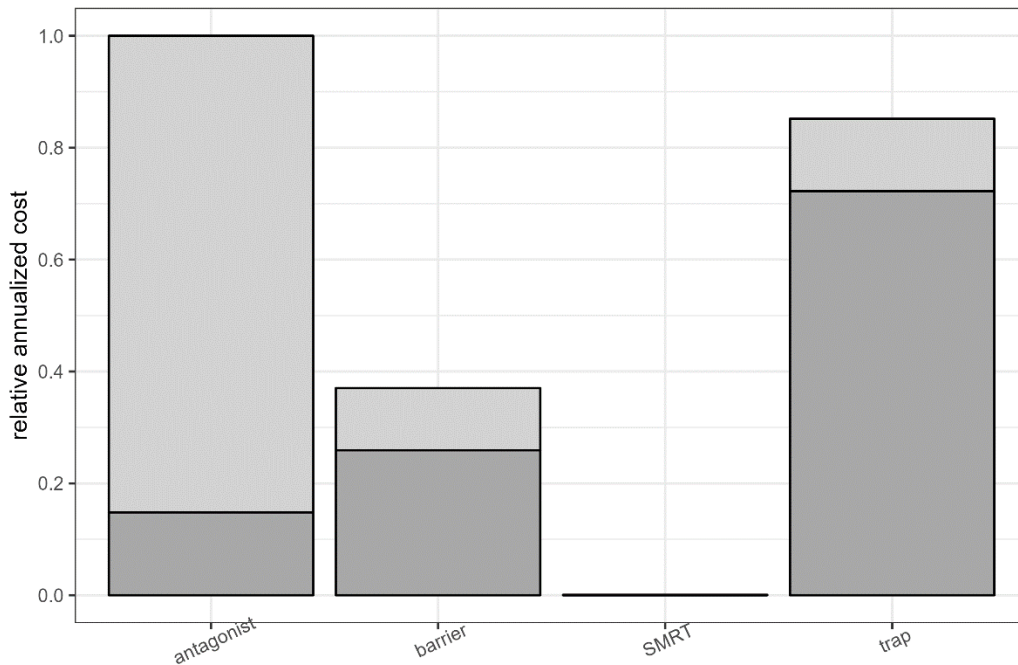
Figure 3.4. Expected relative annual cost of each control tactic broken down by annualized relative equipment and gear costs (light grey) and annual staffing costs (dark grey). The depicted relative cost of disruption tactics (antagonist and SMRT) is for disrupting 1 wild male. The total expected number of wild males to disrupt depends upon the expected starting number of wild males in a stream and the expected percentage of these that evade removal and diversion.

The measurable attribute for the objective of maximize learning was expected gain in predictive power. We developed a simulation-based method for calculating this gain in predictive power. The prediction of interest was the percent decrease in age-1 larval recruitment rate attributed to an experimental management strategy. Learning about this relationship is made difficult by imperfect estimation of larval and adult abundances (observation error) and un-modeled year-to-year variability in the efficacy of control effort (process error). This was

simulated as

$$\log(R_y) = \log(n_y) + r + XInd_y \cdot \log(c_y)$$

where *R* is the abundance of age-1 larvae produced in year *y*, *n* is the pre-control spawning potential (i.e., number of females capable of producing viable larvae) in year *y*, *r* is the per female recruitment rate, *XInd* is a dummy variable indicating if the experimental management strategy was deployed in year *y*, and *c* is the change in recruitment rate caused by the experimental management strategy. Process error was simulated by modeling control efficacy as

$$c_y \sim Truncated\ Normal(c, [c \cdot 0.1], min = 0, max = 1)$$

where c_y is the realized control efficacy for year *y* and *c* is the long-term average control efficacy. We adopted 90% reduction for *c* to match the technical success age-1 recruitment reduction target applied in our feasibility analysis. Observation error was added by applying a CV of 15% to observations of adult abundance and a CV of 20% to log larval abundance. Datasets were simulated (*n*=1500 per scenario) corresponding to a given experimental strategy being replicated between 1 and 7 times. Each replicate consisted of three years of data without added experimental control and five years of data with experimental control. Simulated datasets were analyzed with the linear model

$$\widehat{\log(R_y)} = \beta_0 + XInd_y \cdot \beta_c + offset(\log(\widehat{n_y}))$$

A predictive power test was applied to the linear model output that consisted of comparing the lower bound of the 80% confidence interval for β_c to an efficacy cutoff. If the lower bound of the 80% confidence interval for β_c did not overlap with the efficacy cutoff (70% reduction in recruitment), the model estimate passed the prediction test and if it did overlap, the model estimate failed the test. A predictive power curve was developed by calculating the probability of passing the prediction test (number of passed prediction tests/number of simulated datasets) as the number of experimental units (i.e., streams) in the simulated dataset increased (Figure 3.5).
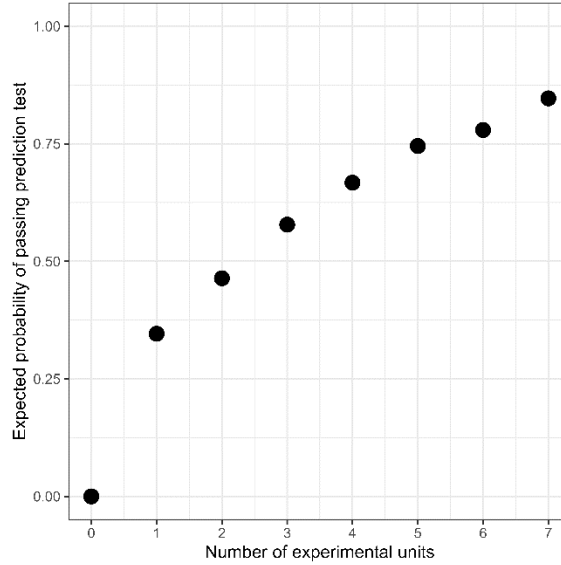
Figure 3.5. Predictive power curve showing the expected probability of passing the prediction test against the number of experimental units in which a given strategy scenario is tested. This curve was developed using simulation methods with assumed levels of process and observation error. The prediction test was passed for a simulated dataset if the estimated 80% confidence interval for larval recruitment reduction efficacy did not overlap with the efficacy cutoff (true efficacy= 90% reduction, efficacy cutoff= 70% reduction).

The expected gain in predictive power index was calculated from this predictive power curve and the experimental design for a given alternative (the number of experimental units assigned to each control strategy). The change in predictive power for control strategy m ($\Delta power_m$) can be written as

$$\Delta power_m = ppass_{m,effortPost} - ppass_{m,effortPre}$$

where the gain in predictive power was equal to predictive power after the management experiment ($ppass_{m,effortPost}$) less the expected predictive power before the experiment ($ppass_{m\ effortPre}$). All strategy scenarios started with 0 experimental units of effort prior to deployment of the alternative except for 4 (SMRT) (starting effort of 3 experimental units) and 9 (Trap + Block + SMRT) (starting effort of 1 experimental unit) based on preexisting experimental management deployments in the Upper Cheboygan watershed and Black Mallard Creek (Johnson et al., 2021a, 2021b). Using these metrics, the expected gain in predictive power index for alternative i (ΔP_i) is the sum of $\Delta power_m$ across all control strategies.

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$$\Delta P_i = \sum_{m=1}^{14} \Delta power_m$$

Tradeoffs

We identified the complete set of non-dominated alternatives to simplify the tradeoffs scenario. A non-dominated alternative performs as good as or better than all other alternatives on at least one objective while performing at least as good as all other alternatives across all other objectives (Hammond et al., 2015). Additionally, we calculated expected utility for scenarios with learning objective weight $w_{learning}$ ranging from 0.01 to 0.99 by 0.01 increments, with the associated expected cost objective weight w_{cost} equal to 1- $w_{learning}$. Expected utility was calculated as

$$E(U_i) = (w_{learning} \cdot u_{learning,i}) + (w_{cost} \cdot u_{cost,i})$$

Partial utilities ($u_{learning}$ and u_{cost}) for alternative i were derived from the expected learning and expected annual cost measurable attributes standardized to a 0 to 1 scale [(outcome$_i$ - worst outcome)/(best outcome - worst outcome)]. Finally, we identified the optimal alternative (the alternative with highest expected utility) for each objective weighting scenario.

Sensitivity Analysis

We evaluated decision sensitivity to assumptions about social and technical feasibility, expected cost, and expected learning outcomes (Table 3.3). Each test (n=7) consisted of calculating expected utility with learning objective weight $w_{learning}$ ranging from 0.01 to 0.99. We examined if and how expected utility and the optimal alternative changed relative to the optimal decision calculated from our baseline assumptions. Comparisons included percent of stream-strategy pairings that matched, percent change in the number of strategy deployments containing electric weirs, percent change in the number of deployments containing traps, and percent change in the number of unique control strategies tested.

Table 3.3. Description of the alternate assumptions investigated with sensitivity analyses, which consisted of reevaluating expected outcomes of either feasibility, expected cost, or expected learning (depending on which prediction the assumption modified). Sensitivity was evaluated by comparing the recommended deployment configurations developed with each alternate assumption (*Test ID* 1 through 7) to the recommended deployment configurations with baseline assumptions (*best guess* scenario).

Category	Test ID	Alternate assumption	Specific test
Best guess	0	NA	-
Social feasibility	1	Electric weirs have high social feasibility in the Traverse River and Bills Creek	Adjust strategies containing electric weir deployments from LOW to HIGH social feasibility for the Traverse River and Bills Creek
Technical feasibility	2	SMRT alone is not a viable strategy for reliably reducing recruitment by 90%	Adjust technical feasibility for SMRT only strategy to LOW across all streams
	3	All streams are possible test sites for pheromone antagonist	Remove the technical constraint limiting pheromone antagonist deployment to Silver Creek (Tawas)
Expected cost	4	Staff day costs were underestimated	Increase staff day costs by 50%
	5	Staff day costs were overestimated	Decrease staff day costs by 50%
Expected learning outcomes	6	age-1 larval recruitment is measured with less observation error	Prediction power simulations conducted with lower larval recruitment observation error (CV=10)
	7	age-1 larval recruitment is measured with more observation error	Prediction power simulations conducted with higher larval recruitment observation error (CV=30)

Results

Feasibility Analysis

Experimental control strategies that included deployment of a seasonal electric barrier were considered a risk to sensitive fish populations and/or a challenge to river access in 5 of 9 streams. These strategy-stream pairings were assigned low social feasibility and excluded from the suite of possible deployment alternatives. Strategies that solely relied on either trapping or blocking were assigned low technical feasibility because they were not expected to reliably reduce reproduction by 90%. Overall, the feasibility analysis substantially constrained the range

of deployment options available for consideration (Figure 3.6). The Traverse River, Bills Creek, Root River, and Crystal Creek had 3 feasible options; the Cranberry River had 4 feasible options; the Potato River and Silver Creek had 5 feasible options; and Furlong Creek and Long Lake Outlet had 6 feasible options.
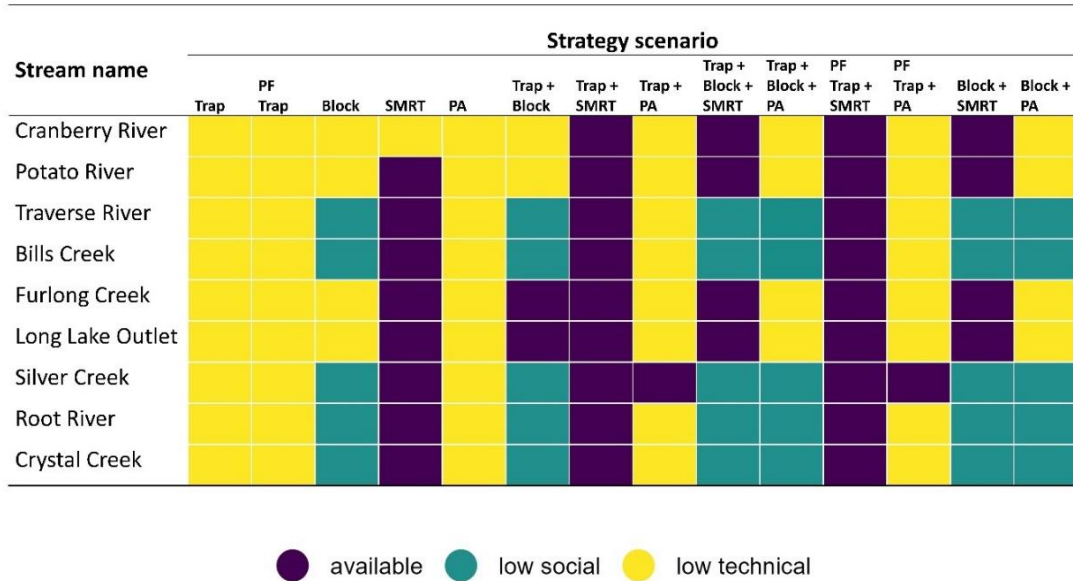
Figure 3.6. Results of the social and technical feasibility assessment. Strategy scenario / stream combinations that are "low social" were expected to have low probability of social acceptance; combinations that are "low technical" were not expected to achieve the 90% reduction in spawning potential benchmark. Strategy scenario / stream combinations that are "available" were considered in the consequences and tradeoffs analysis. PF Trap= passage friendly trap, PA= pheromone antagonist.

Tradeoffs

There were 6 non-dominated alternatives in the suite of 6,432 feasible alternatives (Figure 3.7). The optimal deployment alternative depended upon $w_{learning}$ and included 4 of the non-dominated alternatives (Figure 3.8). At the lowest learning objective weight ($w_{learning} = 0.01$) the optimal alternative included 2 SMRT deployments, 4 SMRT + Trap deployments, and 3 SMRT + electric weir deployments. At low-moderate learning objective weights ($w_{learning} = 0.02$-0.26) the optimal alternative included 2 SMRT deployments, 3 SMRT + Trap deployments, 1 SMRT + Passage-friendly Trap deployment, and 3 SMRT + electric weir deployments. At moderate learning objective weights ($w_{learning} = 0.27$-0.59) the optimal alternative included 2

SMRT deployments, 1 SMRT + Trap deployment, 2 SMRT + Passage-friendly Trap deployments, 3 SMRT + electric weir deployments, and 1 Trap + electric weir deployment. At high learning objective weights ($w_{learning}$ = 0.60-0.99) the optimal alternative included 2 SMRT deployments, 1 SMRT + Trap deployment, 2 SMRT + Passage-friendly Trap deployments, 2 SMRT + electric weir deployments, 1 Trap + electric weir deployment, and 1 Antagonist + Trap deployment.
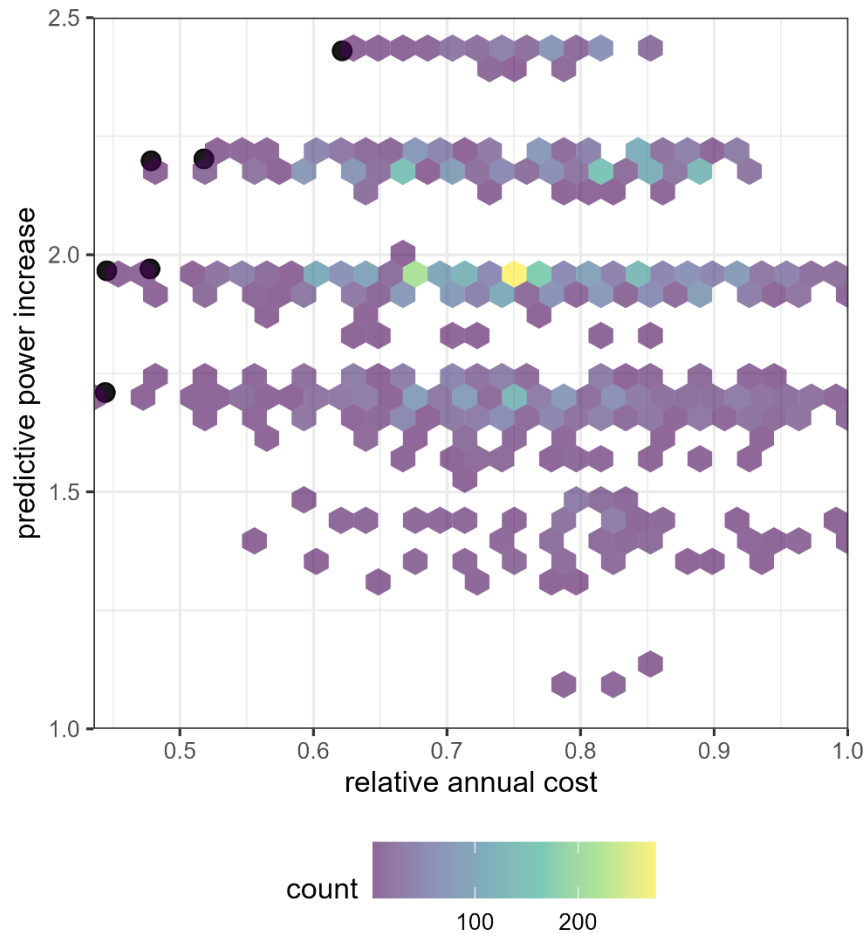
Figure 3.7. Distribution of feasible deployment alternatives with respect to measurable attributes associated with fundamental objectives minimize cost (expected relative annual cost) and maximize learning for external validity (expected predictive power increase). Alternatives that performed as good as or better than all other alternatives on at least one objective while performing at least as good as all other alternatives across all other objectives are identified (black points).
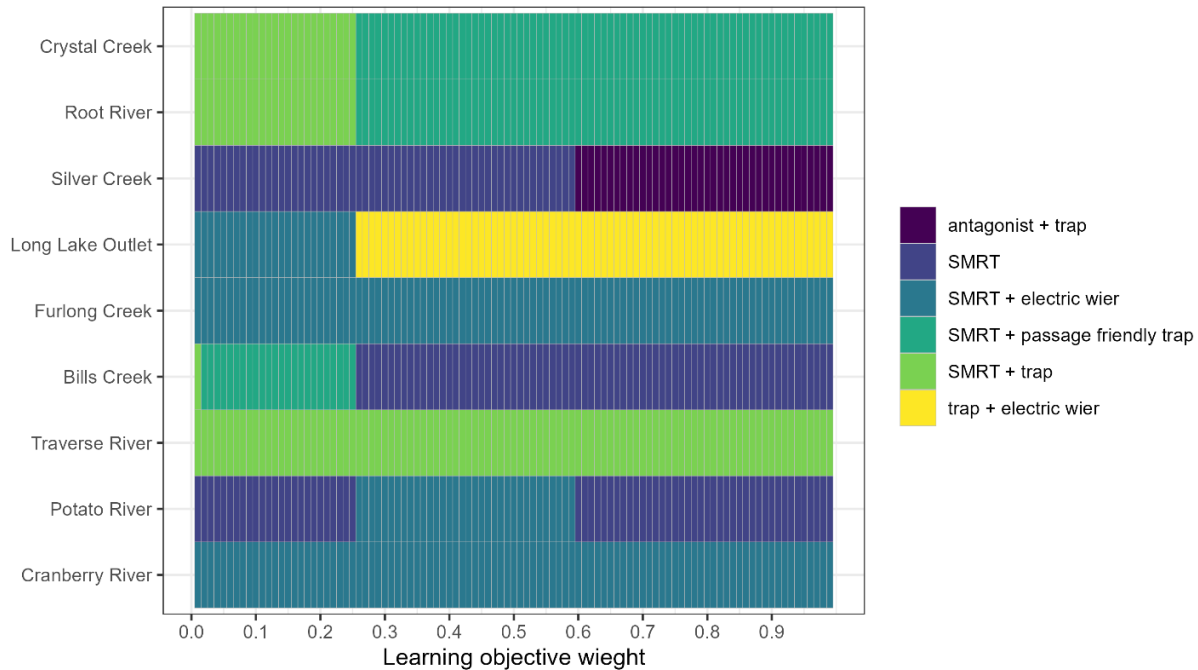
Figure 3.8. Sea lamprey deployment alternatives with the highest expected utility for learning objective weights 0.01-0.99 (the cost objective weight is equal to 1- learning objective weight). All alternatives comprise strategy scenario / stream pairings expected to have both high probability of social acceptance and technical success at reducing spawning potential by 90%.

Sensitivity Analysis

The decision was sensitive to the feasibility and evaluation assumptions we tested, but overall the decision was more sensitive to tests that modified technical or social feasibility compared to tests that modified expected staff day costs or changed the slope of expected learning power by assuming different amounts of larval recruitment observation error (Figure 3.9). However, sensitivity depended upon objective weights and the sensitivity metrics we calculated varied in magnitude and direction. The test removing technical constraints limiting pheromone antagonist deployments to a single stream did not alter the decision for $w_{learning}$<0.52, but at higher values of $w_{learning}$ the less constrained decisions resulted in a greater number of unique deployment strategy scenarios and more strategies that included trapping. The test applying further technical constraints on strategies that rely solely on SMRT resulted in a modified decision across all $w_{learning}$ objective weights, reduced the number of unique strategies across all $w_{learning}$ objective weights, and increased the number of strategies that included traps and barriers. Finally, the test removing social constraints to deploying electric weirs in 2 streams

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resulted in a modified decision across all $w_{learning}$ objective weights, substantially increased the number of unique strategies tested at low-moderate $w_{learning}$ objective weights, increased the percentage of strategies with barriers at $w_{learning}<0.53$, and substantially reduced the percentage of strategies with traps at $w_{learning}<0.32$.
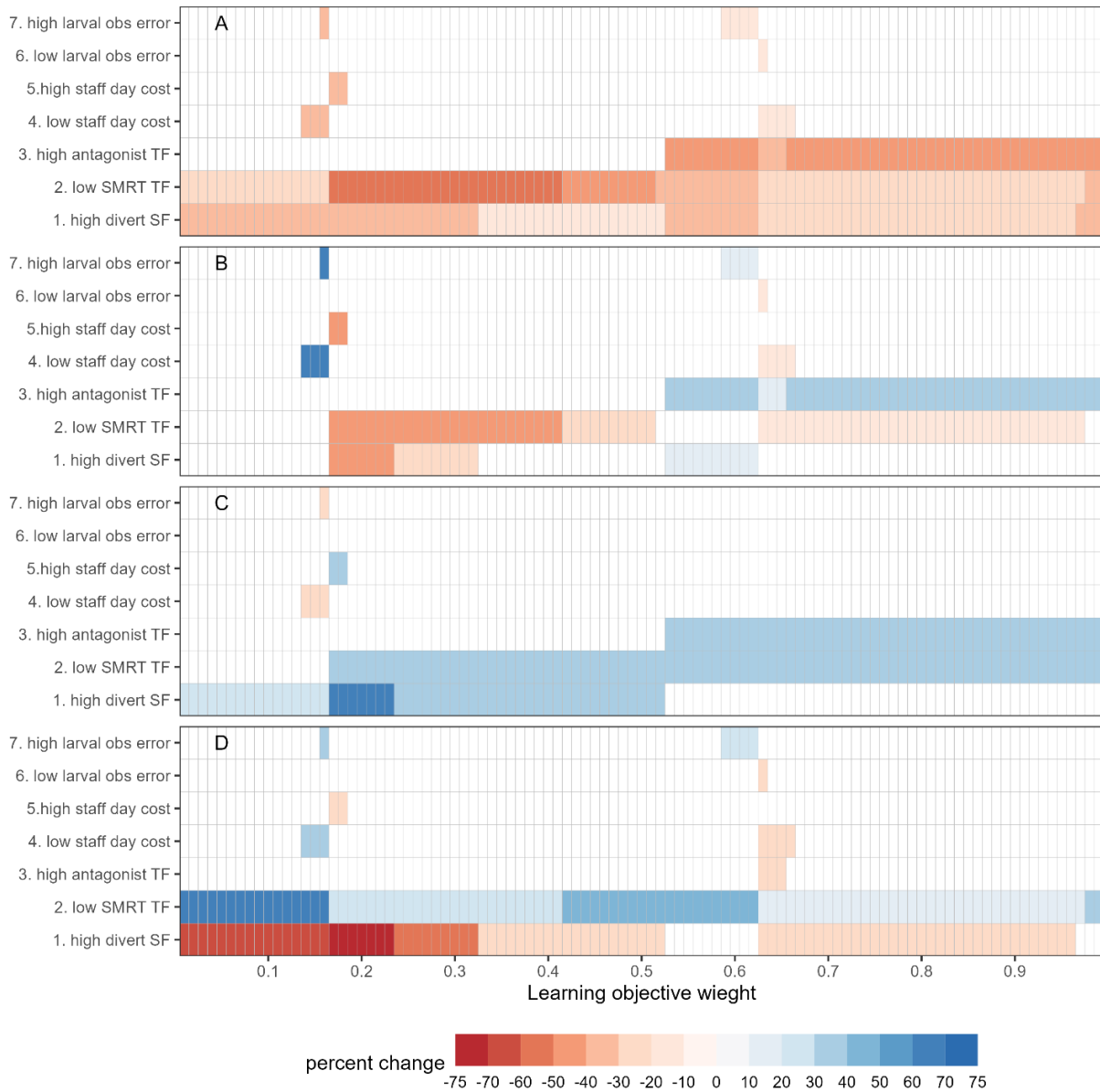
Figure 3.9. Sensitivity of the decision to assumptions about expected outcomes and feasibility. Decision sensitivity is measured by comparing the optimal decision obtained with the modified assumption to the optimal decision obtained with baseline assumptions. Sensitivity metrics include percent reduction in the number of matching stream-scenario pairings (panel A), percent change in the number of unique strategy scenarios deployed (panel B), percent change in the number of strategy scenarios deployed that contain electric weirs (panel C), and percent change in the number of strategy scenarios deployed that contain a trap (panel D). (TF=technical feasibility, SF=social feasibility, obs=observation).

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Discussion

We developed an adaptive management framework for selection and use of novel sea lamprey control tactics that constrained experimental deployment options to those with high expected social and technical feasibility and allowed decision makers to evaluate tradeoffs among cost effectiveness and learning outcomes. This framework can be used to investigate how the optimal deployment decision changes as management priorities shift between minimizing costs and maximizing learning. Furthermore, explicit consideration of both maximize learning and minimize cost as management objectives allowed for acknowledgement of what was left on the table in terms of cost effectiveness to advance learning (and vice versa). Successful, long-term implementation of sea lamprey management experimental designs may depend on transparent and collaborative decision-making processes. For example, effective communication among decision-makers, practitioners, stakeholders, and rightsholders regarding the relative importance of multiple sea lamprey management objectives during the deployment, operation, and decommissioning of an electric weir and fishway on the Pere Marquette River of Lake Michigan could have improved the sea lamprey management and learning outcomes of the experiment. As it happened, lack of effort directed towards developing and communicating objectives and measures of success may have led to the decision to decommission the project, in place of gaining understanding on how to navigate complex sea lamprey management objective tradeoffs through an adaptive management plan (Tews et al., 2020). Effective consideration and communication of multiple sea lamprey management objectives may be necessary to enact long-term, iterative improvement of sea lamprey management outcomes in systems where status quo management is ineffective or jeopardized due to localized environmental and/or social conditions (Lewandoski et al., 2021; Siefkes et al., 2021).

Our adaptive management framework was developed to advance operationalization of IPM principles in invasive sea lamprey management in the Great Lakes. The framework supports iterative refinement of societal and non-target environmental considerations of sea lamprey control tactic selection and use decisions and development of novel sea lamprey control strategies that seek to integrate multiple, compatible control tactics. Spatial and temporal replication of novel control strategy deployments provides power to learn about how sea lamprey ecology interacts with control tactic efficacy, while cross-scale linkages connecting multiple societal and environmental objectives to experimental deployment decisions allows for improved

consideration of societal and environmental consequences of sea lamprey management. Specifically, feedback loops between localized multi-objective decision analysis applications and feasibility assessments conducted at the multi-system level support cross-scale linkages between sea lamprey management decision problems with either multi-system coordination or localized focus.

Future applications of decision analysis that contend with localized invasive/pest species control tactic selection and use decision problems may benefit from this adaptive management framework. Our framework could assist with navigation of cross-scale linkages among multi-system coordination and localized management objectives, a challenge that proved difficult during our decision analysis prototyping efforts focused on sea lamprey control tactic selection and use in a single stream. Localized decision analysis outcomes either support or refute multi-stream feasibility assessments. The localized decision analysis refutes the multi-stream feasibility assessment if operational-scale deployment alternatives (specific control tactics paired with a deployment location on a stream) within the bounds of feasible strategic-level alternatives (combinations of remove, divert, disrupt tactics without reference to deployment locations) do not rank among the preferred alternatives or if operational-scale deployments not within the bounds of feasible strategic-level alternatives do rank. If neither of these incongruences occur, the feasibility assessment conducted within the multi-stream framework is supported by the single-stream framework. Iterative updating of refuted feasibility assessments could support social learning and cross-scale linkages if ideas can be exchanged in a trusting environment (Cundill and Rodela, 2012). Based on our sensitivity analysis, social learning of this nature regarding expected loss of utility due to electric weir deployment disrupting recreational river access, negatively affecting aesthetics, and seasonally blocking non-target fishes may substantially alter expected optimal novel sea lamprey control tactics selection and use decisions, particularly when cost effectiveness is prioritized at the multi-system coordination level.

Quantitative models of sea lamprey population and control dynamics at spatial resolution compatible with operational knowledge bases of sea lamprey management practice could build capacity for future localized decision analysis efforts. At the operational scale, sea lamprey population and control dynamics are represented as one or more specific control tactics deployed to georeferenced deployment locations within a river system, and population dynamics are modeled with enough resolution to capture how expected control outcomes may vary among

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alternative deployment locations. Quantitative models of sea lamprey production with coarse spatial resolution have been developed that make use of sea lamprey control agent and sea lamprey biology and ecology subject matter experts' knowledge (Dawson et al., 2016; Haeseker et al., 2007; Jones et al., 2009; Jubar et al., 2021; Miehls et al., 2021). While these efforts have yielded useful decision-support tools for sea lamprey management decision makers and control agents, the participatory methods used to construct the models may require refinement to elicit knowledge at the operational scale. During our initial localized objectives-scale prototyping, we were unable to develop an agreed-upon operational-scale quantitative model of sea lamprey populations dynamics and control from expert knowledge that was elicited without explicit reference to within-stream spatial heterogeneity. An expert elicitation methodology that allows for experts to provide input on how control efficacy and population dynamics may vary among locations within a river and why (i.e., what key spatial habitat variables are driving the spatial heterogeneity) may be necessary to construct quantitative models that are useful for guiding operational-scale deployment decisions. Furthermore, participatory modeling processes conducted at the operational scale would constitute a rich environment for mobilizing multiple evidence bases and developing enriched understanding of sea lamprey management practices (Tengö et al., 2014). We hypothesize that such modeling approaches would yield more realistic *a priori* predictions of sea lamprey management deployment alternative outcomes compared to similar participatory modeling efforts conducted at coarse spatial scale. Finally, participatory, operational-scale modeling processes may be particularly useful for integrating information collected from monitoring efforts associated with experimental deployments back into the decision framework for iterative decision making (i.e., completing active adaptive management feedback loops), which is imperative for implementation of adaptive management (Williams et al., 2009).

The usefulness of applying adaptive management to advance learning for internal or external validity can be explored by assigning value to what is or could be learned through the application of adaptive management. During our decision analysis application, we found it challenging to compare the value of learning against other objectives of the management experiment and make predictions about learning outcomes. We ultimately developed a learning outcome measurable attribute based on the degree to which uncertainty was expected to be reduced in the relationship between a given experimental sea lamprey management strategy and

reduction in age-1 recruitment rate. However, we applied the simplifying assumption that learning about any experimental sea lamprey management strategy was equally valuable. Value of information (VOI) methods for quantifying the relative value of reducing different uncertainties (Li et al., 2021; Runge et al., 2023, 2011) could improve our decision support frameworks by providing an objective approach to weighting the relative value of learning about a given experimental sea lamprey management strategy. Achievement of experimental sea lamprey management learning objectives related to developing a predictive model of invasive sea lamprey population and control dynamics that incorporates spatial habitat variables and density-dependent factors (Lewandoski et al., 2021) will be influenced by decisions about when/if to apply lampricide management in an experimental sea lamprey management stream, what streams to include in the management experiment, and the monitoring plan. Application of decision analysis to these decision problems would similarly benefit from VOI methods to focus effort towards resolving the most impactful uncertainties and navigate tradeoffs between learning and other management objectives.

In addition to developing quantitative tools capable of assisting with valuing learning objectives, a participatory process that allows access to sea lamprey adaptive management from both multi-system coordination and localized points of view would need to be developed to allow for robust consideration of learning objectives related to both internal and external validation. This would require building connections among localized sea lamprey management practices, multi-system coordination, and resources mobilized to support widespread management of invasive sea lamprey in the Great Lakes Basin. This endeavor appears daunting given the scale of invasive sea lamprey management; roughly 100 streams and hundreds of hectares of lentic habitat are treated with lampricides annually (Sullivan et al., 2021), while partnerships and empirical datasets are developed to maintain over 400 lowermost barriers considered important to management of invasive sea lamprey (Hrodey et al., 2021). However, despite the scale of sea lamprey management in total, sea lamprey control agents routinely develop and rely on social networks and forums to meet localized objectives of minimizing production of juvenile sea lamprey while minimizing collateral damage. Expanding the utility of existing social networks and forums to include implementing adaptive management, which may be perceived as more uncertain and risky than status quo management practices and have learning objectives that are challenging to articulate and measure, could benefit from application

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of multi-objective decision analytic concepts and tools that explicitly examine decision making under uncertainty, offer tools for making tradeoffs among objectives, and provide collaborative and transparent approaches to decision making (Robinson et al., 2021). However, decision analytic tools and theoretical frameworks are not comprehensive. There are few examples of multi-criteria decision analysis applications documented in the literature that fully embrace Indigenous knowledge (Converse, 2020) and decision analytic practice and theory alone may not be well suited to developing pathways that connect Indigenous knowledge to sea lamprey management experiment planning and implementation. Operationalizing Two-Eyed Seeing at both the multi-system coordination and localized levels could address this deficit and further develop pathways for Indigenous knowledge and ways of knowing to coexist with mainstream Western knowledge in support of adaptive management of sea lamprey in the Great Lakes (Nonkes et al., 2023; Reid et al., 2021).

Adaptive management may be broadly useful for operationalizing IPM. Previous theoretical developments and institutional reviews support this conclusion. Leveraging adaptive management learning plans with temporal and spatial replication provides power to resolve critical ecological uncertainties limiting effective control of target invasive species or pest populations (Shea et al., 2002). However, uncertainty in how society values multiple objectives associated with management of invasive or pest populations makes it difficult to assess how societal and non-target environmental effects should be considered in the design and implementation of an IPM program. Overlapping adaptive management feedback loops between learning and decision making at both local and regional scales may allow for iterative refinement of these considerations (Chaffin et al., 2016; DiTomaso et al., 2017; Scarlett, 2013). We further developed these premises for operationalizing IPM by applying decision theory to a multi-level control tactic selection and use decision problem.

The adaptive management framework we developed enables overlapping decision-making processes occurring at the localized and multi-system coordination levels. A key precondition for this functionality was the recognition that multi-system coordination and localized management each have distinct objective sets that must work well in concert. Cross-scale linkages are strengthened by identifying synergies and making transparent tradeoffs between enacting experimental design intended to resolve generalizable social-ecological system uncertainties and improving management practices through collaboration and social learning.

While these features were developed for the decision problem at hand (selection and use of novel sea lamprey control tactics), they may prove useful to other decision problems centered in operationalizing IPM in heterogenous social-ecological landscapes.

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CONCLUSION

- Adult sea lamprey long-term monitoring data are currently analyzed and collected to develop an index of sea lamprey abundance that is then used to gauge the past success or failure of the control program to meet suppression targets in each Great Lake. Using adult sea lamprey capture data to develop a population dynamics model capable of forecasting future control outcomes represents a novel application of these long-term monitoring data. While the research conducted herein hopefully demonstrates the potential benefits of this novel application, further research is needed to rigorously gauge how/if this application represents a useful tool for sea lamprey control policy makers and practitioners. Additional technical work could examine the sensitivity of forecasts to model assumptions, both the prior distributions assigned to demographic rates and model structure used to represent sea lamprey life history and control dynamics. Further application of stakeholder engagement and participatory modeling techniques could be applied to develop agreed-upon standards for acceptable model behavior and diagnostic checks for determining the reliability of the model as a decision-support tool.

- Simulation testing a novel modeling framework for quantifying recruitment, dispersal, and survival rates using sibship and abundance estimation data revealed that this can be a powerful method for learning about spatial population dynamics of fishes. Additional work that builds on this initial proof-of-concept research will be required to understand the utility of this method for learning about the cryptic life history of invasive sea lamprey in the Great Lakes. The next steps will be to apply the model to empirical sibship-abundance datasets collected by the SupCon adaptive monitoring program, develop simulation models intended to represent the biological and sampling processes underlying ongoing field collections, and conduct simulation-based power analyses with status quo sampling effort and alternate possible configurations to guide future monitoring efforts. The vision for this quantitative framework is to provide a method for incorporating learning about sea lamprey population dynamics and control into decision-making processes associated with implementing integrated sea lamprey management with spatial subsetting at the localized tributary scale.

- We developed an adaptive management framework and applied it to a sea lamprey control tactic selection and use decision problem. Adaptive management frameworks that facilitate deliberation of tradeoffs among the multiple objectives of invasive sea lamprey control may

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provide a method for effectively engaging with values-based uncertainties associated with integrated sea lamprey management. Integrating adaptive management with sea lamprey control management practices would require considerable advances in research and practice along multiple fronts, including 1) modifying the adaptive management framework to account for linked decisions outside of experimental control tactic selection and use (e.g., lampricide selection and use; barrier construction, modification, and removal; monitoring), 2) broadening the measurable attribute(s) for learning to accommodate multiple possible learning goals and conducting value of information analyses, and 3) applying decision analysis to multiple localized sea lamprey control decision problems throughout the Great Lakes basin. Thoughtful identification of which localized sea lamprey control decisions are best addressed with status quo sea lamprey control practices and those that may be improved through iterative application of decision analytic tools will be crucial for effective expansion of the use of adaptive management within the invasive sea lamprey control programs.

APPENDIX A: LAKE SUPERIOR SEA LAMPREY POPULATION DYNAMICS MODEL DETAIL

Recruitment and control-induced reduction of Lake Superior sea lamprey recruitment were modeled as

$$u' = n_t^{adult} exp\left(a - b \cdot n_t^{adult} - \beta_{smrt} \cdot X_{SMRT} - \beta_{weir} \cdot X_{weir} + \varepsilon_t\right)$$

where u' is the number of age-1 recruits produced at time $t+1$, n_t^{adult} is the abundance index of adult sea lamprey at time t, a is mean recruitment rate as population size approaches zero, b is a parameter measuring the strength of density-dependence, β_{SMRT} is the effect of SMRT on recruitment rate, X_{SMRT} is an indicator variable indicating which years SMRT was applied, β_{weir} is the effect of electric weir operation on recruitment rate, X_{weir} indicates annual electric weir operation effort (proportion of maximum number of barriers operated), and ε_t is stochastic deviation from mean recruitment rate at year t. Stochastic deviations from the mean recruitment rate were assumed to be a normally distributed white-noise series $\varepsilon_t \sim Normal(0, \sigma_a)$, where σ_a represents annual variability in mean recruitment rate.

Annual larval survival was modeled as

$$S_{l,lotic} = S_l \cdot exp\left(-X_{tfm} \cdot [\beta_{tfm} + \beta_{block} \cdot X_{tfm}]\right)$$
$$S_{l,lentic} = S_l \cdot exp\left(-X_{gB} \cdot \beta_{gb}\right)$$

where S_l is annual larval survival in the absence of lampricide application and β_{tfm}, β_{gB}, and β_{block} are parameters relating lampricide control effort (X_{gB}= kg of active ingredient; X_{tfm}= km of stream treated; X_{block}= km of stream blocked by permanent weirs) to lampricide-induced larval mortality. Kilometers of stream blocked was included in the model for $S_{l,lotic}$ because construction of permanent weirs reduces available habitat for sea lamprey, which concentrates larvae in smaller areas and, at least in theory, increases the mortality level associated with per unit application of TFM.

We used a combination of high-information and low-information priors for fitting our model of sea lamprey population dynamics and control (a table of prior and posterior distributions for all model parameters is provided in S2). Larval metamorphosis probabilities were assigned low-information priors (on the probabilistic scale) but were constrained such that the probability increased with age. We used high-information priors for the probability that juveniles transitioned to the spawning adult life stage in one year, natural mortality of larvae, and natural mortality of juveniles and adults. We chose to use high-information priors for these vital

rates because empirical estimates are available from large-scale mark recapture estimates of Great Lakes sea lamprey populations (Johnson et al., 2016, 2014). Prior distributions for age-1 recruitment parameters (i.e., a and b) were developed based on the long-term population growth rate λ of our sea lamprey stage-age population model evaluated at mean prior distribution values (Caswell, 2000). We assigned a normal prior for a such that 95% of the probability density of λ fell within 1.02 and 1.84. These λ values correspond to the minimum and maximum intrinsic population growth rates estimated for common taxonomic orders of fishes reported by Thorson (2020). We developed a prior for b by considering the population size at which long-term population growth would approach zero with a fixed at the prior distribution mean and a reference population size equal to the mean log catch from the unscaled time series dataset (assessment unit with s fixed at 0, see *Observation model*). Specifically, we used a mean value for our prior on b corresponding to long-term population growth approaching zero at 15 times the reference population size and assumed a CV of 50 to derive a prior variance estimate.

Information on the localized effectiveness of lampricide application is available, but there is limited information on the proportion of larvae inhabiting lampricide-vulnerable habitat. As such, we set priors for the probability of recruiting to lentic and lotic habitat that resulted in a wide spread of distribution probabilities for each habitat. Priors for parameters relating lampricide control effort to lampricide mortality rates were set based on data from localized trials, but we assigned a high CV as these rates have not been rigorously studied.

APPENDIX B: LAKE SUPERIOR SEA LAMPREY POPULATION DYNAMICS MODEL PARAMETERS

Table S1. Process model parameters in the Lake Superior population dynamics and control model. Posterior distribution columns provide the mean, standard error of the mean (sd_mean), quantiles of the distribution, and model diagnostics associated with each parameter.

parameter		prior distribution				posterior distribution								model diagnostics	
symbol	description	family	scale	shape	min	mean	se_mean	sd	2.50%	25%	50%	75%	97.50%	n_eff	Rhat
x3_0	starting abundence index for adult lifestage (log scale)	truc-normal	5.13	2	1	6.2928	0.0237	1.1065	4.5205	5.6574	6.2263	6.784	8.3651	2188.183	1.003
x2a2_0	starting abundence index for age-2 juvenile lifestage	truc-normal	1	100	1	216.7137	0.3066	59.3541	106.947	175.5987	214.4681	255.0463	339.7933	37471.43	1.0001
x2a1_0	starting abundence index for age-1 juvenile lifestage	truc-normal	1	100	1	107.6814	0.2757	69.5425	7.2086	52.8056	98.0143	151.9605	264.9337	63630.87	1
x1a7_0lentic	starting abundence index for age-7+ lentic larval lifestage	truc-normal	1	10000	1	391.1084	1.3394	374.4709	11.6162	119.8424	283.2536	546.4324	1375.044	78166.68	1
x1a6_0lentic	starting abundence index for age-6 lentic larval lifestage	truc-normal	1	10000	1	418.8177	1.4306	399.9382	12.4148	128.822	303.0008	588.4209	1461.559	78155.43	1
x1a5_0lentic	starting abundence index for age-5 lentic larval lifestage	truc-normal	1	10000	1	1231.443	3.9948	1123.509	37.058	395.3966	918.9416	1740.519	4140.356	79098.86	1
x1a4_0lentic	starting abundence index for age-4 lentic larval lifestage	truc-normal	1	10000	1	5902.954	15.392	4282.317	267.0931	2473.286	5136.971	8484.047	15891.83	77404.28	1
x1a3_0lentic	starting abundence index for age-3 lentic larval lifestage	truc-normal	1	10000	1	8297.749	24.0568	6034.744	363.6528	3510.472	7171.687	11872.73	22554.84	62927.73	1
x1a2_0lentic	starting abundence index for age-2 lentic larval lifestage	truc-normal	1	10000	1	9719.341	22.5303	6557.78	496.1824	4534.474	8722.167	13814.62	24684.81	84718.72	1
x1a1_0lentic	starting abundence index for age-1 lentic larval lifestage	truc-normal	1	10000	1	9861.977	25.411	6885.574	473.2915	4331.455	8693.249	14185.97	25790.43	73423.54	1
x1a7_0lotic	starting abundence index for age-7+ lentic larval lifestage	truc-normal	1	10000	1	391.1444	1.3703	376.923	12.0018	118.3933	280.9277	547.3033	1369.017	75658.02	1
x1a6_0lotic	starting abundence index for age-6 lotic larval lifestage	truc-normal	1	10000	1	419.9808	1.4307	407.8695	12.1151	126.5351	301.1947	584.6015	1489.465	81277.9	1
x1a5_0lotic	starting abundence index for age-5 lotic larval lifestage	truc-normal	1	10000	1	1232.347	4.0484	1136.365	35.7519	391.6652	913.5703	1748.82	4163.661	78787.63	1
x1a4_0lotic	starting abundence index for age-4 lotic larval lifestage	truc-normal	1	10000	1	5893.402	15.7683	4278.429	248.1053	2504.224	5113.96	8428.729	15905.76	73620.82	1
x1a3_0lotic	starting abundence index for age-3 lotic larval lifestage	truc-normal	1	10000	1	8250.006	23.2835	6012.847	356.9254	3478.111	7106.309	11797.89	22548.23	66690.41	1
x1a2_0lotic	starting abundence index for age-2 lotic larval lifestage	truc-normal	1	10000	1	9737.917	22.5614	6584.154	508.4082	4502.846	8737.159	13902.39	24730.03	85166.19	1
x1a1_0lotic	starting abundence index for age-1 lotic larval lifestage	truc-normal	1	10000	1	9826.407	24.8093	6831.232	470.9679	4379.474	8676.6	14114.11	25596.84	75817.65	1
x1a7_0inv	starting abundence index for age-7+ invulnerable larval lifestage	truc-normal	1	10000	1	390.1426	1.3246	375.1656	11.4186	120.4215	280.9922	541.8687	1367.32	80223.95	1
x1a6_0inv	starting abundence index for age-6 invulnerable larval lifestage	truc-normal	1	10000	1	418.9509	1.3674	400.7417	12.2503	128.5532	302.7888	585.8244	1474.976	85885.49	1
x1a5_0inv	starting abundence index for age-5 invulnerable larval lifestage	truc-normal	1	10000	1	1237.925	4.0005	1135.139	36.3616	397.1753	927.5606	1743.481	4166.566	80512.91	1
x1a4_0inv	starting abundence index for age-4 invulnerable larval lifestage	truc-normal	1	10000	1	5873.901	15.0988	4278.111	242.9355	2465.788	5090.903	8449.982	15948.07	80281.76	1
x1a3_0inv	starting abundence index for age-3 invulnerable larval lifestage	truc-normal	1	10000	1	8273.831	23.1403	5987.095	372.6728	3530.053	7164.051	11849.1	22441.17	66941.61	1
x1a2_0inv	starting abundence index for age-2 invulnerable larval lifestage	truc-normal	1	10000	1	9743.206	22.7221	6618.14	500.9195	4499.387	8716.563	13880.93	24926.18	84835.28	1
x1a1_0inv	starting abundence index for age-1 invulnerable larval lifestage	truc-normal	1	10000	1	9889.667	25.0666	6893.044	475.626	4396.888	8717.52	14211.41	25691.46	75618.84	1

parameter		prior distribution				posterior distribution								diagnositics	
symbol	description	family	scale	shape		mean	se_mean	sd	2.50%	25%	50%	75%	97.50%	n_eff	Rhat
u	age-1 recruitment rate	Normal	7.1	1.25		6.0378	0.0056	0.7188	4.8354	5.5392	5.9651	6.4588	7.6625	16248.52	1.0006
b	density-dependent effect on age-1 recruitment	Normal	0.00038	0.00019		3.00E-04	0	1.00E-04	1.00E-04	3.00E-04	3.00E-04	4.00E-04	6.00E-04	20312.35	1.0001
surv_river_logit	annual survival of larvae (logit scale)	Normal	0.282	0.25		0.1121	0.001	0.162	-0.1897	-7.00E-04	0.1067	0.218	0.4441	28870.28	1.0001
surv_lake_logit	annual survival of adults and juveniles (logit scale)	Normal	0.405	0.5		0.3349	0.0022	0.3948	-0.3928	0.0631	0.3199	0.5916	1.1522	32574.13	1.0002
sd_q	year-to-year sd of age-1 recruitment rate	Half-normal	0	1		0.8567	0.0012	0.1713	0.5633	0.7372	0.8415	0.9602	1.2334	20407	1.0003
juv_a2_logit	probablity of age-1 juvenile staying in lake for second year	Normal	0	0.2		0.2569	8.00E-04	0.1846	-0.111	0.1345	0.2579	0.3823	0.6142	59666.07	1
p_lentic	probability of age-1 larvae recruiting to lentic habitat (logit scale)	Normal	0	1.4		-0.609	0.0049	1.2112	-3.0184	-1.3978	-0.5972	0.1829	1.7801	60434.3	1
p_lotic	probability of age-1 larvae recruiting to lotic habitat (logit scale)	Normal	0	1.4		1.2422	0.0083	1.3999	-1.8507	0.3853	1.3934	2.2191	3.6521	28545.07	1.0001
b_weir	change in age-1 recruitment rate from electric weir opperation	Normal	0.69	0.4		1.054	0.0015	0.3471	0.3647	0.8227	1.0572	1.2873	1.7301	52471.05	1
b_smrt	change in age-1 recruitment rate from sterile-male-release-technique	Normal	0.35	0.25		0.1428	9.00E-04	0.2215	-0.287	-0.0061	0.1406	0.2895	0.5873	66597.51	1
c_log	rate of increase in larval mortality from TFM application	Normal	-2.3	1		-1.2977	0.0073	1.0578	-3.6187	-1.9581	-1.1721	-0.5724	0.5804	21057.22	1.0002
c_barrier	effect of km of river blocked by permanent weris on c_log	Exponential	2	NA		0.3211	0.0013	0.3374	0.0079	0.0903	0.2159	0.4356	1.2397	70712.11	1
balu_log	rate of increase in larval mortality from Baylucide application	Normal	-0.38	1		-0.6321	0.0034	0.9812	-2.4856	-1.3054	-0.6619	0.019	1.3518	83906.93	1

Table S2. Observation model parameters in the Lake Superior population dynamics and control model. Posterior distribution columns provide the mean, standard error of the mean (sd_mean), quantiles of the distribution, and model diagnostics associated with each parameter.

	parameter	prior distribution			posterior distribution								model diagnostics	
symbol	description	family	scale	shape	mean	se_mean	sd	2.50%	25%	50%	75%	97.50%	n_eff	Rhat
a[1]	scale adjustment for assessment unit 1	Normal	0	2	-2.035	0.0026	0.4096	-2.8222	-2.3127	-2.0395	-1.7648	-1.2152	24936.34	1.0003
a[2]	scale adjustment for assessment unit 2	Normal	0	2	-0.2165	0.0028	0.3918	-0.9833	-0.4792	-0.2178	0.0449	0.5567	19567.19	1.0003
a[3]	scale adjustment for assessment unit 3	Normal	0	2	-1.3487	0.0031	0.5246	-2.342	-1.7094	-1.3601	-0.9988	-0.3008	28726.65	1.0001
a[4]	scale adjustment for assessment unit 4	Normal	0	2	0.2817	0.0021	0.3015	-0.3189	0.0814	0.2838	0.4827	0.8719	21337.42	1.0001
a[5]	scale adjustment for assessment unit 5	Normal	0	2	0.6544	0.0025	0.3096	0.0589	0.446	0.6523	0.8581	1.2774	15866.75	1.0003
a[6]	scale adjustment for assessment unit 6	Normal	0	2	-2.8977	0.0032	0.5771	-3.9884	-3.2721	-2.9201	-2.5457	-1.6764	32602.82	1.0002
a[7]	scale adjustment for assessment unit 7	Normal	0	2	-0.0258	0.0028	0.5198	-1.0735	-0.3604	-0.019	0.3195	0.9776	33491.18	1.0001
a[8]	scale adjustment for assessment unit 8	Normal	0	2	-3.2875	0.0027	0.4564	-4.1747	-3.5934	-3.2902	-2.9871	-2.3799	27630.26	1.0002
a[9]	scale adjustment for assessment unit 9	Normal	0	2	-3.3297	0.004	0.8268	-4.8432	-3.8929	-3.3708	-2.8083	-1.5754	41679.38	1
a[10]	scale adjustment for assessment unit 10	Normal	0	2	-2.2414	0.0025	0.5002	-3.2343	-2.5702	-2.2404	-1.9072	-1.2651	40549.23	1
a[11]	scale adjustment for assessment unit 11	Normal	0	2	-3.2534	0.0029	0.4789	-4.113	-3.5916	-3.2827	-2.9385	-2.2613	27198.89	1.0001
a[12]	scale adjustment for assessment unit 12	Normal	0	2	-3.7765	0.0022	0.4211	-4.5967	-4.0586	-3.7787	-3.5006	-2.9378	37744.19	1
a[13]	scale adjustment for assessment unit 13	Normal	0	2	-0.7255	0.0027	0.4647	-1.6485	-1.0347	-0.7225	-0.4127	0.1777	29637.93	1.0001
a[14]	scale adjustment for assessment unit 14	Normal	0	2	-3.4961	0.0025	0.4122	-4.2787	-3.7687	-3.5066	-3.2358	-2.6507	26349.76	1.0002
a[15]	scale adjustment for assessment unit 15	Normal	0	2	-3.0002	0.0029	0.5724	-4.1333	-3.3733	-2.9999	-2.6268	-1.8682	38702.1	1
a[16]	scale adjustment for assessment unit 16	Normal	0	2	-0.6102	0.0031	0.5761	-1.7464	-0.991	-0.6099	-0.2345	0.5305	34682.28	1.0001
a[17]	scale adjustment for assessment unit 17	Normal	0	2	-2.9756	0.0019	0.2923	-3.5363	-3.1726	-2.9813	-2.7847	-2.3843	24063.21	1.0003
a[18]	scale adjustment for assessment unit 18	Normal	0	2	0.5748	0.0022	0.2791	0.034	0.3858	0.571	0.7581	1.1373	15407.54	1.0005
a[19]	scale adjustment for assessment unit 19	Normal	0	2	-1.0885	0.0035	0.7061	-2.4345	-1.5655	-1.103	-0.6302	0.3445	41060.75	1
a[20]	scale adjustment for assessment unit 21	Normal	0	2	-0.8486	0.0019	0.2402	-1.2981	-1.0124	-0.856	-0.6921	-0.353	16227.75	1.0004
a[21]	scale adjustment for assessment unit 22	Normal	0	2	0.1194	0.0023	0.2512	-0.3619	-0.0518	0.1147	0.2856	0.6227	11743.67	1.0008
a[22]	scale adjustment for assessment unit 23	Normal	0	2	-0.9242	0.0024	0.4202	-1.7561	-1.2028	-0.92	-0.642	-0.1064	31695.02	1.0001
a[23]	scale adjustment for assessment unit 24	Normal	0	2	-1.3955	0.0028	0.5003	-2.3806	-1.7265	-1.3944	-1.0634	-0.4155	31458.71	1.0001
a[24]	scale adjustment for assessment unit 25	Normal	0	2	-2.6289	0.002	0.3181	-3.2507	-2.8413	-2.6298	-2.4187	-1.9963	25653.54	1.0003
a[25]	scale adjustment for assessment unit 26	Normal	0	2	-1.2109	0.0027	0.4604	-2.1225	-1.5169	-1.2082	-0.9051	-0.3053	28938.13	1.0002
a[26]	scale adjustment for assessment unit 27	Normal	0	2	-2.4286	0.0027	0.3831	-3.1725	-2.6791	-2.4328	-2.1864	-1.6507	19991.33	1.0004
a[27]	scale adjustment for assessment unit 28	Normal	0	2	1.6533	0.0023	0.2827	1.1144	1.4622	1.6472	1.8393	2.2262	14594.25	1.0004
a[28]	scale adjustment for assessment unit 29	Normal	0	2	0.3284	0.0019	0.2596	-0.1625	0.1523	0.3214	0.4984	0.8579	18227.12	1.0005
a[29]	scale adjustment for assessment unit 30	Normal	0	2	-0.9347	0.0023	0.3691	-1.6647	-1.1752	-0.9325	-0.692	-0.2106	26859.9	1.0002
a[30]	scale adjustment for assessment unit 31	Normal	0	2	-2.3712	0.0023	0.5237	-3.3769	-2.717	-2.383	-2.0416	-1.3016	51052.85	1
a[31]	scale adjustment for assessment unit 32	Normal	0	2	0.9742	0.0022	0.2217	0.5462	0.8249	0.9712	1.1207	1.4187	10384.85	1.0007
a[32]	scale adjustment for assessment unit 33	Normal	0	2	-3.2963	0.0029	0.5999	-4.4284	-3.7009	-3.3154	-2.9113	-2.0598	43962.59	1.0001
a[33]	scale adjustment for assessment unit 34	Normal	0	2	-0.2031	0.0021	0.3573	-0.8922	-0.445	-0.2088	0.0341	0.5128	30339.26	1.0002
a[34]	scale adjustment for assessment unit 35	Normal	0	2	1.2216	0.0024	0.3258	0.5919	1.001	1.2177	1.4372	1.8685	18532.52	1.0002
a[35]	scale adjustment for assessment unit 36	Normal	0	2	-1.8975	0.0035	0.6336	-3.1884	-2.3177	-1.8754	-1.4555	-0.7178	33113.91	1
a[36]	scale adjustment for assessment unit 37	Normal	0	2	-1.1962	0.0041	0.7529	-2.7055	-1.7003	-1.181	-0.6774	0.2276	33778.64	1
a[37]	scale adjustment for assessment unit 38	Normal	0	2	-2.7641	0.0023	0.4141	-3.5662	-3.0385	-2.7684	-2.4935	-1.941	33730.67	1.0001
a[38]	scale adjustment for assessment unit 39	Normal	0	2	-0.0334	0.0025	0.3478	-0.6841	-0.2713	-0.045	0.1921	0.6804	19524.17	1.0003
a[39]	scale adjustment for assessment unit 40	Normal	0	2	-2.5216	0.0024	0.3169	-3.1346	-2.7316	-2.526	-2.3167	-1.8873	17420.69	1.0004
a[40]	scale adjustment for assessment unit 41	Normal	0	2	-2.2049	0.0021	0.3202	-2.8198	-2.4211	-2.211	-1.9957	-1.559	23656.6	1.0005
a[41]	scale adjustment for assessment unit 42	Normal	0	2	-0.901	0.0026	0.3463	-1.5501	-1.1383	-0.9117	-0.6752	-0.1928	17790.93	1.0001
a[42]	scale adjustment for assessment unit 43	Normal	0	2	-4.1194	0.0027	0.4238	-4.9475	-4.3989	-4.1222	-3.8429	-3.272	24892.43	1.0003
a[43]	scale adjustment for assessment unit 44	Normal	0	2	-3.8977	0.0031	0.5363	-4.8841	-4.2605	-3.9254	-3.563	-2.7634	29409.49	1.0002
a[44]	scale adjustment for assessment unit 45	Normal	0	2	-0.272	0.0024	0.2863	-0.8299	-0.4633	-0.2751	-0.0839	0.303	14486.63	1.0003
a[45]	scale adjustment for assessment unit 46	Normal	0	2	-0.1797	0.0023	0.2491	-0.6608	-0.3474	-0.1827	-0.0147	0.3162	12133.66	1.0007
a[46]	scale adjustment for assessment unit 47	Normal	0	2	-2.4087	0.0024	0.3058	-3.0004	-2.613	-2.4121	-2.2103	-1.7915	16532.92	1.0002
a[47]	scale adjustment for assessment unit 48	Normal	0	2	-0.061	0.0022	0.2539	-0.556	-0.2303	-0.0624	0.1066	0.4451	12744.29	1.0006
a[48]	scale adjustment for assessment unit 49	Normal	0	2	-4.0582	0.0031	0.5059	-5.0086	-4.3895	-4.0775	-3.7454	-3.0029	27484.66	1.0003
a[49]	scale adjustment for assessment unit 50	Normal	0	2	-1.0375	0.0031	0.5984	-2.2074	-1.4293	-1.0441	-0.6504	0.1637	38380.25	1.0001
sd_r[1]	obsevation variance for assessment unit 1	Half-Normal	0	2	0.5373	7.00E-04	0.1764	0.2928	0.4163	0.5045	0.621	0.9695	57164.81	1
sd_r[2]	obsevation variance for assessment unit 2	Half-Normal	0	2	0.8943	7.00E-04	0.1784	0.6191	0.768	0.8702	0.9922	1.3137	69590.75	1.0002
sd_r[3]	obsevation variance for assessment unit 3	Half-Normal	0	2	0.8015	0.001	0.2276	0.4789	0.6413	0.7616	0.918	1.3569	52971.34	1
sd_r[4]	obsevation variance for assessment unit 4	Half-Normal	0	2	0.8168	4.00E-04	0.1092	0.6268	0.7401	0.8081	0.8842	1.0562	64251.65	1.0001
sd_r[5]	obsevation variance for assessment unit 5	Half-Normal	0	2	0.5854	5.00E-04	0.1329	0.3842	0.4914	0.5659	0.657	0.8986	61273.31	1
sd_r[6]	obsevation variance for assessment unit 6	Half-Normal	0	2	0.9396	0.0011	0.2662	0.5724	0.7542	0.8894	1.0704	1.5979	61936.89	1
sd_r[7]	obsevation variance for assessment unit 7	Half-Normal	0	2	1.7416	9.00E-04	0.2579	1.3161	1.5589	1.7144	1.8937	2.3255	84898.68	1
sd_r[8]	obsevation variance for assessment unit 8	Half-Normal	0	2	0.6889	9.00E-04	0.1959	0.4107	0.5517	0.6552	0.7882	1.1633	52510.92	1
sd_r[9]	obsevation variance for assessment unit 9	Half-Normal	0	2	2.0648	0.0018	0.4833	1.3423	1.7212	1.9881	2.3286	3.2217	73846.15	1
sd_r[10]	obsevation variance for assessment unit 10	Half-Normal	0	2	1.9926	0.0014	0.3597	1.4144	1.7372	1.9503	2.1989	2.8101	63617.48	1
sd_r[11]	obsevation variance for assessment unit 11	Half-Normal	0	2	0.9412	0.0014	0.258	0.5646	0.7527	0.8982	1.0844	1.5517	86265.33	1
sd_r[12]	obsevation variance for assessment unit 12	Half-Normal	0	2	1.4428	9.00E-04	0.2631	1.0285	1.2572	1.4085	1.5898	2.0541	78886.51	1
sd_r[13]	obsevation variance for assessment unit 13	Half-Normal	0	2	1.591	8.00E-04	0.2394	1.1984	1.4202	1.5648	1.7331	2.1297	80439.93	1
sd_r[14]	obsevation variance for assessment unit 14	Half-Normal	0	2	1.174	0.0012	0.3013	0.7478	0.9643	1.1208	1.325	1.9073	62011.3	1
sd_r[15]	obsevation variance for assessment unit 15	Half-Normal	0	2	1.3192	0.0014	0.3568	0.8172	1.0688	1.2553	1.4976	2.1956	65426.59	1
sd_r[16]	obsevation variance for assessment unit 16	Half-Normal	0	2	1.7935	0.0013	0.3455	1.253	1.5495	1.748	1.986	2.6034	71762.02	1
sd_r[17]	obsevation variance for assessment unit 17	Half-Normal	0	2	1.3621	6.00E-04	0.1759	1.0663	1.2371	1.3459	1.4679	1.7537	89480.73	1
sd_r[18]	obsevation variance for assessment unit 18	Half-Normal	0	2	0.7127	4.00E-04	0.1178	0.5219	0.6296	0.6986	0.7811	0.9807	70422.36	1
sd_r[19]	obsevation variance for assessment unit 19	Half-Normal	0	2	2.2655	0.0014	0.4068	1.6192	1.9764	2.2139	2.4995	3.1975	81590.82	1
sd_r[20]	obsevation variance for assessment unit 20	Half-Normal	0	2	0.5801	6.00E-04	0.09	0.4291	0.5162	0.5715	0.6342	0.7802	25780.2	1.0002
sd_r[21]	obsevation variance for assessment unit 21	Half-Normal	0	2	0.7237	4.00E-04	0.0966	0.5574	0.6556	0.7154	0.7829	0.9353	60416.63	1
sd_r[22]	obsevation variance for assessment unit 22	Half-Normal	0	2	0.5327	3.00E-04	0.0897	0.3877	0.47	0.524	0.5863	0.7365	71067.68	1
sd_r[23]	obsevation variance for assessment unit 23	Half-Normal	0	2	1.5907	7.00E-04	0.21	1.2381	1.4414	1.5708	1.717	2.0566	83635.84	1
sd_r[24]	obsevation variance for assessment unit 24	Half-Normal	0	2	1.4166	0.001	0.2794	0.986	1.2187	1.3775	1.5699	2.0801	76864.76	1.0001
sd_r[25]	obsevation variance for assessment unit 25	Half-Normal	0	2	1.0661	5.00E-04	0.1569	0.8076	0.9552	1.0495	1.1583	1.4207	82726.05	1
sd_r[26]	obsevation variance for assessment unit 26	Half-Normal	0	2	1.3434	9.00E-04	0.2581	0.9436	1.1603	1.3085	1.4864	1.9502	78218.65	1
sd_r[27]	obsevation variance for assessment unit 27	Half-Normal	0	2	0.4751	6.00E-04	0.1404	0.28	0.3778	0.4499	0.5434	0.8143	49604.22	1
sd_r[28]	obsevation variance for assessment unit 28	Half-Normal	0	2	0.6272	4.00E-04	0.1014	0.4621	0.5552	0.6157	0.6867	0.8581	70973.77	1
sd_r[29]	obsevation variance for assessment unit 29	Half-Normal	0	2	0.7791	4.00E-04	0.1123	0.5911	0.6997	0.7676	0.8466	1.03	76656.16	1
sd_r[30]	obsevation variance for assessment unit 30	Half-Normal	0	2	0.7934	6.00E-04	0.1593	0.544	0.6808	0.7728	0.8831	1.1618	72319.68	1
sd_r[31]	obsevation variance for assessment unit 31	Half-Normal	0	2	1.7997	0.0015	0.3916	1.2062	1.5205	1.741	2.0134	2.7286	71532.42	1
sd_r[32]	obsevation variance for assessment unit 32	Half-Normal	0	2	0.3525	3.00E-04	0.0641	0.2474	0.3072	0.3456	0.39	0.4979	58231.45	1
sd_r[33]	obsevation variance for assessment unit 33	Half-Normal	0	2	1.7569	0.0013	0.359	1.2058	1.5031	1.7059	1.955	2.6028	73028.51	1
sd_r[34]	obsevation variance for assessment unit 34	Half-Normal	0	2	1.4777	7.00E-04	0.192	1.1559	1.3422	1.459	1.5931	1.9057	86453.86	1
sd_r[35]	obsevation variance for assessment unit 35	Half-Normal	0	2	0.8068	5.00E-04	0.135	0.5917	0.712	0.7901	0.8828	1.1167	78044.94	1
sd_r[36]	obsevation variance for assessment unit 36	Half-Normal	0	2	2.0586	9.00E-04	0.2623	1.615	1.8737	2.0332	2.2157	2.6417	76387.46	1.0001
sd_r[37]	obsevation variance for assessment unit 37	Half-Normal	0	2	1.8264	0.0014	0.3756	1.2531	1.5591	1.7728	2.0353	2.7089	76549.37	1
sd_r[38]	obsevation variance for assessment unit 38	Half-Normal	0	2	1.4411	9.00E-04	0.2563	1.0373	1.2598	1.4086	1.5849	2.0332	76210.79	1
sd_r[39]	obsevation variance for assessment unit 39	Half-Normal	0	2	0.8306	7.00E-04	0.1552	0.5893	0.7209	0.8093	0.9163	1.1956	56810.04	1
sd_r[40]	obsevation variance for assessment unit 40	Half-Normal	0	2	0.793	9.00E-04	0.2155	0.4922	0.6425	0.7545	0.8992	1.3172	60796.19	1
sd_r[41]	obsevation variance for assessment unit 41	Half-Normal	0	2	1.214	6.00E-04	0.1596	0.946	1.1008	1.1985	1.3107	1.5704	79947.21	1
sd_r[42]	obsevation variance for assessment unit 42	Half-Normal	0	2	0.6488	5.00E-04	0.13	0.4477	0.5571	0.6308	0.7202	0.9518	69911.03	1
sd_r[43]	obsevation variance for assessment unit 43	Half-Normal	0	2	0.8205	9.00E-04	0.2071	0.5214	0.6753	0.7854	0.9246	1.3278	58308.7	1
sd_r[44]	obsevation variance for assessment unit 44	Half-Normal	0	2	1.0514	0.001	0.2488	0.6885	0.8771	1.0103	1.1791	1.6544	61848.31	1
sd_r[45]	obsevation variance for assessment unit 45	Half-Normal	0	2	0.522	5.00E-04	0.1337	0.3278	0.4285	0.5	0.5891	0.8469	61885.49	1
sd_r[46]	obsevation variance for assessment unit 46	Half-Normal	0	2	0.3934	4.00E-04	0.1047	0.2414	0.3202	0.3764	0.4465	0.6461	63137.47	1
sd_r[47]	obsevation variance for assessment unit 47	Half-Normal	0	2	0.6786	7.00E-04	0.1678	0.4359	0.5614	0.6505	0.7635	1.0879	58629.54	1
sd_r[48]	obsevation variance for assessment unit 48	Half-Normal	0	2	0.3116	4.00E-04	0.0899	0.1771	0.2486	0.2978	0.3591	0.526	62951.24	1
sd_r[49]	obsevation variance for assessment unit 49	Half-Normal	0	2	1.0496	0.0011	0.2642	0.6738	0.8654	1.0025	1.181	1.6585	61770.15	1
sd_r[50]	obsevation variance for assessment unit 50	Half-Normal	0	2	1.6069	0.0014	0.3642	1.0641	1.348	1.5511	1.8034	2.483	72737.86	1
sd_obsCov	standard deviation of year-after-treatment effects	Half-Normal	0	2	0.2805	0.0004	0.0682	0.1691	0.2324	0.273	0.3203	0.4356	33311.78	1
ObsBetas[1]	Year-after-treatment effect for assessment for tributary 1	Dbl Exponential	0	sd_obsCov	-0.3674	9.00E-04	0.1834	-0.7322	-0.491	-0.3668	-0.2424	-0.0136	39494.63	1.0001
ObsBetas[2]	Year-after-treatment effect for assessment for tributary 2	Dbl Exponential	0	sd_obsCov	0.4461	0.0014	0.2923	-0.0849	0.2329	0.4499	0.6515	1.0113	43946.11	1.0001
ObsBetas[3]	Year-after-treatment effect for assessment for tributary 3	Dbl Exponential	0	sd_obsCov	0.096	6.00E-04	0.1269	-0.145	0.0096	0.0896	0.1793	0.3565	43755.72	1
ObsBetas[4]	Year-after-treatment effect for assessment for tributary 4	Dbl Exponential	0	sd_obsCov	-0.0469	0.0012	0.2567	-0.6168	-0.1831	-0.0291	0.0995	0.4537	47171.06	1
ObsBetas[5]	Year-after-treatment effect for assessment for tributary 5	Dbl Exponential	0	sd_obsCov	0.1035	0.0011	0.2534	-0.3698	-0.0506	0.0765	0.2462	0.6653	53764.88	1
ObsBetas[6]	Year-after-treatment effect for assessment for tributary 6	Dbl Exponential	0	sd_obsCov	0.2502	0.001	0.2276	-0.169	0.0879	0.2436	0.4045	0.709	49607.78	1
ObsBetas[7]	Year-after-treatment effect for assessment for tributary 7	Dbl Exponential	0	sd_obsCov	-0.3179	0.002	0.405	-1.2852	-0.5406	-0.239	-0.0313	0.2984	42526.37	1
ObsBetas[8]	Year-after-treatment effect for assessment for tributary 8	Dbl Exponential	0	sd_obsCov	0.535	0.0018	0.3191	-0.0686	0.3022	0.5546	0.7737	1.058	31368.4	1
ObsBetas[9]	Year-after-treatment effect for assessment for tributary 9	Dbl Exponential	0	sd_obsCov	0.2208	0.001	0.2194	-0.1559	0.0606	0.2023	0.3626	0.686	51570.95	1
ObsBetas[10]	Year-after-treatment effect for assessment for tributary 10	Dbl Exponential	0	sd_obsCov	0.2102	0.0013	0.261	-0.2331	0.0259	0.1781	0.3704	0.7874	42788.97	1
ObsBetas[11]	Year-after-treatment effect for assessment for tributary 11	Dbl Exponential	0	sd_obsCov	0.2947	6.00E-04	0.1503	0.0028	0.1923	0.296	0.3963	0.5875	65883.65	1
ObsBetas[12]	Year-after-treatment effect for assessment for tributary 12	Dbl Exponential	0	sd_obsCov	-0.3017	0.0017	0.3708	-1.1699	-0.5174	-0.2346	-0.0359	0.2775	46251.48	1.0001
ObsBetas[13]	Year-after-treatment effect for assessment for tributary 13	Dbl Exponential	0	sd_obsCov	0.182	9.00E-04	0.1099	-0.0129	0.1046	0.1759	0.2522	0.4152	14164.28	1.0006
ObsBetas[14]	Year-after-treatment effect for assessment for tributary 14	Dbl Exponential	0	sd_obsCov	-0.0399	4.00E-04	0.0869	-0.2195	-0.0951	-0.036	0.017	0.1267	56506.56	1.0001
ObsBetas[15]	Year-after-treatment effect for assessment for tributary 15	Dbl Exponential	0	sd_obsCov	0.1987	0.001	0.2078	-0.165	0.0489	0.1807	0.3325	0.6429	47163.19	1
ObsBetas[16]	Year-after-treatment effect for assessment for tributary 16	Dbl Exponential	0	sd_obsCov	0.0942	7.00E-04	0.165	-0.212	-0.0131	0.0818	0.1952	0.4452	55224.22	1
ObsBetas[17]	Year-after-treatment effect for assessment for tributary 17	Dbl Exponential	0	sd_obsCov	0.0398	8.00E-04	0.1708	-0.3074	-0.0589	0.0339	0.1415	0.3887	50512.07	1
ObsBetas[18]	Year-after-treatment effect for assessment for tributary 18	Dbl Exponential	0	sd_obsCov	-0.0481	5.00E-04	0.1242	-0.3075	-0.1246	-0.0424	0.03	0.1941	63892.99	1
ObsBetas[19]	Year-after-treatment effect for assessment for tributary 19	Dbl Exponential	0	sd_obsCov	-0.0617	5.00E-04	0.1397	-0.3547	-0.1485	-0.0538	0.027	0.2066	70715.79	1.0001
ObsBetas[20]	Year-after-treatment effect for assessment for tributary 20	Dbl Exponential	0	sd_obsCov	0.1805	4.00E-04	0.0915	0.0028	0.1189	0.1799	0.2413	0.3612	66469.32	1
ObsBetas[21]	Year-after-treatment effect for assessment for tributary 21	Dbl Exponential	0	sd_obsCov	-0.2336	0.0013	0.3285	-0.9912	-0.4209	-0.1801	-0.0094	0.3047	51990.45	1
ObsBetas[22]	Year-after-treatment effect for assessment for tributary 22	Dbl Exponential	0	sd_obsCov	0.788	7.00E-04	0.1702	0.4446	0.6769	0.7904	0.9018	1.1166	54173.66	1
ObsBetas[23]	Year-after-treatment effect for assessment for tributary 23	Dbl Exponential	0	sd_obsCov	0.4158	0.0018	0.3297	-0.1196	0.1639	0.3886	0.636	1.1199	35488.76	1
ObsBetas[24]	Year-after-treatment effect for assessment for tributary 24	Dbl Exponential	0	sd_obsCov	0.977	0.001	0.2023	0.5484	0.8505	0.987	1.1155	1.3473	43524.52	1
ObsBetas[25]	Year-after-treatment effect for assessment for tributary 25	Dbl Exponential	0	sd_obsCov	-0.1234	7.00E-04	0.1438	-0.4288	-0.2158	-0.1126	-0.022	0.134	47297.07	1
ObsBetas[26]	Year-after-treatment effect for assessment for tributary 26	Dbl Exponential	0	sd_obsCov	-0.0326	0.001	0.2341	-0.5384	-0.1602	-0.0203	0.1025	0.4253	51273.94	1
ObsBetas[27]	Year-after-treatment effect for assessment for tributary 27	Dbl Exponential	0	sd_obsCov	-0.0217	0.0011	0.2649	-0.5903	-0.1645	-0.0135	0.1248	0.5125	60447.63	1
ObsBetas[28]	Year-after-treatment effect for assessment for tributary 28	Dbl Exponential	0	sd_obsCov	-0.2106	0.0012	0.2671	-0.8088	-0.371	-0.1753	-0.0242	0.2373	49076.64	1
ObsBetas[29]	Year-after-treatment effect for assessment for tributary 29	Dbl Exponential	0	sd_obsCov	-0.0888	5.00E-04	0.1393	-0.3583	-0.1704	-0.0825	-0.0037	0.1587	64550.04	1
ObsBetas[30]	Year-after-treatment effect for assessment for tributary 30	Dbl Exponential	0	sd_obsCov	0.1667	9.00E-04	0.214	-0.2279	0.0198	0.1513	0.304	0.6127	54714.79	1
ObsBetas[31]	Year-after-treatment effect for assessment for tributary 31	Dbl Exponential	0	sd_obsCov	-0.1253	4.00E-04	0.1147	-0.3607	-0.1991	-0.1217	-0.0475	0.0887	68510.32	1
ObsBetas[32]	Year-after-treatment effect for assessment for tributary 32	Dbl Exponential	0	sd_obsCov	0.0087	6.00E-04	0.1542	-0.3059	-0.0818	0.0073	0.0995	0.3246	69190.67	1.0001
ObsBetas[33]	Year-after-treatment effect for assessment for tributary 33	Dbl Exponential	0	sd_obsCov	0.0529	4.00E-04	0.1007	-0.142	-0.0107	0.0488	0.1152	0.2634	59655.24	1
ObsBetas[34]	Year-after-treatment effect for assessment for tributary 34	Dbl Exponential	0	sd_obsCov	0.1039	7.00E-04	0.1748	-0.2244	-0.009	0.0903	0.211	0.478	62482.69	1

Table S3. Recruitment deviation model parameters in the Lake Superior population dynamics and control model. Posterior distribution columns provide the mean, standard error of the mean (sd_mean), quantiles of the distribution, and model diagnostics associated with each parameter.

parameter		prior distribution (transformed parameter)				posterior distribution								model diagnostics	
symbol	description	family	scale	shape	multiplier	mean	se_mean	sd	2.50%	25%	50%	75%	97.50%	n_eff	Rhat
pro_dev[1]	annual recruitment deviation for 1953	Normal		0	1 sd_q	1.5646	0.0044	0.5788	0.3819	1.1911	1.597	1.9488	2.6476	17193.34	1.0002
pro_dev[2]	annual recruitment deviation for 1954	Normal		0	1 sd_q	-0.8234	0.0028	0.6824	-2.2989	-1.2428	-0.7789	-0.3522	0.3828	60883	1.0001
pro_dev[3]	annual recruitment deviation for 1955	Normal		0	1 sd_q	-1.0367	0.0029	0.6458	-2.472	-1.4214	-0.9814	-0.5882	0.071	50799.4	1.0001
pro_dev[4]	annual recruitment deviation for 1956	Normal		0	1 sd_q	0.7933	0.0024	0.3903	0.0123	0.5482	0.8021	1.054	1.5278	25994.36	1.0003
pro_dev[5]	annual recruitment deviation for 1957	Normal		0	1 sd_q	-0.1674	0.0029	0.6381	-1.5789	-0.5421	-0.1151	0.2633	0.9447	49574.67	1.0001
pro_dev[6]	annual recruitment deviation for 1958	Normal		0	1 sd_q	-0.3746	0.0026	0.5029	-1.4589	-0.6735	-0.3479	-0.0396	0.533	37253.67	1.0001
pro_dev[7]	annual recruitment deviation for 1959	Normal		0	1 sd_q	-1.0489	0.0024	0.5453	-2.2643	-1.3696	-1.0041	-0.6739	-0.1074	52419.71	1.0001
pro_dev[8]	annual recruitment deviation for 1960	Normal		0	1 sd_q	-0.8315	0.003	0.5815	-2.1317	-1.1702	-0.7751	-0.4304	0.1505	37219.86	1.0002
pro_dev[9]	annual recruitment deviation for 1961	Normal		0	1 sd_q	0.5181	0.0031	0.5367	-0.5416	0.1683	0.5161	0.8716	1.5804	29849.8	1.0001
pro_dev[10]	annual recruitment deviation for 1962	Normal		0	1 sd_q	-0.3104	0.0028	0.6054	-1.6629	-0.6621	-0.2611	0.0993	0.7427	45739.09	1.0001
pro_dev[11]	annual recruitment deviation for 1963	Normal		0	1 sd_q	-0.3088	0.0027	0.5943	-1.6717	-0.6489	-0.245	0.1067	0.6678	50148.17	1
pro_dev[12]	annual recruitment deviation for 1964	Normal		0	1 sd_q	-0.2006	0.0026	0.5902	-1.5573	-0.5379	-0.1393	0.2052	0.7835	53139.65	1
pro_dev[13]	annual recruitment deviation for 1965	Normal		0	1 sd_q	0.5011	0.0019	0.4157	-0.4182	0.2619	0.5315	0.7797	1.2266	45580.38	1.0001
pro_dev[14]	annual recruitment deviation for 1966	Normal		0	1 sd_q	-0.3983	0.0026	0.6318	-1.8165	-0.7665	-0.3359	0.0394	0.6634	57365.8	1
pro_dev[15]	annual recruitment deviation for 1967	Normal		0	1 sd_q	-0.5124	0.0026	0.6514	-1.9702	-0.8992	-0.4521	-0.0562	0.5893	62094.62	1
pro_dev[16]	annual recruitment deviation for 1968	Normal		0	1 sd_q	0.321	0.0027	0.5417	-0.9116	0.0197	0.3765	0.6885	1.2294	41786.22	1
pro_dev[17]	annual recruitment deviation for 1969	Normal		0	1 sd_q	0.0119	0.0027	0.5515	-1.2529	-0.298	0.0702	0.3889	0.9301	40965.79	1
pro_dev[18]	annual recruitment deviation for 1970	Normal		0	1 sd_q	-0.262	0.0027	0.5838	-1.6126	-0.5879	-0.1928	0.1421	0.6893	47708.15	1
pro_dev[19]	annual recruitment deviation for 1971	Normal		0	1 sd_q	-0.117	0.0025	0.5505	-1.3613	-0.4318	-0.0625	0.2574	0.814	50348.52	1
pro_dev[20]	annual recruitment deviation for 1972	Normal		0	1 sd_q	-0.6477	0.0026	0.6283	-2.0483	-1.0235	-0.5897	-0.2113	0.4215	60119.85	1
pro_dev[21]	annual recruitment deviation for 1973	Normal		0	1 sd_q	0.2018	0.0035	0.6719	-1.3399	-0.186	0.2756	0.671	1.3149	36306.81	1
pro_dev[22]	annual recruitment deviation for 1974	Normal		0	1 sd_q	0.9377	0.0039	0.6164	-0.4371	0.5776	0.9903	1.3575	1.9979	25275.73	1.0002
pro_dev[23]	annual recruitment deviation for 1975	Normal		0	1 sd_q	-0.0796	0.0028	0.7638	-1.7288	-0.5517	-0.0284	0.4486	1.2766	74571.34	1
pro_dev[24]	annual recruitment deviation for 1976	Normal		0	1 sd_q	-0.0331	0.0027	0.6725	-1.5453	-0.4287	0.0288	0.4308	1.1206	62041.21	1.0001
pro_dev[25]	annual recruitment deviation for 1977	Normal		0	1 sd_q	0.1807	0.0029	0.6553	-1.2999	-0.1972	0.2415	0.6294	1.2957	51572.19	1
pro_dev[26]	annual recruitment deviation for 1978	Normal		0	1 sd_q	0.2173	0.0028	0.6431	-1.233	-0.1542	0.2754	0.658	1.3209	54257.62	1
pro_dev[27]	annual recruitment deviation for 1979	Normal		0	1 sd_q	-0.0713	0.0027	0.6573	-1.5131	-0.4631	-0.0155	0.3833	1.0726	58058.02	1
pro_dev[28]	annual recruitment deviation for 1980	Normal		0	1 sd_q	-0.3289	0.0025	0.6383	-1.7472	-0.7099	-0.2765	0.1099	0.7807	65389.21	1
pro_dev[29]	annual recruitment deviation for 1981	Normal		0	1 sd_q	-0.2329	0.0025	0.6164	-1.621	-0.5882	-0.1718	0.1892	0.8088	59313.69	1
pro_dev[30]	annual recruitment deviation for 1982	Normal		0	1 sd_q	0.2809	0.0023	0.5022	-0.8545	-0.0023	0.3274	0.6199	1.1361	48736.18	1
pro_dev[31]	annual recruitment deviation for 1983	Normal		0	1 sd_q	-0.2371	0.0026	0.6605	-1.7133	-0.6292	-0.1706	0.2238	0.8687	62564.35	1
pro_dev[32]	annual recruitment deviation for 1984	Normal		0	1 sd_q	0.1948	0.0029	0.6431	-1.2724	-0.1671	0.2639	0.6349	1.2678	50726.22	1
pro_dev[33]	annual recruitment deviation for 1985	Normal		0	1 sd_q	0.3297	0.0024	0.4956	-0.7639	0.0386	0.3653	0.6659	1.1996	42149.57	1.0002
pro_dev[34]	annual recruitment deviation for 1986	Normal		0	1 sd_q	-1.104	0.0024	0.6051	-2.4488	-1.462	-1.0535	-0.6845	-0.066	62801.38	1
pro_dev[35]	annual recruitment deviation for 1987	Normal		0	1 sd_q	-1.2185	0.0024	0.5938	-2.5262	-1.5746	-1.1699	-0.8062	-0.188	63555.02	1
pro_dev[36]	annual recruitment deviation for 1988	Normal		0	1 sd_q	-0.3029	0.0028	0.6136	-1.683	-0.6594	-0.2417	0.1186	0.7391	47879.29	1
pro_dev[37]	annual recruitment deviation for 1989	Normal		0	1 sd_q	0.2523	0.0026	0.5367	-0.9298	-0.0631	0.2963	0.6164	1.1876	44190.96	1.0001
pro_dev[38]	annual recruitment deviation for 1990	Normal		0	1 sd_q	-0.1626	0.0026	0.6351	-1.5622	-0.5374	-0.1046	0.2706	0.9332	60362.95	1
pro_dev[39]	annual recruitment deviation for 1991	Normal		0	1 sd_q	-0.3288	0.0027	0.6954	-1.8293	-0.7524	-0.2812	0.1462	0.9117	67763.16	1
pro_dev[40]	annual recruitment deviation for 1992	Normal		0	1 sd_q	0.9099	0.0032	0.6074	-0.469	0.5667	0.9611	1.3167	1.9584	37081.98	1
pro_dev[41]	annual recruitment deviation for 1993	Normal		0	1 sd_q	0.628	0.0039	0.7391	-1.0307	0.1962	0.6932	1.1374	1.8914	36138.88	1
pro_dev[42]	annual recruitment deviation for 1994	Normal		0	1 sd_q	0.6427	0.0037	0.7646	-1.1074	0.2059	0.7298	1.1744	1.9121	41791.93	1
pro_dev[43]	annual recruitment deviation for 1995	Normal		0	1 sd_q	0.6243	0.0038	0.8026	-1.1492	0.1366	0.6945	1.1847	2.0117	43537.64	1
pro_dev[44]	annual recruitment deviation for 1996	Normal		0	1 sd_q	0.0474	0.0031	0.7035	-1.5412	-0.3662	0.119	0.5359	1.2382	50582.63	1
pro_dev[45]	annual recruitment deviation for 1997	Normal		0	1 sd_q	0.4312	0.0028	0.5531	-0.8569	0.1322	0.496	0.8084	1.3271	39107.28	1
pro_dev[46]	annual recruitment deviation for 1998	Normal		0	1 sd_q	0.081	0.0032	0.7015	-1.4891	-0.3348	0.1466	0.5724	1.2659	48723.31	1
pro_dev[47]	annual recruitment deviation for 1999	Normal		0	1 sd_q	0.4873	0.0034	0.6946	-1.1196	0.0905	0.5706	0.9744	1.6144	42694.51	1
pro_dev[48]	annual recruitment deviation for 2000	Normal		0	1 sd_q	0.6491	0.0035	0.6549	-0.8289	0.2717	0.7136	1.0992	1.7564	34826.22	1
pro_dev[49]	annual recruitment deviation for 2001	Normal		0	1 sd_q	0.0985	0.0032	0.7337	-1.5196	-0.3428	0.1663	0.608	1.356	51388.94	1.0001
pro_dev[50]	annual recruitment deviation for 2002	Normal		0	1 sd_q	0.3482	0.003	0.6361	-1.1219	-0.0029	0.4194	0.783	1.3995	45254.69	1
pro_dev[51]	annual recruitment deviation for 2003	Normal		0	1 sd_q	0.3218	0.0032	0.6694	-1.1999	-0.0663	0.3902	0.7846	1.4512	43875.52	1.0001
pro_dev[52]	annual recruitment deviation for 2004	Normal		0	1 sd_q	0.1308	0.0028	0.6453	-1.3601	-0.2353	0.203	0.5771	1.1966	51637.43	1
pro_dev[53]	annual recruitment deviation for 2005	Normal		0	1 sd_q	-0.2648	0.0028	0.6867	-1.7855	-0.6753	-0.2008	0.2112	0.9115	61396.71	1
pro_dev[54]	annual recruitment deviation for 2006	Normal		0	1 sd_q	0.8042	0.0024	0.4505	-0.1611	0.5383	0.8302	1.1011	1.6206	34238.9	1
pro_dev[55]	annual recruitment deviation for 2007	Normal		0	1 sd_q	-0.5644	0.0027	0.6504	-1.9821	-0.9593	-0.5176	-0.1175	0.5853	60137.71	1
pro_dev[56]	annual recruitment deviation for 2008	Normal		0	1 sd_q	-0.9395	0.0023	0.6251	-2.2973	-1.3198	-0.8945	-0.5086	0.1572	72573.62	1.0001
pro_dev[57]	annual recruitment deviation for 2009	Normal		0	1 sd_q	-0.2479	0.0037	0.7268	-1.8283	-0.694	-0.1924	0.2582	1.0161	38147.44	1.0001
pro_dev[58]	annual recruitment deviation for 2010	Normal		0	1 sd_q	1.5125	0.0024	0.4357	0.6029	1.2414	1.5297	1.8027	2.3268	31929.17	1.0001
pro_dev[59]	annual recruitment deviation for 2011	Normal		0	1 sd_q	-0.3744	0.0026	0.6955	-1.8966	-0.7938	-0.3182	0.1052	0.8394	71882.49	1.0001
pro_dev[60]	annual recruitment deviation for 2012	Normal		0	1 sd_q	-0.5684	0.0024	0.6529	-2.0074	-0.9614	-0.5169	-0.1173	0.5628	75649.73	1
pro_dev[61]	annual recruitment deviation for 2013	Normal		0	1 sd_q	-0.2247	0.0026	0.7714	-1.839	-0.7095	-0.1952	0.3012	1.1967	91004.76	1
pro_dev[62]	annual recruitment deviation for 2014	fixed at 0	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
pro_dev[63]	annual recruitment deviation for 2015	fixed at 0	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
pro_dev[64]	annual recruitment deviation for 2016	fixed at 0	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
pro_dev[65]	annual recruitment deviation for 2017	fixed at 0	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
pro_dev[66]	annual recruitment deviation for 2018	fixed at 0	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
pro_dev[67]	annual recruitment deviation for 2019	fixed at 0	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA

Table S4. Adult abundance index model parameters in the Lake Superior population dynamics and control model. Posterior distribution columns provide the mean, standard error of the mean (sd_mean), quantiles of the distribution, and model diagnostics associated with each parameter.

parameter					posterior distribution					model diagnostics	
symbol	description	mean	se_mean	sd	2.50%	25%	50%	75%	97.50%	n_eff	Rhat
x3[1]	adult abundance index for 1953	4.9932	0.0017	0.2375	4.5083	4.8373	4.9997	5.1566	5.4401	19253.84	1.0005
x3[2]	adult abundance index for 1954	5.7455	0.0021	0.2472	5.2507	5.5811	5.7483	5.9135	6.2199	14170.12	1.0005
x3[3]	adult abundance index for 1955	6.3076	0.0022	0.2311	5.8441	6.1545	6.3119	6.4647	6.7505	11552.09	1.0007
x3[4]	adult abundance index for 1956	6.6784	0.0021	0.2227	6.2294	6.5314	6.6823	6.8296	7.1043	11051.99	1.0007
x3[5]	adult abundance index for 1957	6.7307	0.0021	0.2193	6.2884	6.586	6.7344	6.8793	7.1513	10682.51	1.0007
x3[6]	adult abundance index for 1958	6.3775	0.0022	0.2363	5.9041	6.2204	6.3804	6.5382	6.8292	11212.36	1.0006
x3[7]	adult abundance index for 1959	6.5324	0.0021	0.2252	6.0795	6.3827	6.5354	6.6854	6.9637	11109.71	1.0007
x3[8]	adult abundance index for 1960	7.1849	0.0021	0.2164	6.7481	7.042	7.1887	7.3317	7.5987	10663.23	1.0007
x3[9]	adult abundance index for 1961	6.7671	0.0023	0.2318	6.2982	6.614	6.7715	6.9242	7.211	10062.55	1.0008
x3[10]	adult abundance index for 1962	5.4272	0.0021	0.2314	4.9662	5.2741	5.428	5.5821	5.8794	11765.11	1.0008
x3[11]	adult abundance index for 1963	5.6315	0.0022	0.2274	5.1721	5.4814	5.636	5.7868	6.0677	10308.43	1.0008
x3[12]	adult abundance index for 1964	5.46	0.0023	0.2307	4.9997	5.3075	5.4624	5.6172	5.9032	10346.89	1.0009
x3[13]	adult abundance index for 1965	4.9716	0.0022	0.2332	4.5053	4.8171	4.9739	5.1294	5.421	11646.74	1.0006
x3[14]	adult abundance index for 1966	4.6588	0.0023	0.2415	4.1741	4.4994	4.6618	4.8216	5.122	11239.42	1.0007
x3[15]	adult abundance index for 1967	4.7202	0.0023	0.2392	4.2421	4.5609	4.7231	4.882	5.1801	11226.68	1.0007
x3[16]	adult abundance index for 1968	5.2401	0.0022	0.247	4.7469	5.0747	5.2431	5.4078	5.7175	12805.68	1.0004
x3[17]	adult abundance index for 1969	5.2149	0.0022	0.2455	4.7261	5.0514	5.2163	5.3806	5.6911	12807.29	1.0005
x3[18]	adult abundance index for 1970	4.9469	0.0022	0.2528	4.4426	4.7782	4.9492	5.1192	5.4359	13183.54	1.0005
x3[19]	adult abundance index for 1971	5.1689	0.0022	0.268	4.6411	4.99	5.1703	5.3495	5.6924	14217.24	1.0005
x3[20]	adult abundance index for 1972	5.4799	0.0022	0.2564	4.9635	5.31	5.4839	5.6535	5.9713	13646.19	1.0006
x3[21]	adult abundance index for 1973	5.1954	0.0022	0.2556	4.6819	5.0253	5.1987	5.3683	5.686	13600.51	1.0007
x3[22]	adult abundance index for 1974	4.6792	0.0022	0.2679	4.1413	4.5023	4.6814	4.8608	5.1967	14734.51	1.0006
x3[23]	adult abundance index for 1975	4.981	0.0023	0.2724	4.4365	4.7998	4.9849	5.167	5.5029	14551.9	1.0006
x3[24]	adult abundance index for 1976	5.1794	0.002	0.2432	4.6858	5.0176	5.1842	5.345	5.6424	14375.55	1.0006
x3[25]	adult abundance index for 1977	5.081	0.0019	0.2293	4.616	4.9294	5.0852	5.2369	5.5179	14973.28	1.0005
x3[26]	adult abundance index for 1978	4.9547	0.002	0.235	4.4771	4.8004	4.9598	5.1158	5.4018	14327.79	1.0006
x3[27]	adult abundance index for 1979	4.939	0.0022	0.2534	4.4268	4.7726	4.9434	5.1141	5.4165	13494.59	1.0006
x3[28]	adult abundance index for 1980	5.546	0.0019	0.2846	4.9824	5.3564	5.5467	5.7365	6.1064	21683.18	1.0002
x3[29]	adult abundance index for 1981	5.927	0.0016	0.283	5.3567	5.7403	5.9324	6.1201	6.4676	32346.58	1.0002
x3[30]	adult abundance index for 1982	5.604	0.0016	0.2946	5.009	5.4095	5.6112	5.8073	6.1607	34488.91	1.0003
x3[31]	adult abundance index for 1983	5.2337	0.0016	0.2911	4.6573	5.0393	5.2347	5.4305	5.7994	31844.03	1.0002
x3[32]	adult abundance index for 1984	5.3895	0.0015	0.2786	4.8341	5.2043	5.3935	5.5766	5.9278	35640.79	1.0001
x3[33]	adult abundance index for 1985	5.4357	0.0016	0.2828	4.8666	5.2489	5.4408	5.6281	5.9753	31386.69	1.0002
x3[34]	adult abundance index for 1986	5.2556	0.0018	0.2857	4.6812	5.0648	5.261	5.4509	5.8031	26481.83	1.0002
x3[35]	adult abundance index for 1987	5.1267	0.0017	0.2741	4.576	4.9445	5.1312	5.3127	5.6515	26292.81	1.0002
x3[36]	adult abundance index for 1988	5.4618	0.0016	0.263	4.9286	5.2881	5.4678	5.6403	5.9636	26284.46	1.0002
x3[37]	adult abundance index for 1989	5.8296	0.0016	0.2583	5.3075	5.659	5.834	6.0062	6.3184	25079.82	1.0003
x3[38]	adult abundance index for 1990	5.7893	0.0017	0.2636	5.2557	5.6164	5.7956	5.9675	6.2919	23691.8	1.0003
x3[39]	adult abundance index for 1991	5.7339	0.0019	0.2778	5.1711	5.5503	5.7392	5.9229	6.2634	22003.66	1.0002
x3[40]	adult abundance index for 1992	5.7543	0.0018	0.2634	5.2164	5.5821	5.7612	5.9338	6.2521	20566.51	1.0003
x3[41]	adult abundance index for 1993	5.3015	0.0019	0.2757	4.7435	5.1201	5.3069	5.4901	5.8257	22146.95	1.0004
x3[42]	adult abundance index for 1994	4.739	0.002	0.2933	4.1462	4.5451	4.7447	4.9401	5.297	22134.27	1.0002
x3[43]	adult abundance index for 1995	5.2079	0.002	0.2817	4.6375	5.0217	5.2142	5.4004	5.7462	19623.16	1.0003
x3[44]	adult abundance index for 1996	5.737	0.002	0.2872	5.1492	5.5478	5.744	5.9339	6.2805	21010.29	1.0004
x3[45]	adult abundance index for 1997	5.7817	0.0017	0.2576	5.2578	5.6128	5.788	5.9565	6.2692	23541.25	1.0003
x3[46]	adult abundance index for 1998	5.8505	0.0015	0.2559	5.3338	5.6811	5.8554	6.0243	6.3386	27947.29	1.0002
x3[47]	adult abundance index for 1999	6.4051	0.0017	0.2603	5.8797	6.2332	6.4117	6.5831	6.8975	22364.8	1.0003
x3[48]	adult abundance index for 2000	6.5607	0.0017	0.2521	6.0514	6.394	6.5653	6.7322	7.0429	21094.48	1.0003
x3[49]	adult abundance index for 2001	6.3471	0.0017	0.2639	5.8147	6.1725	6.3517	6.5269	6.8499	23280.31	1.0003
x3[50]	adult abundance index for 2002	6.0489	0.0017	0.2542	5.5267	5.8829	6.0564	6.2231	6.5231	21758.96	1.0002
x3[51]	adult abundance index for 2003	5.8669	0.0016	0.2528	5.3529	5.7019	5.8738	6.0394	6.3449	24952.14	1.0002
x3[52]	adult abundance index for 2004	6.0865	0.0017	0.2559	5.564	5.9193	6.0948	6.2626	6.5658	21754.37	1.0003
x3[53]	adult abundance index for 2005	6.1839	0.0018	0.2645	5.6491	6.0099	6.1906	6.3637	6.6875	20920.61	1.0003
x3[54]	adult abundance index for 2006	6.2987	0.0019	0.2925	5.7118	6.1053	6.3054	6.4984	6.8592	22580.94	1.0003
x3[55]	adult abundance index for 2007	6.4184	0.002	0.2838	5.8346	6.2324	6.4282	6.6143	6.9492	21061.72	1.0003
x3[56]	adult abundance index for 2008	6.2744	0.0019	0.2788	5.705	6.0899	6.2834	6.468	6.7921	21781.46	1.0004
x3[57]	adult abundance index for 2009	6.1625	0.0019	0.2731	5.6075	5.9824	6.1702	6.3492	6.68	20240.94	1.0003
x3[58]	adult abundance index for 2010	6.0849	0.0021	0.2924	5.487	5.894	6.0935	6.2868	6.634	19759.51	1.0003
x3[59]	adult abundance index for 2011	5.8852	0.002	0.2812	5.3074	5.7016	5.8943	6.0796	6.409	19616.22	1.0003
x3[60]	adult abundance index for 2012	5.7817	0.0019	0.2734	5.2259	5.6024	5.7881	5.969	6.2971	20836.14	1.0003
x3[61]	adult abundance index for 2013	6.0329	0.002	0.2721	5.4672	5.8576	6.0434	6.2211	6.5375	18871	1.0002
x3[62]	adult abundance index for 2014	5.7648	0.0019	0.2617	5.2304	5.5925	5.7721	5.9449	6.2596	19533.21	1.0002
x3[63]	adult abundance index for 2015	5.1119	0.0018	0.2982	4.5097	4.9162	5.1173	5.3149	5.6805	27162.8	1.0003
x3[64]	adult abundance index for 2016	5.7837	0.002	0.2912	5.1921	5.5937	5.7917	5.9832	6.3352	21835.75	1.0003
x3[65]	adult abundance index for 2017	6.5008	0.0022	0.3058	5.8641	6.3026	6.5126	6.7139	7.0657	19300.91	1.0004
x3[66]	adult abundance index for 2018	6.2117	0.0022	0.2934	5.6049	6.0206	6.2203	6.4134	6.7606	18608.37	1.0004
x3[67]	adult abundance index for 2019	5.3346	0.0019	0.3064	4.7169	5.1311	5.3402	5.5443	5.9196	26513.23	1.0002

APPENDIX C: LAKE SUPERIOR POPULATION DYNAMICS MODEL POST-POSTERIOR CHECKING METHODS AND RESULTS

We simulated a dataset from each MCMC iteration using the *generated quantities* code block in our *stan* model. Simulated datasets were graphed (mean and 95% credibility intervals) with observed data and examined visually. We noted that residuals for some assessment units appeared to show strong autocorrelation, but, overall, most observations fell within 95% confidence intervals (Figure S1). We were interested in average temporal trends in autocorrelation to see if there tended to be over or under prediction of adult abundance during any given time period. We examined this by scaling residuals for each assessment unit by their mean, calculating annual mean residual from the scaled assessment-unit specific residuals, and plotting the results (Figure S2). We did not observe strong autocorrelation in the mean annual residuals from visual examination of the plot. We ran a Durbin-Watson test for lag-1 autocorrelation to examine this further. Based on this test, there was weak evidence supporting autocorrelation of the mean annual residuals (DW-stat= 1.76; p-value=0.24).
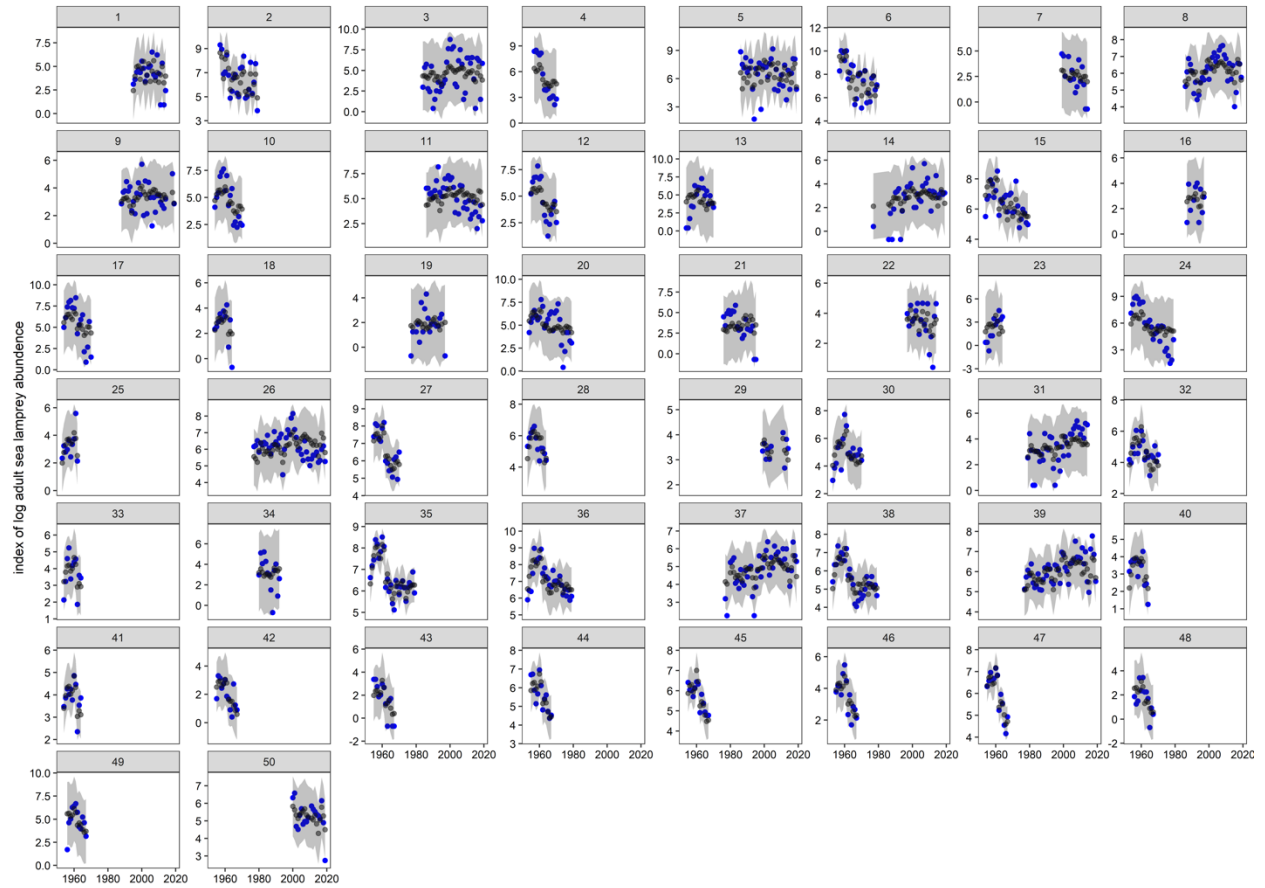
Figure S1. Plot of post-posterior checking results for each assessment unit. Dark-grey points show the model predicted value and blue points show observed values. Grey band is the 95% credibility interval.
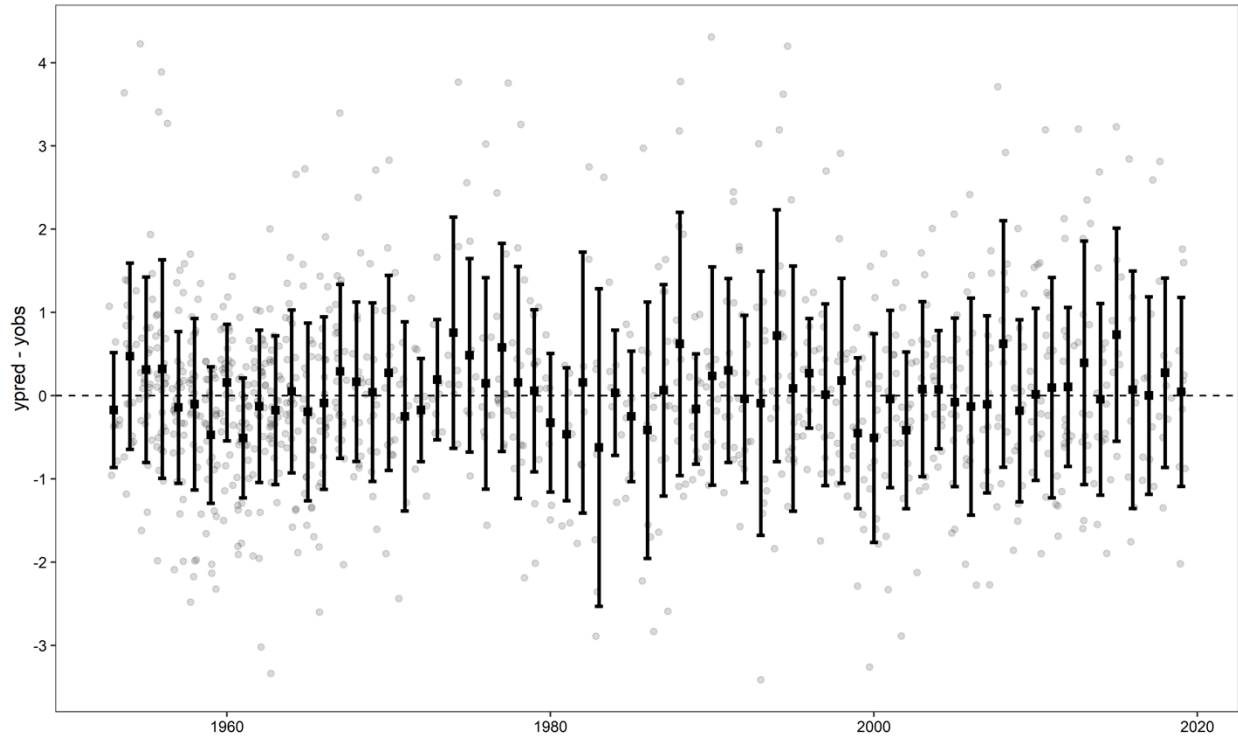
Figure S2. Mean average annual residual (model predicted – observed). Error bars are +/- one sd, light grey points show individual assessment unit residuals.

APPENDIX D: SEA LAMPREY CONTROL TACTIC FEASIBLITY ASSESSMENT
AND COST MODEL DETAIL

Social Feasibility

Social feasibility was assessed by assigning a score to each control tactic-candidate experimental stream pairing. The score (yes=2, maybe=1, no=0) was a guess as to whether collateral damage from the deployment would decrease trust between the Sea Lamprey Control Program and partners, stakeholders, rightsholders, and resource users. The specific collateral damage dimensions considered were aesthetic impact, recreational opportunity/river access, and blocking and/or mortality of non-target fishes. The sum of these responses constituted an expected negative societal effect score (NSES) for a given stream-tactic pairing. Resulting NSES ranged from 0 to 5. NSES >0 were assigned for some trap and electric weir tactic-stream combinations, while passage-friendly trap and distribution tactics (pheromone antagonist and SMRT) all were assigned NSES of 0. The maximum social impact score of the control tactics included in a given control strategy was used to assess the social feasibility of control strategy-stream pairings. Strategy-stream pairings with NSES ≤ 2 were deemed socially feasibility and those with NSES > 2 were deemed not social feasibility.

Table S5. Table of negative societal effect scores (NSES) for each control tactic-stream pairing. Each cell contains the sub scores for aesthetic impact, recreational opportunity/river access, and blocking and/or mortality of non-target fishes and the sum (bold).

Stream/Tactic	Trap	Passage-friendly trap	Electric weir	SMRT	Pheromone antagonist
Cranberry River	0+0+0=**0**	0+0+0=**0**	0+0+0=**0**	0+0+0=**0**	0+0+0=**0**
Potato River	0+0+0=**0**	0+0+0=**0**	0+0+0=**0**	0+0+0=**0**	0+0+0=**0**
Traverse River	0+1+1=**2**	0+0+0=**0**	1+2+1=**4**	0+0+0=**0**	0+0+0=**0**
Bills Creek	0+0+1=**1**	0+0+0=**0**	0+1+2=**3**	0+0+0=**0**	0+0+0=**0**
Furlong Creek	0+0+0=**0**	0+0+0=**0**	0+1+0=**1**	0+0+0=**0**	0+0+0=**0**
Long Lake Outlet	0+0+0=**0**	0+0+0=**0**	0+1+0=**1**	0+0+0=**0**	0+0+0=**0**
Silver Creek	0+1+1=**2**	0+0+0=**0**	1+2+2=**5**	0+0+0=**0**	0+0+0=**0**
Root River	0+1+0=**1**	0+0+0=**0**	1+2+2=**5**	0+0+0=**0**	0+0+0=**0**
Crystal Creek	0+0+0=**0**	0+0+0=**0**	1+1+2=**4**	0+0+0=**0**	0+0+0=**0**

Expected Percent Reduction in Sea Lamprey Spawning Potential

A deterministic probability tree (Figure S1) was developed for predicting expected percent reduction in sea lamprey spawning potential associated with each control strategy-stream pairing. The conditional probability of being trapped, blocked, or disrupted represents the

expected reduction in spawning potential associated with a given control strategy-stream combination. Starting spawning potential (i.e., the size of the migratory spawning run) was assigned based on adult sea lamprey assessment data for each stream. Control tactics were assumed to be applied sequentially in the remove, divert, disrupt order. Probabilities in the probability tree include the probability of being available to be targeted by a given control tactic (max capture and max block) and control tactic effectiveness probabilities (capture prob, block prob, disrupt prob) (Figure S3, Table S6). Probability of being available to removal tactics was assigned a base value of 0.9 because we don't expect traps to be operated for 100% of the run (on average), with a few adult lamprey migrating into streams either very late or very early in the spawning migration. Additionally, traps are expected to be ineffective under flood conditions, when they become inundated. In these conditions, existing trap operations are typically suspended and gear removed from the stream to prevent equipment loss and damage. Especially flashy streams, prone to flooding (Cranberry River and Potato River) and moderately prone to flooding (Furlong Creek) were assigned a further reduced probability of being available to traps to account for reduced expected effectiveness under more frequently occurring flood conditions. Probability of being available to diverting tactics was set to 0.75 across all streams and is interpreted as the percentage of the run unavailable to traps that are available to diversion tactics. This value is greater than zero because we expect electric weir operations to be more feasible to operate for a greater portion of the spawning run and be more resilient to flood conditions, compared to traps.

Typical adult sea lamprey assessment traps recapture 20-40% of marked individuals. We assumed that removal tactics would constitute enhanced trap deployments that make use of available technologies expected to increase capture efficacy (e.g., electric leads and chemosensory push-pull methods) and/or novel trap designs to boost capture probability to 55%. Finally, we assumed deployment of two enhanced traps and calculated the final probability as $1-(1-0.55)^2=0.80$ (the probability of being captured in one of the 2 traps). We estimated passage-friendly trap probability by reducing the expected capture probability of each trap from 0.55 to 0.40, based on the assumption that accommodating passage-friendly needs would somewhat reduce the effectiveness of the trap. The final capture probability for passage-friendly traps was $1-(1-0.40)^2=0.64$.

Electric weirs are expected to have high blocking capabilities, when deployed in optimal

locations. For example, no adult sea lamprey have been captured above an electric weir deployed in such a location on the Black Mallard River in 8 years of operation. We assigned a blocking probability of 0.90, lower than what we expect for electric weir deployments in optimal conditions, to account for anticipated challenges optimizing deployment location and operations for new deployments.

SMRT disruption probability at a 40:1 sterile to wild male ratio was assigned 0.90 across all streams. Theoretically, if males and females are randomly paired for mating, this ratio should cause successful reproduction rates to approach zero. However, we assumed lower efficacy to account for limitations in matching timing of sterile male releases and maturation schedules to the wild male population, which could reduce the effectiveness of SMRT applications (compared to the theoretical maximum).

Pheromone antagonist applications at a 100 3sPZS:100 PZS:1 3kPZS ratio are expected to cause reproduction rates to approach zero, based on experimental trials conducted in the Carp Lake Outlet. We assigned a base probability of 0.90 because the deployment of this tactic would be targeted to a 3–4-week peak spawning window, and we expect that misidentification of peak spawning and/or a prolonged spawning period would result in some mature adult lamprey not being inundated with pheromone antagonists while they are sexually mature.

Using the probability tree, expected availability and control efficacy probabilities, and starting spawning potentials, the expected proportional reduction in spawning potential was calculated for each control strategy-stream combination (Table S6). Combinations with an expected reduction less that 0.90 were considered *low* technical feasibility and those with expected reduction of 0.90 or greater passed this portion of the technical feasibility assessment (and were assigned *high* feasibility if they met maximum cost and sterile male availability requirements).
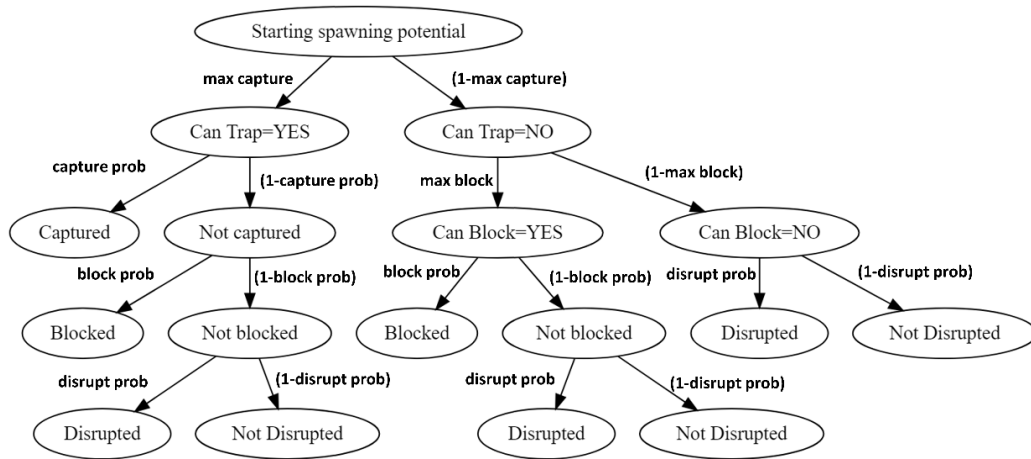
Figure S3. Probability tree for estimating the expected reduction in spawning potential for a given control strategy possibility containing remove, divert, and disrupt control tactics.

Table S6. Values included in the probability tree used to estimate expected reduction in sea lamprey spawning potential. Rows correspond to candidate streams for experimental sea lamprey control deployments. Mean spawning run size was assigned based on monitoring data while control efficacy probabilities (*max capture*=expected probability of availability to capture tactics, *capture prob*=expected probability of capturing capture-available adults, *max block*=expected probability of adults not available to capture tactics being available to blocking tactics, *block prob*=expected probability of blocking adults available to capture or blocking tactics, *disrupt prob*= expected probability of disrupting reproduction) were assigned based on expert judgement of the authors of this manuscript. (SMRT=sterile male release technique; PF Trap=passage-friendly trap).

Parameter	Mean spawning run size	max capture	capture prob		max block	block prob	disrupt prob	
Tactic/stream		Trap/PF Trap	Trap	PF Trap	Block	Block	SMRT	Antagonist
Potato	10	0.6	0.8	0.64	0.75	0.90	0.90	0.70
Cranberry	235	0.6	0.8	0.64	0.75	0.90	0.90	0.70
Traverse	125	0.9	0.8	0.64	0.75	0.90	0.90	0.90
Bills Creek	32	0.9	0.8	0.64	0.75	0.90	0.90	0.90
Furlong Creek	32	0.8	0.8	0.64	0.75	0.90	0.90	0.90
Root River	37	0.9	0.8	0.64	0.75	0.90	0.90	0.90
Crystal Creek	17	0.9	0.8	0.64	0.75	0.90	0.90	0.90
Long Lake Outlet	147	0.9	0.8	0.64	0.75	0.90	0.90	0.90
Silver Creek	8	0.9	0.8	0.64	0.75	0.90	0.90	0.90

Expected Cost Model

Expected annual cost was estimated for each control tactic and was broken down into staff day and gear/equipment costs. Expected number of staff days was highest for a removal tactic deployment (n=28), followed by an electric weir deployment, (n=10), application of pheromone antagonist (n=6), and release of sterile males (n=5 per release of 1000 sterile males). One staff day was estimated to cost $1,409, which includes transportation and administrative support costs. Expected annualized equipment and gear costs were estimated by considering one-time equipment expenses annualized by the expected lifespan of the gear plus annual gear costs. Annualized expected cost (USD) was $7,000 for a removal deployment, $6,000 for an electric

weir deployment, $1,000 for release of 1000 sterile males, and $46,000 for synthetizing enough pheromone antagonist to neutralize 1 wild male. Total expected annual cost for each control strategy-stream pairing was calculated by summing all of the individual costs associated with the deployment (Table S8). Disruption costs that depend on the number of wild males to neutralize (either by achieving a 40:1 sterile to wild ratio or 100:100:1 pheromone ratio) were scaled to the expected number of wild males to neutralize. This was calculated as the starting run size * 50% expected male * (1- proportion trapped) * (1-proportion blocked).

The expected cost of synthesizing enough pheromone to neutralize one wild male was calculated from pheromone synthesis costs (per mg) and estimated 3kPZS production rate of a sea lamprey male in a natural setting. We estimated that a sea lamprey male produces 27 mg of 3kPZS per day in a natural setting, based on a Bayesian statistical analysis that included an informative prior for this rate based on lab-based measurements (known number of lamprey in a small tank) and field-based 3kPZS measurements with highly uncertain number of sea lamprey present in the system and uncertain amounts of background 3kPZS production from larval life-stage lamprey. The field data contained high levels of observation error and the informative prior (based off of lab measurements) largely informed our estimate.

Table S7. Estimated proportion of starting spawning potential controlled for each control strategy-stream pairing.

	Antagonist	SMRT	PF Trap	Antagonist + PF Trap	SMRT + PF Trap	Trap	Antagonist + Trap	SMRT + Trap	Barrier	Antagonist + Barrier	SMRT + Barrier	Trap + Barrier	Antagonist + Trap + Barrier	SMRT + Trap + Barrier
Cranberry River	NA	0.90	0.38	NA	0.94	0.48	NA	0.95	0.81	NA	0.98	0.86	NA	0.99
Potato River	NA	0.90	0.38	NA	0.94	0.48	NA	0.95	0.81	NA	0.98	0.86	NA	0.99
Traverse River	NA	0.90	0.58	NA	0.96	0.72	NA	0.97	0.88	NA	0.99	0.95	NA	0.99
Bills Creek	NA	0.90	0.58	NA	0.96	0.72	NA	0.97	0.88	NA	0.99	0.95	NA	0.99
Furlong Creek	NA	0.90	0.51	NA	0.95	0.64	NA	0.96	0.86	NA	0.99	0.92	NA	0.99
Long Lake Outlet	NA	0.90	0.58	NA	0.96	0.72	NA	0.97	0.88	NA	0.99	0.95	NA	0.99
Silver Creek (Tawas)	0.90	0.90	0.58	0.96	0.96	0.72	0.97	0.97	0.88	0.99	0.99	0.95	0.99	0.99
Root River	NA	0.90	0.58	NA	0.96	0.72	NA	0.97	0.88	NA	0.99	0.95	NA	0.99
Crystal Creek	NA	0.90	0.58	NA	0.96	0.72	NA	0.97	0.88	NA	0.99	0.95	NA	0.99

[1]Highlighted cells indicate deployments expected to achieve the 0.90 control target.

Table S8. Estimated annual cost (USD) for each control strategy-stream pairing.

	Antagonist	SMRT	PF Trap	Antagonist + PF Trap	SMRT + PF Trap	Trap	Antagonist + Trap	SMRT + Trap	Barrier	Antagonist + Barrier	SMRT + Barrier	Trap + Barrier	Antagonist + Trap + Barrier	SMRT + Trap + Barrier
Cranberry River	NA	38,000	46,000	NA	70,000	46,000	NA	66,000	20,000	NA	27,000	67,000	NA	72,000
Potato River	NA	2,000	46,000	NA	47,000	46,000	NA	47,000	20,000	NA	20,000	67,000	NA	67,000
Traverse River	NA	20,000	46,000	NA	55,000	46,000	NA	52,000	20,000	NA	23,000	67,000	NA	68,000
Bills Creek	NA	5,000	46,000	NA	49,000	46,000	NA	48,000	20,000	NA	21,000	67,000	NA	67,000
Furlong Creek	NA	5,000	46,000	NA	49,000	46,000	NA	48,000	20,000	NA	21,000	67,000	NA	67,000
Long Lake Outlet	NA	24,000	46,000	NA	56,000	46,000	NA	53,000	20,000	NA	23,000	67,000	NA	68,000
Silver Creek (Tawas)	192,000	1,000	46,000	133,000	47,000	46,000	107,000	47,000	20,000	51,000	20,000	67,000	84,000	67,000
Root River	NA	6,000	46,000	NA	49,000	46,000	NA	48,000	20,000	NA	21,000	67,000	NA	67,000
Crystal Creek	NA	3,000	46,000	NA	48,000	46,000	NA	47,000	20,000	NA	20,000	67,000	NA	67,000

[1]Highlighted cells indicate deployments requiring less than $150,000 USD annual expected cost.