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## Using Integral Projection Models to Explore Management Strategies for Silver Carp (*Hypophthalmichthys molitrix*)

Cameron Coles

*Cornell University*, [cjc378@cornell.edu](mailto:cjc378@cornell.edu)

Elizabeth Balas

*Susquehanna University*, [balas@susqu.edu](mailto:balas@susqu.edu)

James Peirce

*University of Wisconsin-La Crosse*, [jpeirce@uwlax.edu](mailto:jpeirce@uwlax.edu)

Greg Sandland

*University of Wisconsin-La Crosse*, [gsandland@uwlax.edu](mailto:gsandland@uwlax.edu)

Richard Erickson

*USGS Upper Midwest Environmental Sciences Center, La Crosse, WI*, [rerickson@usgs.gov](mailto:rerickson@usgs.gov)

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# Using Integral Projection Models to Explore Management Strategies for Silver Carp (*Hypophthalmichthys molitrix*)

Cameron Coles<sup>1</sup>, Elizabeth Balas<sup>2</sup>, James Peirce<sup>3,\*</sup>, Gregory Sandland<sup>4</sup>, Richard Erickson<sup>5</sup>

\*Correspondence:  
Prof. James Peirce,  
Dept. of Mathematics &  
Statistics, University of  
Wisconsin-La Crosse,  
La Crosse, WI 54601, USA  
jpeirce@uwlax.edu

## Abstract

Silver carp (*Hypophthalmichthys molitrix*) are planktivorous fish that were originally introduced to the United States for use in fish production ponds and have since escaped these enclosures and are invading the Mississippi River Basin. The silver carp invasion of the Illinois River has a myriad of negative effects on native ecosystems. In this paper, we introduce key dependencies that are likely important in the population dynamics of silver carp: length-dependent egg production and density-dependent growth. Using movement data between two adjacent pools of the Illinois River, we conduct numerical simulations to explore the theoretical effect of harvesting and the use of movement barriers. Results of our model provide insights on how the number of silver carp may respond to movement barriers placed between adjacent harvesting sites.

**Keywords:** population model, invasive species management, Mississippi River Basin, silver carp

## 1 Introduction

Silver carp (*Hypophthalmichthys molitrix*) are planktivorous fish that are native to freshwater systems in eastern Asia, ranging from Russia to China to possibly northern Vietnam [36]. Because silver carp are lower trophic-level filter feeders, they were imported to the United States in the 1970s for use in aquaculture, plankton control, and sewage processing [16, 36]. Subsequent escapes of silver carp into the Mississippi River in the 1990s led to their establishment in the Mississippi River Basin, including the Illinois River [23, 36]. Further expansion is of substantial concern because the Illinois River is connected to Lake Michigan, which to date remains free of silver carp. As a result of the potential direct and indirect effect on native fish species and the Great Lakes ecosystem, societal concerns have been raised regarding the potential catastrophic ecological and financial effects if silver carp reach the Great Lakes [6].

Establishment of silver carp in the Mississippi River has been associated with negative impacts on the native ecosystem. Phytoplankton and zooplankton levels have decreased due to silver carp foraging [7]. Additionally, the composition of zooplankton communities has shifted,

with rotifers becoming significantly more common post-silver carp establishment [37]. Native fish have also been affected, with both body condition and abundance of gizzard shad (*Dorosoma cepedianum*) and bigmouth buffalo (*Ictiobus cyprinellus*) decreasing after the establishment of silver carp [21, 25, 31].

Even though silver carp have disrupted the food webs in their invaded habitats, the long-term effects of this species on native ecosystems remain unknown. Thus, minimizing the threat that silver carp pose to native ecosystems and preventing their spread into new regions such as the Great Lakes has become a high priority for management agencies. To that end, a variety of harvesting strategies and movement barriers have been used to reduce silver carp populations. In one harvesting method, commercial fishers will bang on their boats and adjust motor speeds to make sounds that drive the fish into gill nets where they are captured and removed. For example, the Enhanced Contract Fishing Program uses targeted contract fishing in Alton, La Grange, and Peoria pools of the Illinois River to remove millions of pounds of invasive carp annually [20].

Along with harvesting, a variety of movement barriers have been proposed and developed to control silver carp. For example, an electric barrier is maintained in the Chicago Sanitary and Shipping Canal to prevent movement of silver carp from the Illinois River into Lake Michigan [27]. Electric barriers induce avoidance behaviors in carps and other fishes. Carbon dioxide (CO<sub>2</sub>) barriers

<sup>1</sup>Central College, Pella, IA, USA, <sup>2</sup>Susquehanna University, Selinsgrove, PA, USA, <sup>3</sup>Department of Mathematics & Statistics, University of Wisconsin, La Crosse, WI, USA, <sup>4</sup>Department of Biology, University of Wisconsin, La Crosse, WI, USA, <sup>5</sup>U.S. Geological Survey, Upper Midwest Environmental Sciences Center, La Crosse, WI, USA

have also been tested as a silver carp deterrent. These barriers release CO<sub>2</sub> into the water leading to avoidance behaviors in fish, including silver carp. In addition, silver carp are particularly sensitive to 20–2000 Hz signals, resulting in acoustic barriers being up to 95% effective as a deterrent [29, 33]. Many other barriers have also been developed and used, including strobe lights, bubble curtains, and pheromones [29].

Because of the silver carp’s invasion potential, a substantial amount of research has been done to better understand their life histories. Silver carp typically reach reproductive maturity between four and eight years of age in their native ranges; however, individuals have been reported to mature in as few as two years in the United States [28]. Fecundity in silver carp is related to body size, with larger fish producing more eggs [18, 36]; however, there is some discrepancy over how many eggs are produced by a single silver carp female. Some studies have reported that a single female can produce up to five million eggs in a year [28], while other research indicates that the number is as low as 1.65 million eggs [36]. Silver carp are noted for incremental spawning, where females engage in several smaller spawning events in a year rather than a large, single spawning event [36]. Eggs require constant water flow to survive and develop. Thus, most silver carp spawning occurs in long stretches of fast-flowing water [9, 17]. Silver carp have a high natural rate of mortality, particularly in early development; however, specific estimates of mortality across different developmental stages of these fish are not well known [18].

## 1.1 Integral Projection Models

An Integral Projection Model (IPM) is a relatively new form of population modeling that closely ties model components to patterns seen in life-history data. A comprehensive description of traditional IPMs can be found in [35]. An IPM is characterized by a discrete time step,  $t$ , where a census of fish sizes  $z$ , is recorded for the population. For the silver carp model in this paper, we measure the size of an individual by its total length (in millimeters). The population census at time  $t$  is represented by a continuous density function of the length,  $n(z, t)$ . Note that for any particular  $z$ ,  $n(z, t)$  does not represent the number of individuals of length  $z$ , but rather a density. The number of individuals with a length between  $a$  and  $a + h$  can be obtained by integrating,

$$\int_a^{a+h} n(z, t) dz.$$

The length distribution of the population is updated, or projected, from census time  $t$  to  $t + 1$  through the

following formula:

$$n(z', t + 1) = \int_L^U K(z', z) n(z, t) dz \quad (1)$$

where  $z'$  is the length at time  $t + 1$ ,  $K(z', z)$  is an integral kernel, and  $[L, U]$  is the interval of all possible lengths. The kernel function represents the contribution that an individual of length  $z$  at time  $t$  will have on the population at time  $t + 1$ . The kernel is defined by adding and multiplying functions closely related to the life-history traits of individuals in the population.

Due to the complexity of the life-history functions used in the IPM, a closed form analytic solution to the projection equation above is typically unknown. Instead, we use the Midpoint Rule to approximate solutions to the model. As a result, the IPM computationally acts in a similar way to classical matrix projection models, as the kernel function becomes a transition matrix and the population function becomes a vector. The accuracy of the approximation can be increased by using smaller length bins, and therefore, more sample points.

### 1.1.1 Meta-population IPM

Often an IPM only accounts for the body sizes of organisms within a single population; however, the Mississippi and Illinois Rivers are divided into navigation pools by locks and dams, which likely restrict the movement of fish (and other taxa) along these waterways. As such, modeling silver carp in these rivers may best be achieved using a meta-population approach where regional groups of fish are potentially connected via movement through these structures [41]. Dynamic meta-population models utilize a network-node framework to describe changes in population dynamics at discrete nodes and the movements between nodes. The network-node framework describes “nodes” (i.e., discrete habitat patches) that are connected by edges to form a network. For each of these nodes, many papers capture population changes with time and age-/stage-/sex-structure matrix or difference equations models (for example, [15, 14, 22, 45]).

Recent work has expanded the network-node framework to model the growth of individual grass carp as a continuous variable using an IPM rather than a matrix model within each node [12]. This merged the benefits of an IPM and network-node models. Recently, the authors have created a Python package, Meta-population Integral Projection Model (MetaIPM), and outlined its use in modeling silver carp populations in the Illinois River [13].

In this paper, we modified the MetaIPM package to include two functions that are likely important in the population dynamics of silver carp: length-dependent egg

production and density-dependent growth. Strengthening our understanding of how factors such as movement and harvest influence silver carp populations is critical for predicting the local dynamics of this species and the potential for this invader to spread throughout connected freshwater systems. We applied the model to silver carp populations in two pools of the Illinois River as a means to investigate the effects of fish movement and harvest in these two pools.

## 2 Model Development and Parameter Estimation

To create the MetalIPM for silver carp in two pools of the Illinois River, we (1) define the assumptions made for the annual change in the length distribution of the population at each node, and (2) describe the annual movement rates of fish between the pools. In each pool we will use an IPM (Equation 1) where the integral kernel is constructed from functions that capture the survival, growth, reproduction, and harvesting of silver carp (summarized in Figure 1).

### 2.1 Density-dependent growth and survival

For a silver carp of length  $z$  at time  $t$ , the function  $P(z', z)\Delta z$  is the probability that the individual is alive at time  $t + 1$ , and its size is in the interval  $[z', z' + \Delta z]$  (as with  $n(z, t)$  this is an approximation that is valid for small  $\Delta z$ , and the exact probability is given by an integral). In fisheries science, the biomass of an invasive species can be used as a quantitative benchmark for evaluating management or conservation actions [3]. Density-dependent growth rates have been observed in silver carp populations [2, 5] and we modeled the effects of density exclusively on the growth and survival kernel. Let  $P(z', z, B_t) = s(z)G(z', z)e^{-gB_t}$  where  $s(z)$  is the annual survival probability,  $G(z', z)$  describes the annual increase in length,  $B_t$  is the biomass of silver carp at time  $t$ , and  $g$  is a measure of the effect of density on growth and survival. The total biomass in year  $t$  is defined as  $B_t = \int_L^U W(z)n(z, t) dz$  where  $W(z)$  is the weight (in grams) of a silver carp of length  $z$ . The relationship between silver carp body length and weight is

$$\log(W(z)) = \alpha_W \log(z) + \beta_W, \quad (2)$$

where  $\alpha_W$  is a measure of how  $\log(W)$  scales with  $\log(z)$ , and  $\beta_W$  is the intercept (Figure 2b). The specific number of silver carp found in our target system has not been well established, so we explored this uncertainty with different values for  $g$ , settling on a value that produced a biologically reasonable carrying capacity.

A nonlinear model for fish length  $L$  as a function of time is the von Bertalanffy model [43]:

$$L(t) = L_\infty \left(1 - e^{-K_G(t-t_0)}\right)$$

where  $t$  is time,  $t_0$  represents the theoretical ‘time’ when a fish is length 0,  $L_\infty$  represents the maximum possible length of the fish, and  $K_G$  is a growth constant (Figure 2a). The fish length function at time  $t$  can be expressed in a recursive form [11] to find length  $z'$  at time  $t + 1$  based on length  $z$  at time  $t$ :

$$z' = (1 - e^{-K_G})L_\infty + e^{-K_G}z.$$

We assumed the growth kernel is a normal distribution with mean,  $\mu_G$ , predicted by the von Bertalanffy growth function based on current length  $z$  and standard deviation  $\sigma_G$ . Thus,  $G(z', z) = \text{Prob}(z' | z, L_\infty, K_G) = \text{NormPDF}(\mu_G, \sigma_G)$ .

We assumed that silver carp less than  $\alpha_s$  in length have a very low survival rate while lengths larger than  $\alpha_s$  approach a maximum survival probability  $s_{\max}$ . This survival pattern has been reported for many fish species and can arise due to several biotic (e.g., predation) and/or abiotic (e.g., temperature) factors [30, 32]. As a consequence, we assumed the survival function (Figure 2c) is the three-parameter logistic function of the length,

$$s(z) = \frac{s_{\max}}{1 + e^{-\beta_s(z - \alpha_s)}}.$$

Survival data on silver carp are scarce, especially in relation to fish length. Grass carp (*Ctenopharyngodon idella*) longer than 450 mm in length are large enough to avoid largemouth bass (*Micropterus salmoides*) predation [39]. Therefore, we assumed  $\alpha_s = 450$  mm for our silver carp MetalIPM. The upper bound on the survival percentage  $s_{\max}$  is estimated using the following equation [40] (adapted to length measured in mm):

$$s_{\max} = 1 - 8.804K_G^{0.73}L_\infty^{-0.33}.$$

### 2.2 Reproduction

$F(z', z)\Delta z$  is the number of new silver carp that spawn in the length interval  $[z', z' + \Delta z]$  present at time  $t + 1$ , per length- $z$  individual at time  $t$ . The fecundity kernel is

$$F(z', z) = \text{egg}(z) \nu C_1(z') \quad (3)$$

where  $\text{egg}(z)$  is the mean number of eggs produced,  $\nu$  is the probability that an egg is viable and produces an age-0 fish that survives to the next census, and  $C_1(z')$  is the length distribution of new recruits at age-1 (when they are first censused in the model). During 2004 and 2005, the number of eggs within mature silver carp females in the lower Illinois River was recorded [8] and we

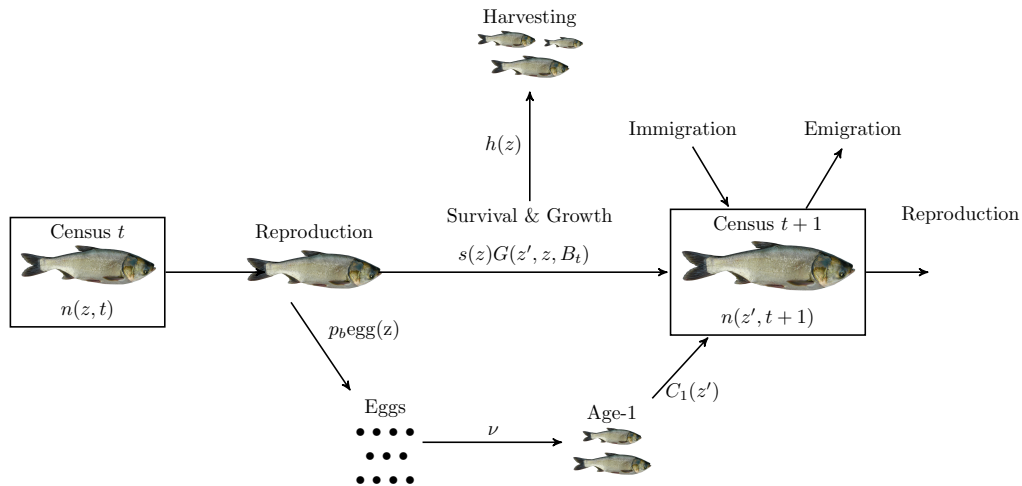


Figure 1: Life cycle diagram and census points for pre-reproduction census of silver carp. The diagram is a visualization of the MetaIPM kernel. Individuals undergo growth, survival, and reproduction between every census. At census time, individuals also may immigrate or emigrate from the populations. Image courtesy of Dan O’Keefe, Michigan Sea Grant (CC BY-NC-ND 2.0).

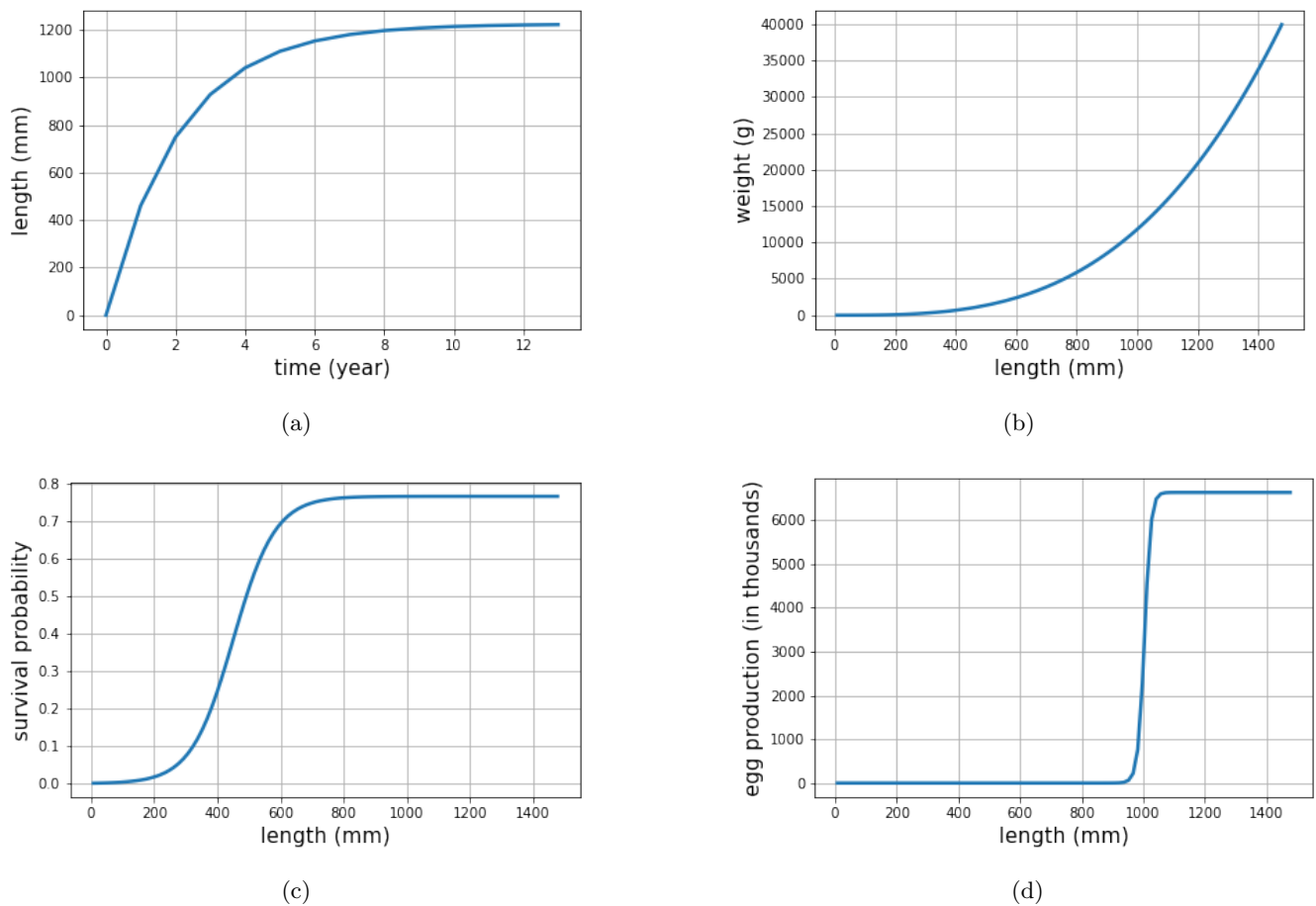


Figure 2: Functions for (a) length  $L(t)$ , (b) weight  $W(z)$ , (c) survival  $s(z)$ , and (d) egg production  $\text{egg}(z)$  used in the integral kernels of the silver carp MetaIPM.

used the data to fit a linear model for egg production and weight. We extended this model to the weight interval  $(0, W_\infty)$  by equating all negative predicted egg production values to zero. Because egg production is not a trait that starts when a fish reaches a specific weight, the logistic parameters for the mean number of eggs produced by females of a certain weight were obtained by fitting a three-parameter logistic function:

$$\text{egg}(z) = \frac{e_{\max}}{1 + e^{-\beta_e(W(z) - \alpha_e)}},$$

with  $e_{\max}$  corresponding to the linear predicted value at maximum weight  $W_\infty$  [8] (Figure 2d).

Recruit size was assumed to be independent of parent size. Specifically,  $C_1(z') = \text{NormPDF}(\mu_R, \sigma_R)$  with  $\mu_R$  representing the size at year one predicted by the von Bertalanffy equation and standard deviation  $\sigma_R$ .

### 2.3 Harvesting

Harvesting was modeled in two ways, (1) as a constant function  $h(z) = h_0$ , and (2) as a piecewise function,

$$h(z) = \begin{cases} h_0, & \text{if } z > z_c \\ 0 & \text{otherwise} \end{cases}$$

where  $z_c$  represents a length threshold after which harvesting efforts become effective. The piecewise representation is more aligned with current harvesting methods, which tend to target larger fish [1].

### 2.4 Population model

Finally, the IPM for the length distribution of silver carp populations in the Illinois River at the next census (summarized in Figure 1) is

$$n(z', t + 1) = \int_L^U K(z', z, B_t) n(z, t) dz$$

where the projection kernel  $K$  summarizes the combined effects of survival, growth, reproduction, and harvesting:

$$K(z', z, B_t) = (1 - h(z))s(z)G(z', z)e^{-gB_t} + \text{egg}(z)\nu C_1(z').$$

Throughout this paper, we will summarize the effect harvesting and movement has on the silver carp populations (integrated over all lengths) in adjacent pools of the Illinois River.

### 2.5 Annual movement rates for the MetalIPM

Radio telemetry was used to study the movement patterns of silver carp in pools of the Illinois River [5]. This work provided monthly movement probabilities across the six

pools of the Illinois River (Figure 3a). We used a Markov Chain to convert these estimates into yearly movement rates for two of the pools, La Grange and Peoria. Each pool is regarded as a separate state and it is assumed that individual fish do not migrate beyond these pools. In Markov Chains, a transition matrix is used to tabulate the probabilities of transitioning from one state (pool) to another. The row is associated with the source pool, while the column is associated with the destination pool. Thus, values along the diagonal represent the probability of a fish remaining in the current pool. To determine transition probabilities after  $n$  time steps, the transition matrix is raised to the  $n$ th power. A transition matrix,  $X$ , was constructed using the monthly movement rates between the La Grange and Peoria pools rates and then projected 12 months into the future to obtain a matrix of yearly rates:

$$X^{12} = \begin{bmatrix} 0.9695 & 0.0305 \\ 0.0214 & 0.9786 \end{bmatrix}^{12} = \begin{bmatrix} 0.722346 & 0.277654 \\ 0.194813 & 0.805187 \end{bmatrix}.$$

A graphical representation of the annual movement rates of silver carp between two pools (La Grange and Peoria) is shown in Figure 3b.

## 3 Analysis

Three numerical experiments were conducted to explore how harvesting and movement barriers influence silver carp populations. The mean values of parameters used are listed in Table 1. Using the Midpoint Rule with 100 length bins, we created large approximating matrices at every census time,  $t$ , to numerically solve the integral equation for 75 years to ensure that a steady state was reached. It should be noted that these experiments are theoretical exercises inspired by management practices used in the upper Mississippi River. Factors such as river flow direction, interspecific interactions, and/or movement of fish beyond our specified domain (i.e. only the La Grange and Peoria pools) were not considered as part of these *in silico* simulations.

### 3.1 Numerical Experiment A: constant harvesting of silver carp in the La Grange pool with changing harvesting rates in Peoria pool

In the first scenario of the MetalIPM, the model was simulated with the harvesting rate held constant in the La Grange pool at 40% annually, but varied from 0% to 40% (in 10% increments) in the Peoria pool. Movement probabilities between pools were held constant at their empirically determined levels. The primary goal of this numerical experiment was to understand how changing

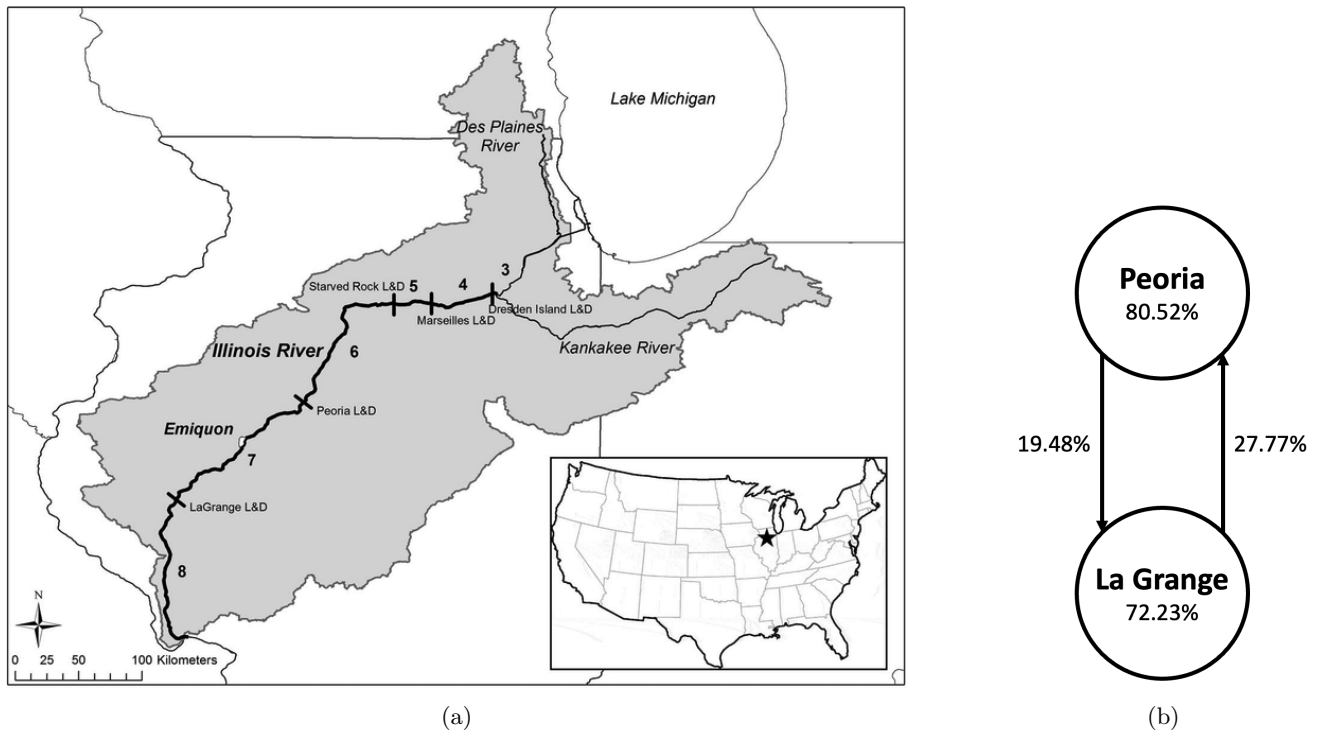


Figure 3: (a) Navigation pools of the Illinois River [44] licensed under CC BY 4.0. Pools are separated by locks and dams (L&D), indicated by perpendicular black lines. (b) Estimated mean annual movement percentages (converted from monthly estimates) for silver carp in the La Grange and Peoria Pools of the Illinois River [4].

Table 1: The names of parameters used in the silver carp IPM with their mean value.

Parameter	Symbol	Value	Source
Length-weight slope	$\alpha_W$	3.122	[21]
Length-weight intercept	$\beta_W$	-5.294	[21]
von Bertalanffy maximum length	$L_\infty$	1224	[19]
von Bertalanffy growth constant	$K_G$	0.173	[19]
Growth standard deviation	$\sigma_G, \sigma_R$	60	[46]
Density effect	$g$	$10^{-10}$	
Maximum survival	$s_{max}$	0.76585	[40]
Survival inflection	$\alpha_s$	450	[39]
Survival slope	$\beta_s$	0.015	[11]
Maximum egg production	$e_{max}$	6636993	[8]
Egg production intercept	$\alpha_e$	11965.07	[8]
Egg production slope	$\beta_e$	0.002565	[8]
Egg viability and survival of age-0	$\nu$	0.00005	[11, 34]

harvest rates at one location affects the population size of silver carp at both pools without changes in movement. Because the harvesting rate changes in the Peoria pool, while held constant in the La Grange pool, changes in population size for the Peoria pool could indicate the effectiveness of harvesting, while changes in population size for the La Grange pool could provide insight into the effect of harvesting on nearby pools. Any differences in the La Grange pool could follow from the various harvest rates at the Peoria pool and its effect on the number of migrants.

### 3.2 Numerical Experiment B: varying rates of silver carp movement between pools, while harvesting silver carp at a constant rate in the La Grange pool

Movement barriers may influence the effectiveness of silver carp harvesting by altering fish transitions into a harvested pool. To explore this scenario, we held harvesting at 40% in the La Grange pool (with no harvesting in Peoria) and varied movement from 0% to 100% (in 25% increments) of the empirical movement rates between pools. Altering silver carp transitions allows us to assess the usefulness of harvesting under differing movement scenarios and provides insight into how movement barriers affect local (within a pool) versus multi-pool dynamics of invasive silver carp.

### 3.3 Numerical Experiment C: altering the minimum-lengths of harvested silver carp

In practice, the effectiveness of harvesting can depend on the methodologies (e.g., electrofishing versus nets) used to capture the fish. This can lead to a situation where fish are only captured if they occur within a certain range of sizes. To explore this scenario in silver carp, we ran five simulations where fish capture was restricted to those individuals from >800 mm to >1000 mm (in 50 mm increments) and compared the population projections against a population with minimum harvest length. Fish smaller than the thresholds were assumed to escape harvest while those larger than the thresholds were harvested at a rate of 20% in both La Grange and Peoria pools. For this numerical experiment, silver carp movement probabilities (between pools) were held constant at their original, empirically determined levels. Outputs from these numerical experiments could be important for identifying (and subsequently harvesting) the fish sizes that result in the greatest reduction in overall silver carp numbers in the two pools.

## 3.4 Sensitivity analysis

Sensitivity analysis was conducted following previous methods used with IPMs [10]. An IPM has a dominant eigenvalue  $\lambda$  that represents the population's asymptotic growth rate. Sensitivity describes the change in  $\lambda$  resulting from a change in demographic parameters. For the analysis of a particular parameter, all other parameters were held at the values used in the model (Table 1).

We examined the growth rate  $\lambda$  over time  $t$  rather than absolute values to ensure comparability between pools and conditions. The sensitivity  $S$  of  $\lambda$  to a parameter  $x$  is defined as  $S = \frac{\partial \lambda}{\partial x}$ . The sensitivity was computed for several different values of each parameter. Note that  $\lambda$  varies over time, thus  $S$  is also a function of time.

## 4 Results

### 4.1 Numerical Experiment A

As expected, the implementation of length-independent harvesting of silver carp in the La Grange and Peoria pools resulted in substantial reductions in silver carp populations at both locations. Increased harvesting in the Peoria pool continued to reduce the silver carp population in that pool along with the population in the La Grange pool. Collapse of the silver carp population in both pools was only achieved once harvesting rates reached 30% in both the La Grange and Peoria locations. (Figure 4).

### 4.2 Numerical Experiment B

When 100% of the movement was allowed, both simulated populations reached a steady state with a greater density of silver carp in the Peoria pool (Figure 5). This is expected, since dispersal is asymmetric with more silver carp moving from the La Grange pool to the Peoria pool (Figure 3b). Reducing the movement of silver carp between La Grange and Peoria pools increased the effect of harvesting at the La Grange location (Figure 5). In fact, when silver carp movement was reduced to 25% or less of the original rates, harvesting drove the population to collapse within the La Grange pool. Reduced silver carp movement generated a very different pattern within the unharvested (Peoria) pool. When 0% of movement was assumed, harvesting drove the density of silver carp in the La Grange pool towards zero while excluding the removal of silver carp from the Peoria pool. Our simulations indicated that restricting the movement of silver carp may have unintended consequences for controlling these fish at the local (pool) level in the absence of additional control measures (e.g., harvesting).



### 4.3 Numerical Experiment C

Length thresholds for size-dependent harvesting had a nonlinear relationship with the population size, with large decreases in the steady population levels when the threshold was reduced from 1000 to 800 mm. Subsequent population reductions were negligible when length thresholds were lowered further (Figure 6).

### 4.4 Sensitivity analysis

Sensitivity analysis revealed a continued, non-zero sensitivity  $S$  to certain parameters over time (e.g., the maximum survival probability). Conversely, the sensitivity to other parameters (e.g., intra-specific density coefficient) decayed to zero. Examples are shown in Figure 7a and Figure 7b. Note, the growth rate became more sensitive when the maximum survival probability was low. At a maximum survival probability of 0.316, the growth rate has a sensitivity of approximately 1.5 for the entire 75-year period for which the model was run, whereas, the sensitivity on the intra-specific density coefficient  $g$  decays to approximately zero near year 40.

## 5 Discussion

Since their introduction into the southern reaches of the Mississippi River, invasive carp have migrated northwards into connected systems within the Mississippi River region, including the Illinois River. Due to their adverse effects on native ecosystems, several measures have been proposed and/or implemented to control the population growth and spread of silver carp. The goal of our work was to explore the effects of two control methods (harvesting and movement barriers) on silver carp populations in two interconnected pools of the Illinois River using a novel modeling approach (MetalIPM).

Previous work has shown that high harvest rates are required to collapse silver carp populations within their invaded habitats [42]. Using a two-pool model, we found that to be the case as well. In fact, our work indicates that the local extirpation of silver carp can only be achieved if harvesting rates are maintained at 30% (or higher) in both the La Grange and Peoria pools. One of the assumptions of our harvesting rate, however, is that it includes individuals across all lengths. Because current harvesting methods preferentially remove larger fish, actually implementing a 30% length-independent harvesting target may not be feasible [1]. Size-dependent harvesting rates are largely unknown, although estimates of the distribution of sizes of harvested silver carp have been provided in [26]. Previous work predicted that 76% of carp greater than 500 mm in length or that 27–33% of fish

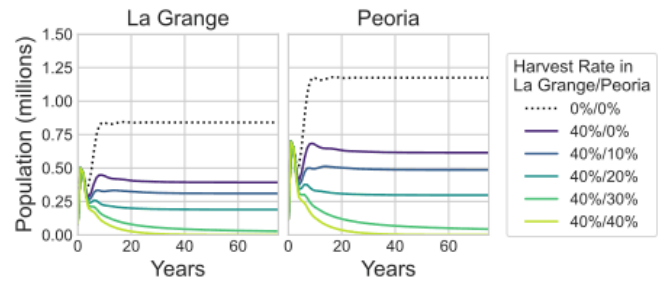


Figure 4: Results from Numerical Experiment A. Total population projections of silver carp at the La Grange and Peoria pools of the Illinois River under varying harvesting scenarios. Harvest rates were held constant for the La Grange pool at 40%, while the harvest rates at the Peoria pool varied from 0% to 40% (in 10% increments).

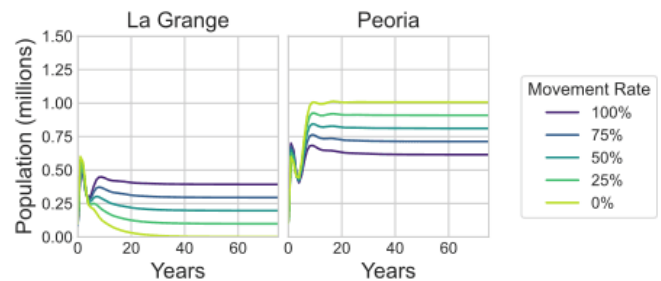


Figure 5: Results from Numerical Experiment B. Total population projections of silver carp at the La Grange and Peoria pools of the Illinois River when movement barriers with differential effects on movement probabilities are present. The harvesting rate was fixed at 40% in the La Grange pool (with no harvesting in the Peoria pool) and the movement rate varied from 0% to 100% (in 25% increments) of the empirical movement rates between the pools.

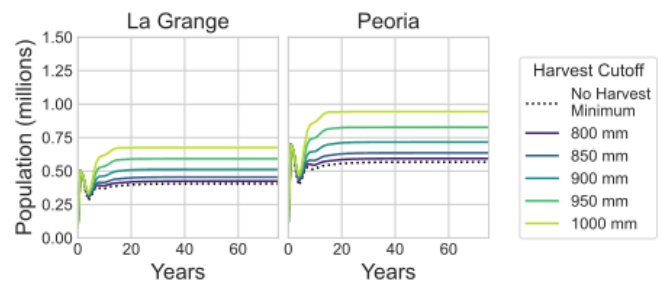


Figure 6: Results from Numerical Experiment C. Total population projections of silver carp at the La Grange and Peoria pools of the Illinois River when harvesting targets 20% for all sizes of individuals above the harvest cutoff lengths of 800 mm to 1000 mm (in 50 mm increments).

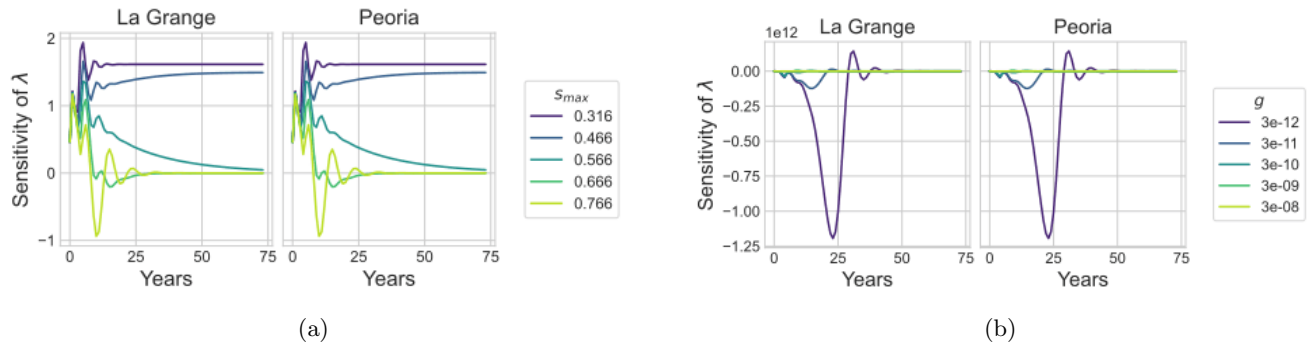


Figure 7: Sensitivity of the growth rate  $\lambda$  to the silver carp (a) maximum survival parameter  $s_{max}$ , and (b) intra-specific density coefficient  $g$  over time at the La Grange and Peoria pools of the Illinois River.

greater than 300 mm in length have to be captured in order to reduce reproductive success to a level that greatly reduces the silver carp population [38]. After incorporating length-thresholds, our model indicates that reducing the size-threshold of harvested fish (to a point) will decrease silver carp population levels; however, lowering the threshold below 800 mm had minimal effect on the silver carp population. This may be due to smaller individuals contributing little to overall reproduction within the population. Our results indicate harvest is most effective when the rate of harvest is increased and a wider range of fish lengths are targeted.

In our two-pool model, harvesting in the La Grange pool alone was not enough to collapse the silver carp population when fish movements remained at empirically estimated levels. Indeed, silver carp movement has been proposed as a key mechanism for maintaining population densities, even in the face of increasing harvesting efforts [26]. It was only after movement rates were reduced to 50% of recorded levels that the silver carp population collapsed, and this only happened in the harvested pool (La Grange). This result indicates that using a combination of both harvesting and barriers (e.g., electrical, chemical, acoustic) may be a more feasible way to control silver carp from target pools. This theoretical scenario also demonstrated the potential consequence of using just a single method for silver carp control, as restricting fish movement led to an increased population of silver carp in the non-harvested, upstream pool (Peoria). This could exacerbate the effects of silver carp at the local (pool) level if fish movement is limited between locations.

Our two-pool model displayed the strongest sensitivity to parameters pertaining to survival and growth rate. These parameters influence how quickly individuals grow to become larger fish and their likelihood of being able to continue reproducing. Sensitivity to movement rates was low. This may indicate that small changes to movement will not have a large effect. Rather, the substantial movement reductions explored in this study may be required to

noticeably reduce silver carp populations. Research is ongoing to assess whether electrical,  $CO_2$ , and/or acoustic barriers can reduce silver carp movements to this degree.

A notable challenge in developing a MetaIPM is acquiring accurate data on the many key life-history traits for the organism(s) of interest. Although bigheaded carps (including silver carp) have received substantial interest since being introduced into the Mississippi River, several important life-history traits remain poorly understood. For example, quantitative assessments of silver carp mortality across age and/or size classes have not been rigorously undertaken. This led us to use estimates of mortality based on the von Bertalanffy growth function [40]. Additionally, few studies have specifically quantified recruitment rates within populations of silver carp. To address this informational void, we selected parameters based on biological intuition rather than actual empirical data. Finally, we introduced a density dependence in the growth and survival term of the model. However, studies focusing on the effects of density of native fishes [21] have observed decreases in body condition (the ratio of the weight of a fish to its weight predicted by a length-weight relationship) at high density levels. Future iterations of the model may explore the effect of density on maximum length using a density-dependent von Bertalanffy growth function [24].

Recent meta-population models for silver carp [22] have incorporated movement data that were recorded for pools along the Illinois River [4]. For these modeling studies, movement rates among pools were applied without regard to fish size, fish sex and/or population density. Fish density at each node could be a key factor (along with fish size, sex, and season) that may drive movement patterns and is planned as the focus of future work.

Future studies will also focus on quantifying the effectiveness of management practices using more ecologically and economically relevant methods. By connecting the costs of management practices with their predicted effects on silver carp populations, the model can estimate re-

turn on investments that would allow better comparisons between control strategies. Additionally, incorporating competition into the overall MetaIPM structure would allow evaluation of the effects of management practices on the population and length-structure of native fishes. Bigmouth buffalo and gizzard shad are prime candidates for this type of approach, given their dietary overlap with silver carp. Incorporating results from both the ecological and economic perspectives could allow managers to make more nuanced decisions regarding silver carp harvesting and movement reduction practices.

## Data Availability

Code available on CC GitHub repository:  
<https://github.com/camjay99/SilverCarpIPM>.

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## Author Contributions

C. Coles: conceptualization, methodology, software, validation, formal analysis, writing (original draft). E. Balas: conceptualization, methodology, formal analysis (original draft). J. Peirce: conceptualization, methodology, writing (original draft). G. Sandland: conceptualization, methodology, writing (original draft). R. Erickson: conceptualization, software, writing (review & editing).

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