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Using a Coupled Integral Projection Model to Investigate Interspecific Competition During an Invasion: An Application to Silver Carp (*Hypophthalmichthys molitrix*) and Gizzard Shad (*Dorosoma cepedianum*)

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ABSTRACT

As a generalization of stage-based matrix models, integral projection models (IPMs) have been used to describe the size-based dynamics of wildlife and fisheries populations. Although some matrix models have explicitly included species interactions, few IPMs have expanded beyond single species, which limits their ability to describe the competitive dynamics of co-occuring taxa. We present a coupled system of IPMs where intra- and inter-specific competition may reciprocally affect the life-histories of two species. We investigated the potential role that competition has on two overlapping fish species in the upper Mississippi River system: the native gizzard shad (*Dorosoma cepedianum*) and the invasive silver carp (*Hypophthalmichthys molitrix*). Numerical simulations of this system indicated that the coupled IPMs could exhibit asymptotic behaviors similar to traditional, non-linear competition models. Specifically, by altering the competition coefficients, we demonstrate this model's ability to detect competitive exclusion, species coexistence, and dual extinction outcomes.

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1 Introduction

Globalized transport and commerce, and the widespread cultivation of economically valuable species have been implicated in the widespread introduction of potentially detrimental non-native fishes (Mack et al., 2000; Rahel, 2000; Toussaint et al., 2016; Perrin et al., 2021). Although relatively few introductions have had measurable effects on native fish communities (Gozlan, 2008), their suspected influence has been recognized for decades (Elton and Elton, 1958; McKinney and Lockwood, 1999) and their establishment is thought to have contributed to declines in native freshwater fishes worldwide (Reynolds et al., 2002; Dudgeon et al., 2006; Cucherousset and Olden, 2011). These effects include population decreases and even the displacement of native fish due to predation and competition, transmission of foreign parasites, and the physical disruption of habitat (Vitule et al., 2008; Korsu et al., 2010; Cucherousset and Olden, 2011; Cooke et al., 2016; Britton, 2022). Despite the potential negative effects that non-native fishes may have on native species, relatively little is known about the conditions under which interspecific interactions influence native fishes, and how the strength of these effects alter their populations (Gallardo et al., 2016).

Silver carp (*Hypophthalmichthys molitrix*) and gizzard shad (*Dorosoma cepedianum*) are two fish species found in abundance in the upper Mississippi River system (LTRM, 2022). Silver carp have invaded aquatic ecosystems throughout the Mississippi River Basin of North America (Williamson and Garvey, 2005). Populations of silver carp are highly fecund, grow rapidly, and reach maturity early in life (Williamson and Garvey, 2005) and, consequently, can increase their numbers rapidly in invaded habitats; however, local abundance may be limited through density-dependence mechanisms (Broaddus and Lamer, 2022). Silver carp feed at multiple trophic positions and exhibit high consumption rates, which make them a potentially competitive threat to numerous fish species including native gizzard shad (Kolar et al., 2007). Although little is known about interactions

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between silver carp and gizzard shad, previous work has indicated that silver carp densities may alter both the growth and survival of gizzard shad in areas where both species occur (Buynak et al., 1992; Welker et al., 1994; Michaletz, 2010). For example, in the La Grange Reach of the Illinois River, the presence of silver carp has corresponded with a reduction in the abundance and body condition of gizzard shad (Irons et al., 2007; Love et al., 2018). These patterns might be attributed to interspecific competition between young gizzard shad and silver carp for prey sources (notably zooplankton) (Irons et al., 2007). Although interspecific competition may also influence other gizzard shad life stages, little work has been conducted to address these associations (DiCenzo et al., 1996).

Mathematically describing the interactions between species continues to be a keystone in the building of mathematical models predicting population dynamics. Competition terms have been included in models ranging from classic differential equations and discrete-time matrix models, to individual based models (for example, Brauer and Castillo-Chavez, 2012 and Grimm and Railsback, 2013). A size-structured integral projection model (IPM) framework, first introduced by Easterling et al. (2000), has been used as a generalization of stage-based, matrix model for population dynamics (refer to Ellner et al., 2016, for a review) In an IPM, future size states are predicted using size-dependent survival and growth functions of the current state, and the recruitment of new individuals from reproduction and immigration. Just as with the classical models, an increase in population density can affect intraspecific and interspecific competition, and many IPMs for a single species include intraspecific density dependence (refer to Ellner et al., 2016, Chapter 5). Few IPMs represent interspecific competition and explicitly model multiple species. For example, Bassar et al. (2017) developed an IPM with competition, including niche shifts based on organism length, to study species coexistence.

In this paper, we present a coupled system of IPMs for populations where the density of competitors can affect growth, survival, and reproduction of both species. Freshwater fish are an ideal group to study using an IPM approach as many species have received substantial management attention and are associated with robust life-history information and standardized sampling (for example, Erickson et al., 2017; Heather et al., 2018; Schindler et al., 2013). As an application of the coupled IPM, we numerically explored how varying the interspecific competition coefficients can affect the population densities of gizzard shad and silver carp. Results from this study may allow managers to better understand the potential for interspecific competition between these two species and the possible consequences of silver carp invasions.

2 Materials and Methods

An integral projection model is characterized by a discrete time step, t, where a census of the sizes, z, of individuals in the population is recorded (Easterling et al., 2000). The population census at time t is represented by a continuous density function of the size, $n(z,t)$. The size distribution of the population is updated, or projected, to census time $t+1$ through the formula:

$$n(z',t+1) = \int_{\Omega} K(z',z)n(z,t)\,dz, \tag{1}$$

where Ω is the interval of all possible sizes and $K(z',z)$ is an integral kernel often defined as $K(z',z) = P(z',z) + F(z',z)$. For an individual of size z at time t, $P(z',z)\Delta z$ is the probability that the individual remains alive at time $t+1$ and has grown to a size in the interval $[z', z'+\Delta z]$. $F(z',z)\Delta z$ is the number of new offspring in the size interval $[z', z'+\Delta z]$ present at time $t+1$ per individual of size z at time t.

2.1 Density-dependence competition model

Intraspecific and interspecific competition can affect the survival, growth rates, and reproduction of individuals during their lifetime (Connell, 1983; Gustafsson and Ehrlén, 2003; Ward et al., 2006). If there are N species competing for similar resources, the size-distributions of each species can be modeled by a system of N coupled density-dependent IPMs:

$$n_i(z',t+1) = d_{P,i}(\vec{n}) \int_{\Omega_i} P_i(z',z)n_i(z,t)\,dz + d_{F,i}(\vec{n}) \int_{\Omega_i} F_i(z',z)n_i(z,t)\,dz, \qquad \text{for } i = 1,\ldots,N, \tag{2}$$

where $d_{P,i}$ and $d_{F,i}$ are non-increasing scalar functions with respect the total individuals in each species and $\vec{n}$ is the vector of size distributions. Equation 2 allows for models in which density-dependent effects may reduce (1) the survival and growth of the current population, and/or (2) the recruitment observed in the next population census.

2.2 Application to gizzard shad and silver carp

We assumed the sequence of events in the life cycle of gizzard shad and silver carp are the same (Figure 1) and depend on the size variable z, representing the length of an individual (measured in millimeters). For the current population of fishes

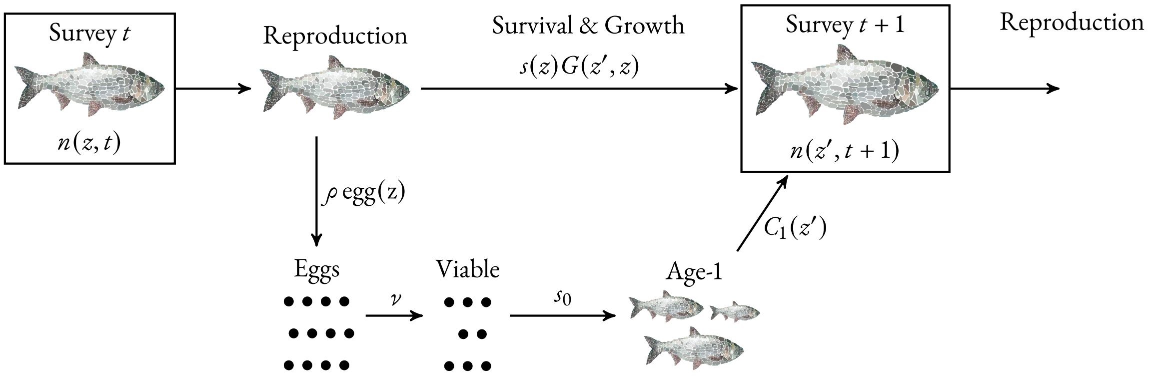

Figure 1: An example of the life cycle diagram and pre-reproduction survey points used in an IPM model for freshwater fish species.

$P(z',z) = s(z)G(z',z)$ where $s(z)$ is the annual survival probability and $G(z',z)$ is the growth function that describes annual length transitions. Survival was represented as a four-parameter logistic function, and the growth function was a two-variable normal distribution centered around a modified von Bertalanffy function of the length at time t (measured in years). The forms for the functions used in the model are summarized in Table 1, and more detail can be found in the references to Peirce et al. (2023) and Coles et al. (2023).

In the gizzard shad and silver carp models, reproduction was described by a two-stage process with ρ representing the probability a female fish spawns, and egg(z) is the mean number of eggs produced by a female of length z. A small probability ν of eggs will develop to age-0 individuals and those fish recruit to be observed during the next survey with probability s_0. $C_1(z')$ is the length distribution of all age-1 fish. A pre-reproductive survey leads to the fecundity kernel used for both fish species as

$$F(z',z) = \rho\, \text{egg}(z)\, \nu\, s_0\, C_1(z').$$

We assumed the density-dependence in the growth and survival component was

$$d_P(\vec{n}) = \exp\left(-\sum_{j=1}^{N} p_{ij} B(n_j)\right),$$

where $B(n_j)$ is the biomass density of population j (g per 1000 m^3) computed from the length distribution of each population as

$$B(n_j) = 10^{-3}\int_{\Omega} W(z) n_j(z,t)\, dz, \tag{3}$$

with $W(z)$ representing the length-weight relationship. The parameters p_{ij} measure the effect of the biomass density of population j on the growth and survival of population i. If the species are not in direct competition for resources, then p_{ij} will be zero.

We assumed that the density of new recruits at the next survey depends on current density of recruits with the function

$$d_F(\vec{n}) = \exp\left(-\sum_{j=1}^{N} f_{ij} A_0(n_j)\right),$$

where A_0 is the density (number per 1000 m^3) of each species before the first survey, and f_{ij} are weights on how much age-0 density of population j affects the survival of age-0 fish in population i.

2.2.1 Single-species: gizzard shad and silver carp IPM

The probability of a gizzard shad surviving their first year can depend on many factors including predation, temperature, the mean total length of the individual, and the density of age-0 fish in the population (Michaletz, 2010). As according to Peirce et al. (2023), the probability of survival of an age-0 gizzard shad in this study was assumed to be density-dependent without an assumption of intraspecific competition effects on adult survival ($d_P(\vec{n}) = 1$). As a result, the dynamics of a gizzard shad population were described by a reduced form of Equation 2:

$$n(z',t+1) = \int_{\Omega} P(z',z)n(z,t)\, dz + e^{-f_{11}A_0(n)}\int_{\Omega} F(z',z)n(z,t)\, dz,$$

Table 1: A summary of the functions used in the coupled IPM model for gizzard shad and silver carp. Refer to the supplementary material for the graphs of each function.

Adult survival:	$s(z) = s_{min} + \dfrac{s_{max} - s_{min}}{1 + e^{-\beta_s(z-\alpha_s)}}$ with the minimum and maximum survival probability s_{min} and s_{max}. α_S and β_S are the inflection and slope parameters.
Growth kernel:	$\text{Prob}(z' \mid z, L_\infty, K_g) = \text{NormalPDF}(\mu_g, \sigma_g)$ where $\mu_g = L_\infty\left(1 - e^{-K_g}\right) + z(t)e^{-K_g}$. L_∞ and K_g are the von Bertalanaffy coefficients for maximum length and growth rate.
Recruit length distribution:	$C_1(z') = \text{NormalPDF}(\mu_r, \sigma_r)$
Length-weight relationship	$\log\big(W(z)\big) = \alpha_W \log(z) + \beta_W$ where α_W and β_W are the slope and intercept parameters.
Egg production:	Gizzard shad: $\text{egg}(z) = \dfrac{e_{max}}{1 + e^{-\beta_e(z-\alpha_e)}}$ Silver carp: $\text{egg}(z) = \dfrac{e_{max}}{1 + e^{-\beta_e(W(z)-\alpha_e)}}$ where α_e and β_e are the inflection and slope parameters.
Age-0 survival:	$s_0(d) = \alpha_s e^{\beta_s d}$ where α_s and β_s are the initial value and decay rate parameters and d is the density of age-0 gizzard shad.

where $A_0(n) = 10^{-3}\int_\Omega \rho\,\text{egg}(z)\nu n(z,t)\,dz$ is the density of age-0 fish, and f_{11} is an estimate of how much the intraspecific density affects the survival of age-0 fish. A biologically reasonable value of the parameter f_{11} was estimated from age-0 gizzard shad survival data (Michaletz, 2010).

For the silver carp IPM, intraspecific competition was only included in the survival of adults and therefore $d_F(\vec{n}) = 1$ (Coles et al., 2023). The IPM for silver carp was provided as

$$n(z', t+1) = e^{-p_{22}B(n)} \int_\Omega P(z', z)n(z,t)\,dz + \int_\Omega F(z', z)n(z,t)\,dz,$$

where $B(n)$ is the biomass density defined by Equation 3, and p_{22} is an estimate of how intraspecific density affects adult survival and growth.

2.2.2 Multispecies competitive IPM: gizzard shad and silver carp

Interspecific competition among young gizzard shad and silver carp is possibly due to the similarities in their diet (Sampson et al., 2009), and we assumed the competition between the two species is greatest during their first year (Minder and Pyron, 2018). As a consequence, the coupled density-dependent IPM (Equation 2) applied to gizzard shad and silver carp becomes the model used in our analysis:

$$\begin{aligned} n_1(z', t+1) &= \int_\Omega P(z', z)n_1(z,t)\,dz + e^{-\left(f_{11}A_0(n_1) + f_{12}A_0(n_2)\right)} \int_\Omega F(z', z)n_1(z,t)\,dz, \\ n_2(z', t+1) &= e^{-p_{22}B(n_2)} \int_\Omega P(z', z)n_2(z,t)\,dz + e^{-f_{21}A_0(n_1)} \int_\Omega F(z', z)n_2(z,t)\,dz, \end{aligned} \tag{4}$$

where $n_1(z,t)$ and $n_2(z,t)$ are the current length distributions of gizzard shad and silver carp, respectively. Equation 4 is the previously discussed gizzard shad and silver carp models with an additional density-dependent multiplier on the fecundity integral.

3 Analysis and Results

We numerically solved Equation 4 using the Midpoint Rule with large approximating matrices (Burden and Faires, 2005). During the course of model development, we explored different step sizes for the Midpoint Rule and found that about 400 points provided numerically stable results. We integrated over lengths from 0 mm to 600 mm for gizzard shad and 0 mm to 1200 mm

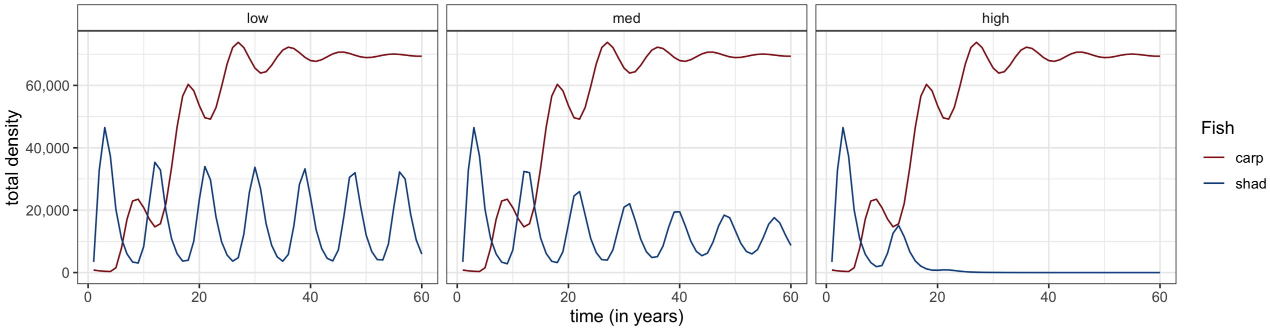

Figure 2: Assuming no effect of gizzard shad density on silver carp ($f_{12} = 0$), the simulated total density of fishes with a low (10^{-4}), medium (10^{-2}), and high (10^{-1}) competitive influence of age-0 silver carp density on the survival of gizzard shad recruits (f_{21}).

for silver carp. The upper limits were chosen based upon numerical stability and consistency of the system (e.g., avoiding eviction or the loss of individuals due to numerical errors; Williams et al., 2012).

We assumed that the initial number of gizzard shad and silver carp in the model were $d_0 = 3437$ and $d_0 = 816$ fish, respectively, representing the average annual catch of fishes caught with all gear types, as reported in the Long Term Resource Monitoring (LTRM, 2022) of the La Grange Reach of the Illinois River from 2000–2020. To begin the model, the initial length distribution for each fish was selected as their density multiplied with the probability of an individual being length z at time $t = 0$. The probability was represented by a normal distribution with mean $0.5L_\infty$ and standard deviation σ_g. Intraspecific competition parameter values were chosen to be $f_{11} = 3 \cdot 10^{-3}$, for the gizzard shad effect on gizzard shad recruitment, and $p_{22} = 5 \cdot 10^{-9}$, for the silver carp effect on silver carp growth and survival. Mean values for the gizzard shad and silver carp parameters used for the simulations have been published by Peirce et al. (2023) and Coles et al. (2023), respectively.

The model was coded in R (R Core Team, 2017), and the scripts are published on JP's GitHub page `https://github.com/jppeirce`.

3.1 Simulation I: Effect of silver carp density on gizzard shad

In the simulation, we assumed that gizzard shad density had no competitive effect on the carp population ($f_{21} = 0$) and we varied the influence of carp density on the survival probability of age-0 gizzard shad (f_{12}) at low (10^{-4}), medium (10^{-2}), and high competition scenarios (10^{-1}). We simulated the total population of both species for 60 years to demonstrate the potential long-term dynamics of the two species at each level of interaction (Figure 2).

For the low value of f_{12}, the density of gizzard shad approached a stable cycle (Figure 2a, blue line). As described by Peirce et al. (2023); the oscillations in the density of gizzard shad follow from the relationship between age-0 density and the survival of age-0 fish, and are similar to patterns of annual length distributions created from the LTRM dataset before silver carp establishment. In contrast, an increase in silver carp densities influenced the adult survival producing a stable equilibrium similar to a logistic growth model (Figure 2a, red line). As the value of f_{12} increased, there was a decay in the amplitude of oscillation and in the mean simulated density of gizzard shad (Figure 2b and 2c, blue line). For the high value of f_{12}, the competitive effect was so strong that the simulated gizzard shad density was approximately zero within 25 years (Figure 2c, blue line).

3.2 Simulation II: Effect of gizzard shad density on silver carp

Here, we assumed that silver carp density has no effect on the shad population ($f_{12} = 0$) and varied the influence of shad density on the survival probability of age-0 silver carp (f_{21}) at low (10^{-5}), medium (10^{-4}), and high competitive scenarios ($2 \cdot 10^{-3}$). We simulated the total population of each species for 60 years to demonstrate the potential long-term effects of gizzard shad competition on the silver carp population (Figure 3).

Even a small dependence of silver carp on age-0 gizzard shad resulted in increased oscillations in the silver carp density (Figure 3a, red line). The amplitude of the oscillation became more evident as the competitive effect increased (Figure 3b, red line). At the high value of the interspecific competition parameter, the density of silver carp oscillated with small amplitude (Figure 3c, red line). When $f_{21} > 2 \cdot 10^{-3}$, the effect of interspecific competition became too great for the persistence of silver carp as its density approached zero.

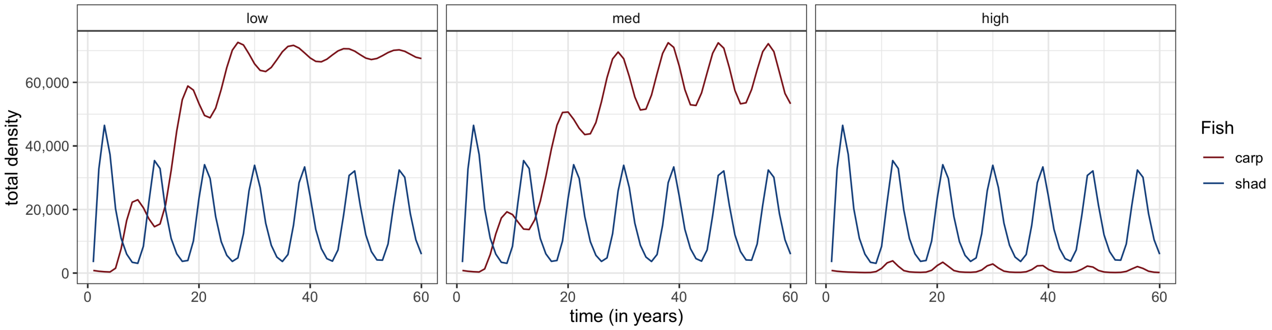

Figure 3: Assuming no effect of silver carp density on gizzard shad ($f_{21} = 0$), the simulated total density of fishes with a low (10^{-5}), medium (10^{-4}), and high ($2 \cdot 10^{-3}$) competitive influence of age-0 gizzard shad density on the survival of silver carp recruits (f_{12}).

3.3 Simulation III: Combined density effects for gizzard shad and silver carp

We varied the interspecific competition parameters $10^{-4} \leq f_{12} \leq 10^{-1}$ and $10^{-5} \leq f_{21} \leq 2 \cdot 10^{-3}$ and simulated the total population of both fish species for 60 years to demonstrate the potential long-term effects of interspecific competition on each population (Figure 4).

When the interspecific competition coefficients were at a low and medium competitive level, both populations of fish were able to survive and coexist. However, the competitive influence was evident in each density. Silver carp totals slightly oscillated due to the density-dependent age-0 survival, while oscillations in the gizzard shad totals declined in amplitude as the mean density of gizzard shad approached a non-zero equilibrium.

In the last column of Figure 4, the competitive effect on gizzard shad from silver carp was set at a high value. When the competition factor from gizzard shad was at low and medium values, the gizzard shad density approached zero after about 30 years. In contrast, when both interspecific competition coefficients were set to high values, the continued presence of gizzard shad delayed the growth of silver carp density when compared to the other simulations by approximately 40 years.

3.4 Simulation IV: Persistence or quasiextinction of gizzard shad and silver carp

In this simulation, we investigated the potential displacement of native gizzard shad following the introduction and establishment of a non-native species. One of the most important and enduring questions in population biology is whether a population of organisms will persist or go extinct (Gerber and González-Suárez, 2010). In this model, as expected, the simulated endpoint of each fish population was associated with the competition coefficients included in the model. To examine this relationship, we compared the final 10-year average of total densities with various quasiextinction thresholds. We consider the quasiextinction threshold to be the population density below which there is a greater likelihood that the population would go extinct.

For the smaller values of the interspecific competition coefficients (f_{12} and f_{21}), both populations coexisted (Figure 5). However, as the values of the parameters increased, one fish population persisted above the threshold, while the other remained below, indicating displacement or community resilience. It should be noted that the range of values for silver carp's competitive effect on gizzard shad shown in Figure 5 was over 300 times larger than the range of values for the effect of gizzard shad on silver carp. As expected, the domain of competition parameters associated with dual quasiextinction (shown as the white region in Figure 5) increased in area as the threshold increased. This area was disproportionately dominated by silver carp as the density of gizzard shad was more likely to drop below the quasiextinction threshold.

4 Discussion

Species introductions can have substantial effects on native populations and communities through several biological processes including competition. In this paper, we developed a coupled IPM that includes interspecific competition, and applied the model to a system with two overlapping fish species, gizzard shad and silver carp. Simulations using varying competition coefficients demonstrated the importance of interspecific competition on the long-term state of each species in areas of the upper Mississippi River system (Figures 4 and 5). More specifically, modeling outputs predicted silver carp to persist at higher densities than gizzard shad across most of our competitive scenarios. These results align with information from an empirical study showing a reduction in the abundance of gizzard shad after the arrival of silver carp into the Illinois River (Irons et al., 2007).

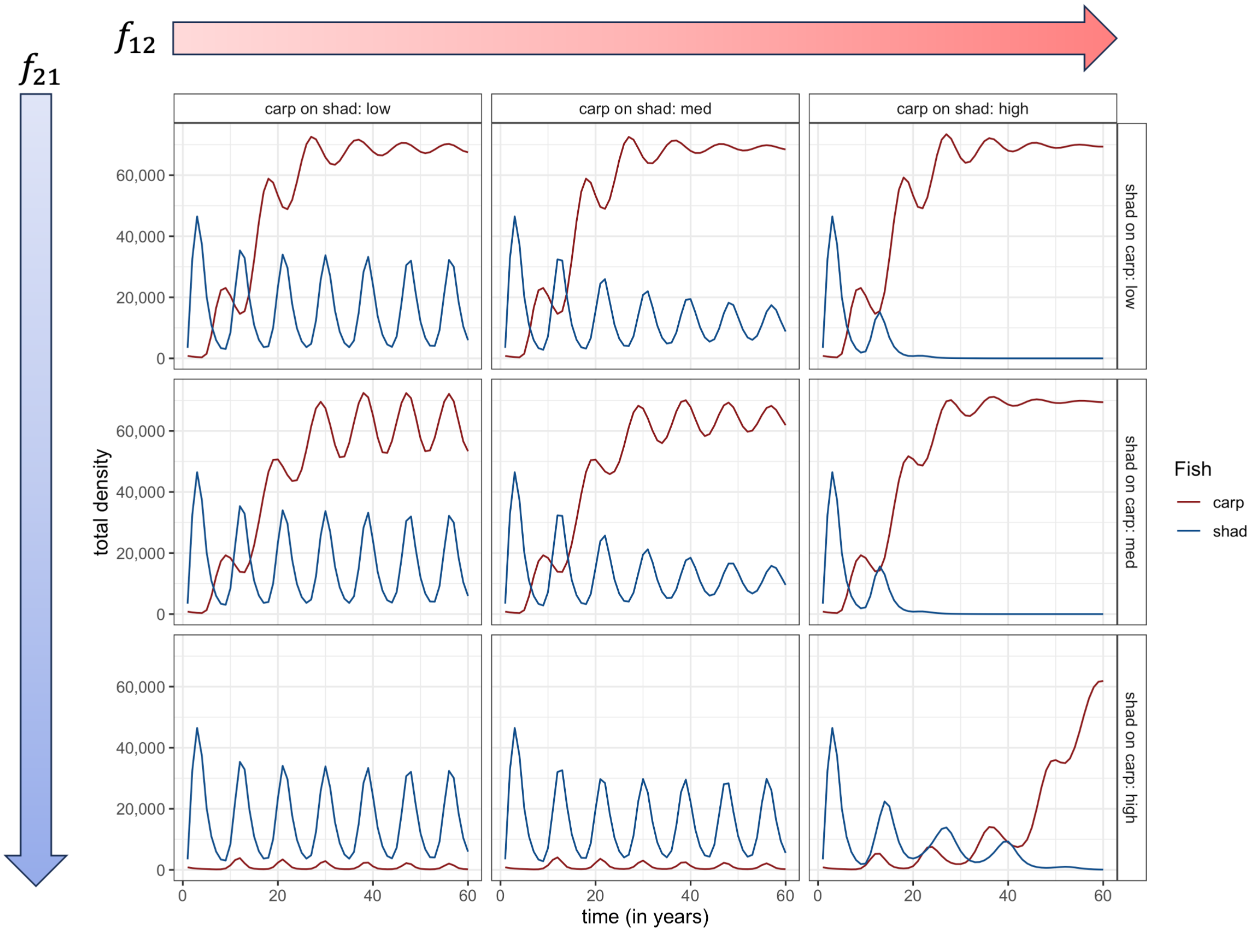

Figure 4: Simulations of total densities of silver carp and gizzard shad for various combinations of interspecies competition factors. Graphs left to right reflect an increase in f_{12}, the competitive effect of silver carp on gizzard shad with low (10^{-4}), medium (10^{-2}), and high (10^{-1}) values. Graphs top to bottom reflect an increase in f_{21}, the competitive effect of gizzard shad on silver carp, with low (10^{-5}), medium (10^{-4}), and high ($2 \cdot 10^{-3}$) values.

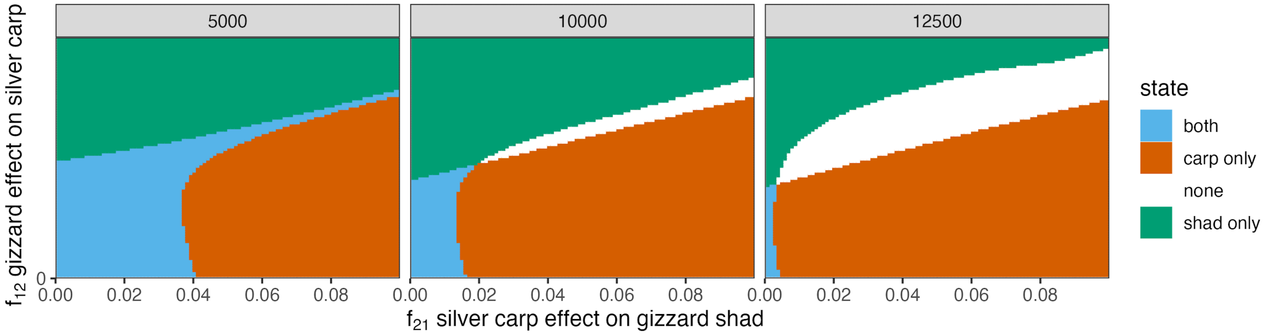

Figure 5: State of gizzard shad and silver carp after 60 years with threshold for persistence (a) 5000 fish, (b) 10000 fish, and (c) 12500 fish.

Modeling gizzard shad and silver carp densities within a coupled IPM framework exhibited long-term patterns consistent with traditional non-linear competition models. In particular, altering the values of the competition coefficients produced three long-term population outcomes: competitive exclusion, species coexistence, and dual quasiextinction (Figure 5). The same behavior has been shown in differential equation-based models for competitive species (for example, Brauer and Castillo-Chavez, 2012). However, the IPM framework may have an advantage over more traditional approaches because a predicted size distribution of individuals can be produced at any time step. In addition, the structure of an IPM has a greater connection to empirical data, which tends to associate growth, survival, and reproduction with individual length as opposed to life stage (Ellner et al., 2016). For competition, this extends to associating niche use and relative competitive strength to length, rather than only discrete life stage (Bassar et al., 2017). In future studies, this modeling approach may allow researchers to identify displacement or community resilience within particular size-groups in each population.

Several different modeling approaches have been used to provide insight into managing invasive carp. For example, Tsehaye et al. (2013) used a dynamic simulation model to show the importance of size-based fish removal when attempting to control silver carp. Yet, to our knowledge, no modeling exercises have simultaneously examined the combined effects of length-based carp removal and interspecific competition on the dynamics of both invasive (carp) and native (i.e., gizzard shad) populations; this is something that could be investigated using our model. Other modeling approaches have focused on the consequences of silver carp in food webs (Rutherford et al., 2021; Kramer et al., 2019). Unlike these food web-based models, however, IPM-based models, such as the one presented in this study, can explore different mechanisms of both intra- and inter-specific competition and examine how these processes interact with management actions aimed at reducing carp numbers. In addition, a more focused modeling approach on one or two fish species rather than broader food-web interactions, may better align with current fisheries-management practices that are species-centric (Foley, 2013).

As invasive species continue to alter native ecosystems, additional theoretical studies could utilize the approach outlined in this paper. For example, there are other native fish species, such as bigmouth buffalo (*Ictiobus cyprinellus*), that appear to be negatively affected by silver carp (Irons et al., 2007). These species would be a good candidates for this model and could provide a more comprehensive appreciation of the influences that invasive carp are having on fish assemblages within invaded waterways. In addition, expansion of a coupled IPM to other species could motivate subsequent empirical work that could aid in elucidating critical life history parameters in both native and invasive species. This information could then be incorporated into future iterations of the model. Parameters from this empericial work would likely include uncertainty, which could be studied more systematically through stochastic iterations of the model that include parameters drawn from the distribution of the estimated parameters, Monte Carlo integration over the joint distribution of all the parameters, or other methods. Other ecological factors, including food availability, migration, and seasonality could be incorporated into the model to further study the mechanisms of competition and the effect of other changes in population density. Understanding size and life-stage vulnerabilities of native fish may help managers to better protect these species from invasive species such as silver carp.

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