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ARTICLE

Analysis of per capita contributions from a spatial model provides strategies for controlling spread of invasive carp

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Abstract

Metapopulation models may be applied to inform natural resource management to guide actions targeted at location-specific subpopulations. Model insights frequently help to understand which subpopulations to target and highlight the importance of connections among subpopulations. For example, managers often treat aquatic invasive species populations as discrete populations due to hydrological (e.g., lakes, pools formed by dams) or jurisdictional boundaries (e.g., river segments by country or jurisdictional units such as states or provinces). However, aquatic invasive species often have high rates of dispersion and migration among heterogeneous locations, which complicates traditional metapopulation models and may not conform to management boundaries. Controlling invasive species requires consideration of spatial dynamics because local management activities (e.g., harvest, movement deterrents) may have important impacts on connected subpopulations. We expand upon previous work to create a spatial linear matrix model for an aquatic invasive species, Bighead Carp, in the Illinois River, USA, to examine the per capita contributions of specific subpopulations and impacts of different management scenarios on these subpopulations. Managers currently seek to prevent Bighead Carp from invading the Great Lakes via a connection between the Illinois Waterway and Lake Michigan by allocating management actions across a series of river pools. We applied the model to highlight how spatial variation in movement rates and recruitment can affect decisions about where management activities might occur. We found that where the model suggested management actions should occur depend crucially on the specific management goal (i.e., limiting the growth rate of the metapopulation vs. limiting the growth rate of the invasion front) and the per capita recruitment rate in downstream pools. Our findings illustrate the importance of linking metapopulation dynamics to management goals for invasive species control.

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KEYWORDS

aquatic invasive species, Bighead Carp, Great Lakes, Illinois River, management, metapopulations, population dynamics

INTRODUCTION

Many species exist across a series, heterogenous patches, or subpopulations connected by dispersal, migration, or other similar movement patterns. Where this is the case, effective species management benefits from the explicit consideration of multiscale effects (Akçakaya et al., 2007; Hastings, 2014). The demography of these species depends on the interaction of the traits and behaviors of the species with the location-specific qualities and connectivity of the landscape. Metapopulation models (i.e., models of populations of subpopulations) exist as one method for examining these systems (Hanski, 1999).

To date, metapopulation concepts and models have been combined with data to inform various aspects of conservation and species management such as habitat protection, regulation of harvest, reserve design, and reintroduction (reviewed in Akçakaya et al., 2007). Similarly, they have been used to inform management of a diversity of invasive species including birds (Lenda et al., 2010), fish (Tamburello et al., 2019), mammals (Lurgi et al., 2016), gastropods (Facon & David, 2006), insects (Bogich & Shea, 2008), and plants (James et al., 2011; Maxwell et al., 2009). In addition, there have been a number of general theoretical treatments of invasive species management in spatially structured populations (e.g., Baker, 2017; Pepin et al., 2020; Perry et al., 2017). These studies have employed a diversity of methods from analytically simple incidence function models (Hanski, 1994; Tamburello et al., 2019)—which uses distance between patches, size of patches, and presence/absence data—to systems of reaction–diffusion equations that model population dynamics over a continuous spatial domain (Baker, 2017).

The diversity of methods that have been used is, at least partially, driven by practical constraints. For example, detailed data on demographic parameters and especially movement rates are both very important to understanding metapopulation dynamics that can be difficult, expensive, and time-consuming to obtain. As a result, each study must adopt methods to make the best use of the incomplete information available given the system-specific constraints.

Despite the variation in methods employed and specific definitions of management success, these previous studies had similar goals, to identify either a general “rule-of-thumb” or specific strategy for which set of

subpopulations to target to limit or eradicate an invasive population. The strategies they recommend vary in the particulars but can be summarized as targeting management efforts to those subpopulations that are some combination of (1) the largest subpopulations (e.g., Pepin et al., 2020; Tamburello et al., 2019), (2) most highly connected (e.g., Perry et al., 2017), and (3) most likely to act as sources to uninfected areas (e.g., Baker, 2017).

However, trying to apply these insights to manage particular populations can be difficult. For example, defining and identifying which subpopulations are sources is often not straightforward (see Runge et al., 2006), especially for species with complex within-generation migratory or movement patterns (see Erickson et al., 2018). Runge et al. (2006) and Erickson et al. (2018) provide some remedy to the need to determine source and sink subpopulations using information provided by linear matrix models. The benefit of the matrix model approach is that the within-subpopulation demographic and movement information are both encoded to inform the per capita contributions of each subpopulation to one another and the metapopulation as a whole. This approach is useful for invasive species management because the per capita contribution of subpopulation A on B can be directly interpreted as the number of individuals reduced in subpopulation B in period $T + 1$ caused by removing an individual from subpopulation A in period T .

Moreover, review of previous work suggests that both local- and metapopulation-scale phenomena may be relevant for different population management goals. For example, if the goal is control of the population landscape-wide, focusing control effort in areas most important to metapopulation-scale parameters would be best. However, in the case of an outward-spreading invasion, limiting the subpopulation size and growth rate at the margins of the invasion might be the most important objective of population management. The “per capita contribution” suggested by Runge et al. (2006) and Erickson et al. (2018) is useful because it provides direct analytical connections between subpopulation-scale and metapopulation-scale dynamics and phenomena.

To illustrate these concepts, we use a linear matrix model to derive the per capita contributions and metapopulation-scale metrics to provide management insights for Bighead Carp (*Hypophthalmichthys nobilis*), an invasive fish, in the Illinois River. Bighead Carp first

appeared in the Mississippi River Basin in the early 1970s and have since spread to connected subbasins including the Illinois River (see Kolar, 2007 for their invasion history). In locations where Bighead Carp have invaded, they cause large-scale ecological and economic damage (Hansen, 2010), especially when they reach high abundances, such as in parts of the Illinois River (e.g., Silver Carp [*H. nobilis*] and Bighead Carp combined up to 80% fish biomass; Coulter, MacNamara, et al., 2018). For example, native planktivores are negatively impacted by invasive Bighead Carps (Fritts et al., 2018; Tristano et al., 2019) and plankton assemblages are altered (e.g., Collins & Wahl, 2018). The Illinois Waterway has been a focal point for Bighead Carp management because this waterway connects the Mississippi River Basin to the valuable fisheries resources of the Laurentian Great Lakes via man-made canal systems. If Bighead Carp establish in the Great Lakes, there would likely be large impacts to those ecosystems, resulting in potential economic and ecologic value loss (Cuddington et al., 2014; Ivan et al., 2020; Zhang et al., 2016). The goal of this work is to use the spatial structure of the Illinois River, which is formed by a series of movement-limiting dams that divide it into a set of pools, and existing data on movement among pools to inform management strategies to prevent the spread of Bighead Carp to the Great Lakes.

We created a simple, spatial linear matrix model of population dynamics to examine the per capita effects of harvest of Bighead Carp from different locations in the Illinois River. We combined monthly observational data about survival and movement rates among pools of the Illinois River (Coulter, Brey, et al., 2018; data release: Coulter et al., 2022) with local demographic parameterization to derive pool-level (i.e., subpopulation) contributions to both population pressure at the invasion front and at the scale of the whole metapopulation. We focused on pool-specific per capita effects since these can be interpreted directly as estimates of the per individual efficiency of culling one individual on future populations. The goal is to provide insights about this system to guide management efforts and to help direct and prioritize future data collection efforts to aid management.

METHODS

Study system description

The study area covers the Illinois River main stem, which flows south and west from the confluence of the Kankakee and Des Plaines rivers until it flows into the Mississippi River at Alton, IL, USA, as well as the lower portion of the Des Plaines River, downstream of Brandon

Road Lock and Dam (Figure 1). The study area is divided by a series of locks and dams creating pools of varying sizes and gradients (upper three pools have higher gradient than lower pools; Koel & Sparks, 2002). The upstream-most pool, Dresden Island Pool, is 23 river kilometers (rkm) long, with Brandon Road Lock and Dam at the upstream end and Dresden Island Lock and Dam at the downstream end. Next is Marseilles Pool, which is 39 rkm long. It is bounded by Dresden Island Lock and Dam at the upstream end and Marseilles Lock and Dam at the downstream end. Starved Rock Pool is 26 rkm in length. It is demarcated by Marseilles Lock and Dam at the upstream end and Starved Rock Lock and Dam at the downstream end. These three pools are collectively referred to as the Upper Illinois River. The next pool downstream is Peoria Pool, which is 118 rkm in length. It is bounded by Starved Rock Lock and Dam at the upstream end and Peoria Lock and Dam at the downstream end. Next is La Grange Pool, which is 125 rkm in length and surrounded by Peoria Lock and Dam at the upstream end and La Grange Lock and Dam at the downstream end. The most downstream pool in the study area is Alton Pool, which is 129 rkm in length. It is delineated at the upstream end by La Grange Lock and Dam. No dam exists at the downstream end of Alton Pool at the confluence with the Mississippi River. The three downstream pools are collectively known as the Lower Illinois River.

The Lower Illinois River has highest abundance of invasive carps (Coulter, MacNamara, et al., 2018), whereas Dresden Island Pool consistently has the lowest abundance of invasive carps within the study area (Coulter, MacNamara, et al., 2018). Locks and dams within the study area have varying permeability to Bighead Carp movement due to structural and operational differences. Movement probability is greatest through the two most downstream dams (Coulter, Brey, et al., 2018). La Grange and Peoria dams are wicket-style dams where wickets are lowered for portions of the year, allowing water to flow freely. Other dams in the study area are gated dams where water velocities can be higher, making passage more difficult. For this analysis, we treat the populations within pools as subpopulations of the metapopulation (comprised of all pools) due to restricted movement among pools (Coulter, Brey, et al., 2018).

Movement data collection and analysis

Individual Bighead Carp ($N = 248$) movements were tracked with internally implanted acoustic tags (V16, 60-s ping interval, Innovasea, Nova Scotia, Canada; Southern Illinois University Animal Care and Use Protocols

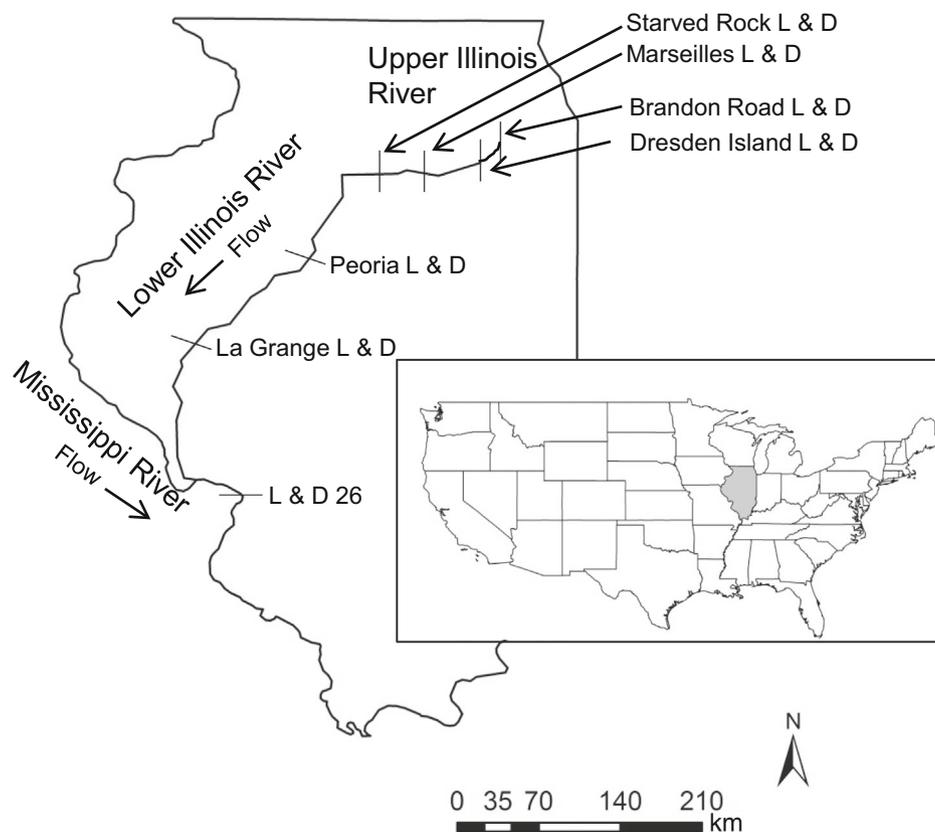


FIGURE 1 Map of Illinois River with location of the locks (L) and dams (D) that define the pools. Inset map highlighting the position of the State of Illinois. Upper pools (Dresden Island through Starved Rock pools) tend to be shorter and higher gradient than downstream pools (Peoria through Alton Pools): Dresden Island (Pool 1), 23 km; Marseilles (Pool 2), 39 km; Starved Rock (Pool 3), 26 km; Peoria (Pool 4), 118 km; La Grange (Pool 5), 125 km; Alton (Pool 6), 129 km.

11-010, 14-015, 14-025) in the Illinois River using an array of VR2W and VR-tx stationary receivers (Innovasea). Full details about tagged fish characteristics, tagging procedures, and receiver deployment can be found in Coulter, Brey, et al. (2018). The Illinois River was divided into its six pools or “states” delineated by the dams and locks and where the Illinois River joins the Mississippi River. Individual movements were condensed into monthly capture histories covering 20 months of movement (May 2012–August 2015; Coulter, Brey, et al., 2018). The pool a fish was considered to have resided in during a given month was the pool it was last detected within during that month. Month was selected as a time step because this was the smallest time step that minimized zeros within capture histories while still maintaining some temporal resolution (Coulter, Brey, et al., 2018).

Capture histories were then used to parameterize and evaluate open mark–recapture multistate models (Brownie et al., 1993; Hayden et al., 2014; Hestbeck et al., 1991) in program MARK (White & Burnham, 1999) with the goal of estimating pool to pool transition

probabilities (Coulter, Brey, et al., 2018; Hayden et al., 2014). In addition to transition probabilities, multistate models also estimate survival and detection probability. Assumptions of multistate models include those of all Cormack–Jolly–Seber mark–recapture models (e.g., tagging does not influence survival/recapture; Cormack, 1964; Jolly, 1965; Seber, 1965) and additional assumptions that (1) mortality occurs before movement and (2) movement among states (or pools) occurs simultaneously. The multistate models that were evaluated in program MARK included all possible combinations of transition, survival, and detection probabilities varying by state, time, both, and neither. Additionally, different season parameterizations (two, three, or four seasons per year) were evaluated (details in Coulter, Brey, et al., 2018). Since there was little substantial difference among seasons, within this manuscript we used the model that provided a constant rate across seasons. However, the derivation described below is general with respect to this choice and could easily be updated if new information is provided. For simplicity, we will refer to the final estimates as movement probabilities.

For the top models for Bighead Carp, three Markov chain Monte Carlo (MCMC) chains resulting from the analysis described above were used to generate hyperdistributions for each estimated parameter from 10,000 steps after 4000 tuning steps and 1000 burn-in steps, respectively (following Cooch & White, 2019). Random number seed was zero. The MCMC hyperdistributions were used to estimate the uncertainty in these relationships by resampling the posterior distribution of the monthly transition probabilities and carrying results through the subsequent calculations. For this application, the transition probability estimates returned by the MCMC fit were treated as movement probabilities, which assumes that the probability of survivorship during transition, S in Equation (1) below, is very high (estimated as 0.99 ± 0.0021 in Coulter, Brey, et al., 2018).

For model development, we followed the usual convention of using a numeric index for pools ordered by position in the river such that $k=1$ indicates most upstream pool and $k=6$ indicates the most downstream pool. This results in the assignments: Dresden Island ($k=1$), Marseilles ($k=2$), Starved Rock ($k=3$), Peoria ($k=4$), La Grange ($k=5$), and Alton ($k=6$).

Model description and development

Here, we describe how we used the monthly survival and movement estimates to develop an annual time-step model with variation among seasonal demographic parameters. As described in Coulter, Brey, et al. (2018), the per capita probability of survival in pool h and movement from pool h to pool k in the monthly time step Δt is described by the parameter ϕ_{kh} , where $h, k \in \{1, \dots, 6\}$ are indices of pool membership. As a mnemonic device to remember which is which, h can be thought of as the originating or “home” pool. If we assume no recruitment in the short time Δt , then the population in pool k at time $t + \Delta t$, $n_k^{t+\Delta t}$, can be described by the following equation:

$$n_k^{t+\Delta t} = S \left(1 - \sum_{h \neq k} \phi_{hk} \right) n_k^t + \sum_h \phi_{kh} n_h^t. \quad (1)$$

For each pool, k , this can be written in matrix notation as follows:

$$\mathbf{n}^{t+\Delta t} = \mathbf{A}^t \mathbf{n}^t, \quad (2)$$

where \mathbf{n}^t is the 6×1 vector of population values at time t and \mathbf{A}^t is the 6×6 matrix of transition probabilities at time t . With this formulation, the matrix element a_{kh} is

the per capita contribution of individuals from pool h to pool k at time t . Note that the superscript indicating time is an index, not an exponent.

From Equation (2), we find the expression for \mathbf{n}^t is,

$$\mathbf{n}^t = \mathbf{A}^{t-\Delta t} \mathbf{n}^{t-\Delta t}. \quad (3)$$

Substituting Equation (3) into Equation (2) gives the expression for $\mathbf{n}^{t+\Delta t}$ over the $2\Delta t$ interval,

$$\mathbf{n}^{t+\Delta t} = \mathbf{A}^t \mathbf{A}^{t-\Delta t} \mathbf{n}^{t-\Delta t}. \quad (4)$$

In Equation (4), the product $\mathbf{A}^t \mathbf{A}^{t-\Delta t}$ is a 6×6 matrix \mathbf{A}' , of which the kh th element is,

$$a'_{kh} = \sum_{i=1}^6 a_{ki}^t a_{ih}^{t-\Delta t}. \quad (5)$$

The recursive substitution of $\mathbf{n}^{t-j\Delta t}$ by $\mathbf{n}^{t-(j+1)\Delta t}$ can be continued until for $j = (0, \dots, T)$ to give an overall time step of $T + 1$.

For this model, we assumed subpopulation censuses were done in March of every year. We use annual time steps but allow demographic parameters to vary seasonally. To accomplish this, we defined four seasonal transition matrices as $\mathbf{A}^w = \mathbf{A}^2 \mathbf{A}^1 \mathbf{A}^{12}$, $\mathbf{A}^f = \mathbf{A}^{11} \mathbf{A}^{10} \mathbf{A}^9$, $\mathbf{A}^{su} = \mathbf{A}^8 \mathbf{A}^7 \mathbf{A}^6$, and $\mathbf{A}^{sp} = \mathbf{A}^5 \mathbf{A}^4 \mathbf{A}^3$, where the notation {w, f, su, sp} refers to season {winter, fall, summer, spring} and the number refers to the month (i.e., January = 1, February = 2, etc.). Thus, winter = {December, January, February}, fall = {September, October, November}, etc. We assume that recruitment into the size class detectable by surveys occurs during summer and varies by pool; and that individuals in smaller size classes remain in natal pools. Putting these elements together gives,

$$\mathbf{n}^{T+1} = \mathbf{A}^w \mathbf{A}^f (\mathbf{A}^{su} + \mathbf{B}) \mathbf{A}^{sp} \mathbf{n}^T, \quad (6)$$

where T is the year, \mathbf{B} is a diagonal matrix such that $b_{kh} = 0$ for all $k \neq h$. Thus, b_{11} is the per capita recruitment in Pool 1. From here on, when referring to b , we drop one of the indices, (e.g., $b_{kk} = b_k$). The resulting entries in the matrix $\mathbf{A}' = \mathbf{A}^w \mathbf{A}^f (\mathbf{A}^{su} + \mathbf{B}) \mathbf{A}^{sp}$ are complicated combinations of the month-based parameters ϕ_{hk} and the seasonal parameters b_k that reflect the mixing of the populations among the pools at the shorter timescales. It contains information about both local- and metapopulation-scale dynamics. For example, at the local scale, a'_{kh} gives the per capita contribution of an individual in pool h on the population in pool k the following spring. At the metapopulation scale, the dominant eigenvalue of \mathbf{A}' gives the long-term per capita growth rate of the

metapopulation and the dominant eigenvector, the stable population distribution across pools (i.e., proportion of the metapopulation in each pool) (Runge et al., 2006).

In the next section, we analyze how the local and metapopulation dynamics depend on pool-specific combinations of migration probabilities and demographic parameters. For each analysis, the uncertainty in the target metric to variability in the underlying measurements, such as detection, was assessed by resampling the posterior distribution of movement probabilities and reported as standard error.

Sensitivity of metapopulation growth rate

As discussed above, the dominant eigenvalue, λ_1 of the matrix \mathbf{A}' is an estimate of long-term growth rate of the metapopulation. The sensitivity of the metapopulation growth rate to each movement probability can be calculated as follows:

$$s_{\phi_{kh}} = \left. \frac{\partial \lambda_1}{\partial \phi_{kh}} \right|_{\theta^*}, \quad (7)$$

where θ^* is the set $\{\boldsymbol{\phi}, \mathbf{b}\}$ in which movement probabilities, $\boldsymbol{\phi}$, were set at observed values and recruitment rates, \mathbf{b} , were set to values to cause the dominant eigenvalue to be slightly larger than 1, that is, $\lambda_1 = 1.01$. Note that positive or negative sensitivity is possible since any increase in the inter-pool movement probability $\phi_{k \neq h}$ necessitates a corresponding decrease in the retention probability of the source pool $\phi_{k=h}$. We found that the sensitivities are an approximately linear function of the per capita birth rates b . Thus, for any selection of b away from the origin, the ordering of the sensitivities is constant. Additionally, because the estimated values of ϕ^* vary widely, we report these elasticities, calculated as $s_{\phi_{kh}} \phi^* / \lambda_{1^*}$, where the asterisk indicates the quantities were calculated for the median values of the observed movement rates. Thus, sensitivities can be interpreted as the absolute change in growth rate given a small positive change in movement probability, and elasticity as the proportional change in growth rate given a small positive change in movement probability. We have made the simplifying assumption that equal per capita recruitment rates in the lower pools, $b_4 = b_5 = b_6 = b > 0$, and that $b_1 = b_2 = b_3 = 0$ to reflect the current evidence of no in-site recruitment in the upper pools. The elasticities resulting from these assumptions can be interpreted as the proportional change in the metapopulation growth rate given a small proportional change in the parameter ϕ_{kh} .

Similarly, the sensitivity of the metapopulation growth rate to changes in per capita recruitment rates in

Alton (Pool 6), La Grange (Pool 5), and Peoria (Pool 4) were calculated as follows:

$$s_{b_h} = \left. \frac{\partial \lambda_1}{\partial b_h} \right|_{\theta^*}, \quad (8)$$

where the repeated subscript on b was replaced by the single index for $h = \{4, 5, 6\}$.

Sensitivity of invasion front (Dresden Island Pool) growth rate

The per capita contribution of each pool to the population of Dresden Island (Pool 1) are represented in the vector $\mathbf{a}_1 = a_{11}, \dots, a_{16}$ of the matrix \mathbf{A}' . The sensitivity of the per capita contribution in individuals of each pool to the growth rate of Dresden Island (Pool 1) to changes in the movement probabilities was calculated as follows:

$$s_{a_{1h}}^{\phi} = \left. \frac{\partial a_{1h}}{\partial \phi_{kh}} \right|_{\theta^*}. \quad (9)$$

The elasticities were calculated as $s_{a_{1h}} \phi^* / a_{1h}^*$, where the asterisk indicates the quantities were calculated for the median values of the observed movement rates.

The sensitivity of the per capita contribution of each pool to the growth rate in Dresden Island (Pool 1), to changes in the recruitment rates in Alton (Pool 6), La Grange (Pool 5), and Peoria (Pool 4) were calculated as follows:

$$s_{a_{1h}}^{b_j} = \left. \frac{\partial a_{1h}}{\partial b_j} \right|_{\theta^*}, \quad (10)$$

where j indicates the pool where recruitment occurred and h indicates the pool through which the effects are conveyed. For example, $s_{a_{16}}^{b_4}$ represents the sensitivity of the per capita effect of Alton (Pool 6) on Dresden Island (Pool 1) given a change in recruitment in Peoria (Pool 4). The elasticities were calculated as described above.

RESULTS

Sensitivity of metapopulation growth rate

Overall, the metapopulation growth rate is not sensitive to small increases in the movement rates out of the upper pools (Figure 2, top row). It is most sensitive to movement from Dresden Island to the three lower pools

(Alton, ϕ_{61} ; La Grange; ϕ_{51} ; and Peoria, ϕ_{41}), which result in an increase in metapopulation growth rate. The metapopulation growth rate is very sensitive to movement from the lower pools (Alton, La Grange, and Peoria) to the upper pools (Starved Rock, Marseilles, and Dresden Island) (Figure 2, bottom row). The largest impacts result from movement out of La Grange (Pool 5) and to a much lesser extent Alton (Pool 6), each of which has a large negative effect on the metapopulation growth rate. The elasticity of those rates is very small compared with the sensitivities because the observed movement

probabilities from lower to upper pools are currently small.

The sensitivity of the metapopulation growth rate to changes in per capita recruitment rates in Alton (Pool 6), La Grange (Pool 5), and Peoria (Pool 4) is shown in Figure 3. As was found with the movement rates, the metapopulation growth rate is very sensitive to the dynamics of La Grange Pool (b_5). The metapopulation growth rate is about seven times more sensitive to changes in the recruitment rate in La Grange (Pool 5) than in Alton (Pool 6) and about 34 times more sensitive

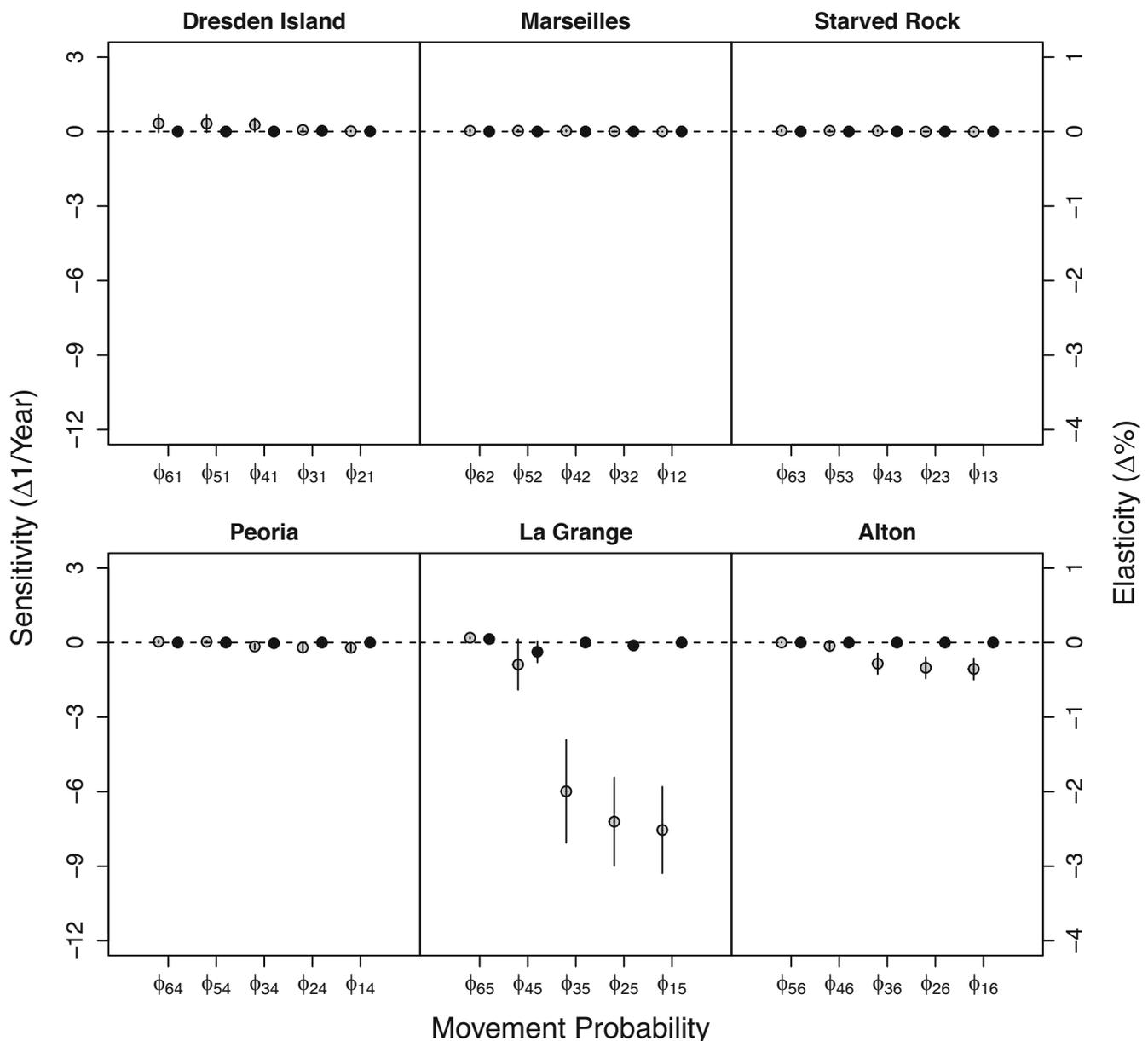


FIGURE 2 Sensitivity (gray points) and elasticity (black points) of metapopulation growth rate movement probabilities. Panels gather effects of the origin of migrants and the axis labels present the parameter identity. Error bars show resampling based on 95% confidence intervals.

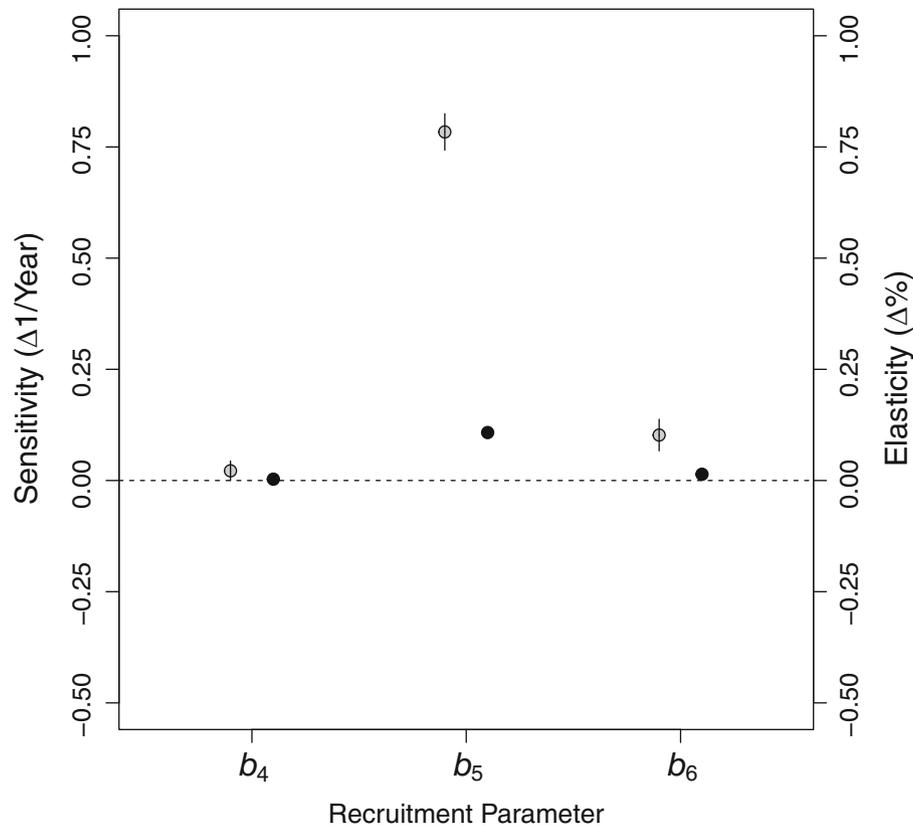


FIGURE 3 Sensitivity (gray points) and elasticity (black points) of metapopulation growth rate to per capita recruitment rate in the lower three pools: Alton (b_6), La Grange (b_5), and Peoria (b_4). Error bars show resampling based on 95% confidence intervals.

than to changes to recruitment in Peoria (Pool 4). The pattern of the elasticities follows that for the sensitivities.

Sensitivity of invasion front (Dresden Island Pool) growth rate

The per capita population contribution of each pool to the population in Dresden Island (Pool 1) is represented in the vector $\mathbf{a}_1 = a_{11}, \dots, a_{16}$ of the matrix \mathbf{A}' . The sensitivity of the per capita contributions of each pool to the growth rate of Dresden Island (Pool 1) to changes in the movement probabilities is shown in Figure 4.

As would be expected, the growth rate of the Dresden Island (Pool 1) population is most sensitive to movement out of Dresden Island. Small changes in the movement rates from Dresden Island to every other pool have a negative effect on its per capita growth rate (Figure 4, panels $\phi_{61}, \phi_{51}, \phi_{41}, \phi_{31}$, and ϕ_{21}). These changes are realized via reduction in the per capita contributions of each of the three upper pools (a_{11}, a_{12} , and a_{13}). With respect to positive changes, the per capita growth rate of Dresden Island population is sensitive movement out of La Grange (Figure 4, panels ϕ_{35}, ϕ_{25} , and ϕ_{15}). These changes are realized via increases in the per capita

contributions of each of the three lower pools (a_{16}, a_{15} , and a_{14}). The elasticities of the parameters with the largest magnitude (positive and negative) sensitivities are variable, but very close to zero, indicating that currently the observed values of those movement rates are near zero.

The pattern of elasticities is different than that of the sensitivities. The largest elasticities are associated with changes in movement from Starved Rock to Dresden Island (ϕ_{31}), Peoria to Starved Rock (ϕ_{34}), and La Grange to Peoria (ϕ_{45}). Each of these is realized via increase in the per capita contribution of each of the lower pools (a_{16}, a_{15} , and a_{14}) (Figure 4).

The sensitivity and elasticity of the per capita growth rate of the Dresden Island population to changes in the recruitment rates in Alton (b_6), La Grange (b_5), and Peoria (b_4) are shown in Figure 5. The sensitivities are all near zero except for the effect of b_4 , as conveyed via the per capita contribution of Peoria on Dresden Island (a_{14}) (Figure 5, panel b_4). The elasticities of the growth rate are largest for changes in recruitment in Peoria (b_4) and La Grange (b_5). The effects of the change in the recruitment rate in Peoria (b_4) are conveyed via the per capita contributions of each of the lower three pools (a_{16}, a_{15} , and a_{14}) (Figure 5, panel b_4). The effects of the change in the

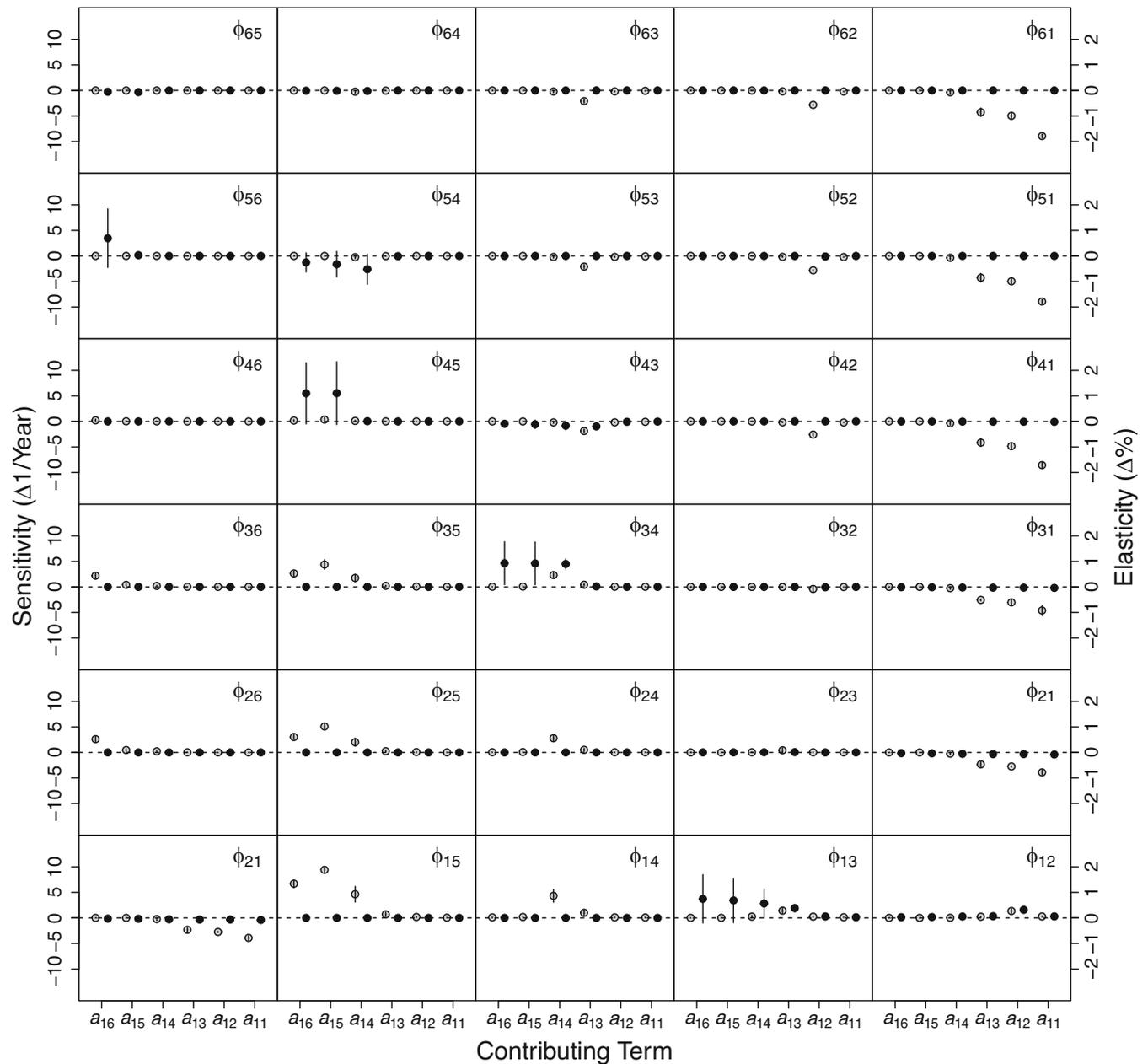


FIGURE 4 Sensitivity (gray points) and elasticity (black points) of movement probabilities (ϕ_{kh}) on the per capita contributions of each pool to the local population growth rate of Bighead Carp in Dresden Island Pool (a_{1h}). For example, the panel labeled ϕ_{61} presents the change in each per capita contribution (a_{1h}), given a small increase in the probability of movement from Dresden Island (Pool 1) to Alton (Pool 6). Error bars show resampling based on 95% confidence intervals.

recruitment rate of La Grange (b_5) are conveyed via the per capita contributions of each of La Grange and Alton (a_{16} and a_{15}) (Figure 5, panel b_5).

Rank order of each pool’s per capita contribution to invasion front (Dresden Island Pool) growth rate

The per capita effect of each pool on the population growth rate in Dresden Island (Pool 1) can be interpreted directly

as an estimate of the per individual efficiency of culling on the future population in Dresden Island (Pool 1). Assuming equal culling efficiency in each pool, those pools with the highest per capita effects represent the highest priority targets of management. We calculated the per capita contributions of each pool to the growth rate of Dresden Island (Pool 1) over a gradient of recruitment rates. Given the observed movement rates and assuming $b_6 = b_5 = b_4 = b$, at low recruitment rates, the highest per capita effects are from upper pools, Dresden Island (Pool 1), Marseilles (Pool 2), and Starved Rock (Pool 3), respectively

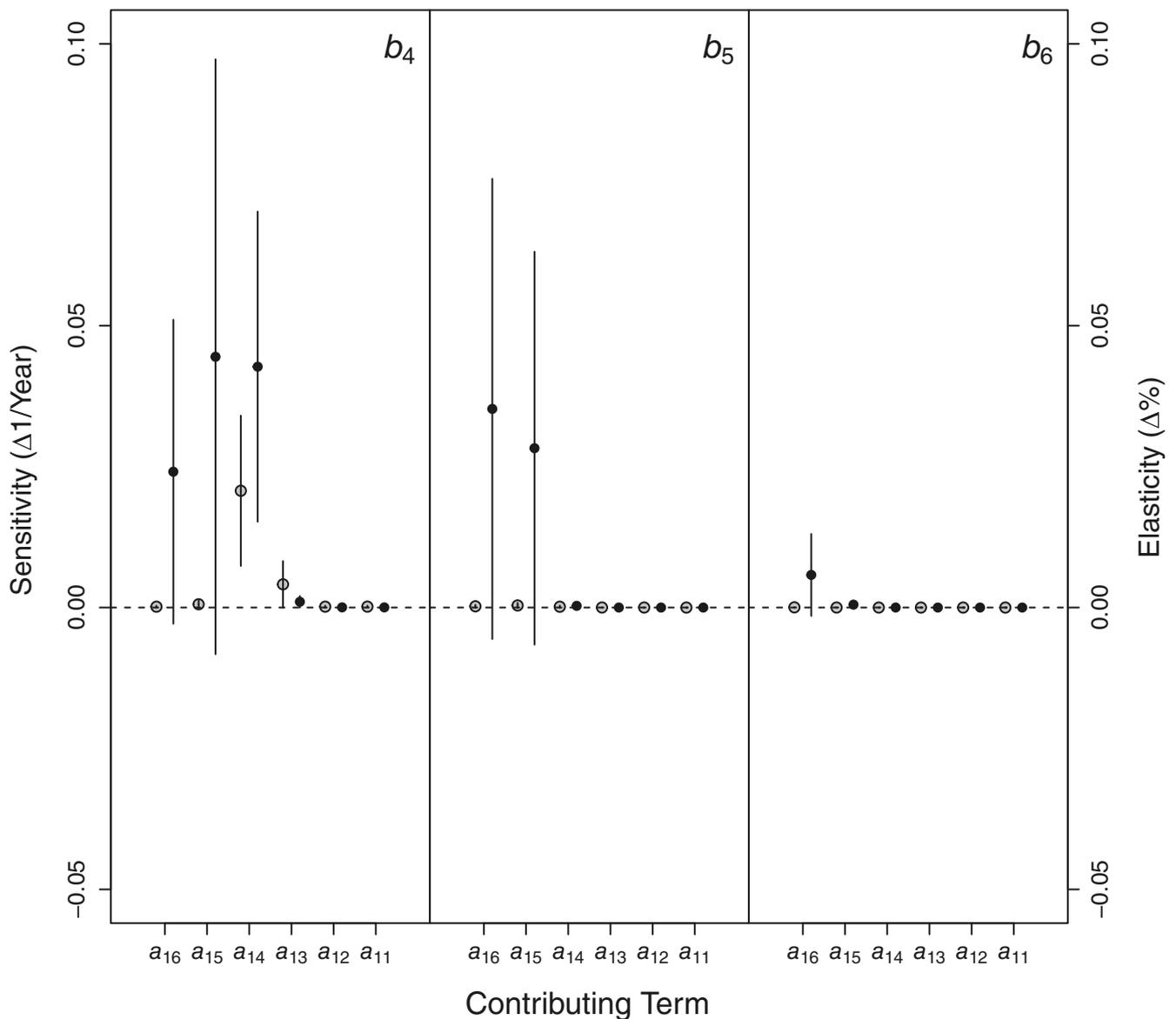


FIGURE 5 Sensitivity (gray points) and elasticity (black points) of recruitment rates (b_i) on the per capita contributions of each pool to the local population growth rate of Bighead Carp in Dresden Island Pool (a_{1h}). For example, the panel labeled b_4 presents the change in each per capita contribution a_{1h} , given a small increase in the recruitment rate in Peoria (Pool 4). Error bars show resampling based on 95% confidence intervals.

(Figure 6). However, the per capita effects of Starved Rock (Pool 3) and especially Peoria (Pool 4) increase quickly with increasing recruitment rate relative to the others, resulting changes in rank order near $b \approx 40$, with the per capita effect of Peoria (Pool 4) becoming the largest at $b \gtrsim 45$, although the uncertainty is large (Figure 6).

DISCUSSION

Managers dealing with invasive species are often faced with limited resources (e.g., person hours or funds)

and incomplete information. Models that can provide targeted insight in the face of the gaps in system information to guide management planning and efficient allocation resources can be valuable. Here, we have combined a very simple spatial model with robust observational data on species movement to provide insight on the cross-pool contributions to the per capita growth rates at the invasion front and to the metapopulation as a whole. The model was able to produce these insights even without specific information on the population levels in the pools or within pool recruitment rates. We used multiple strategies to

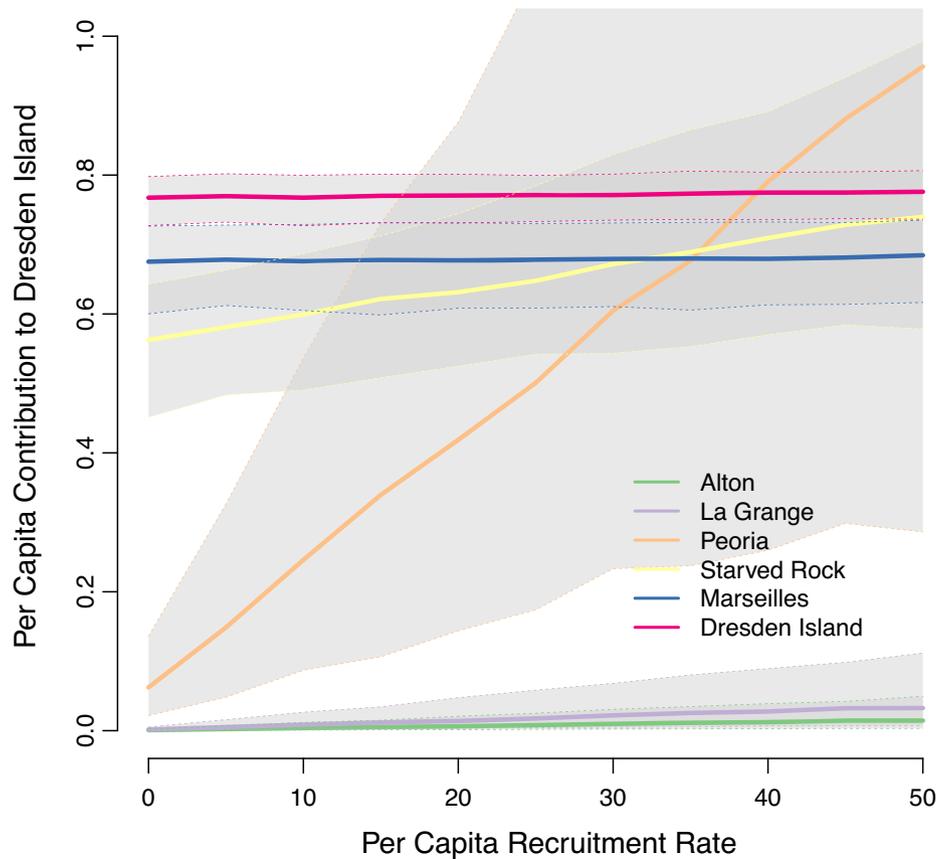


FIGURE 6 Per capita contributions of each pool on the population growth rate of Bighead Carp in Dresden Island Pool as a function of increasing recruitment rate. Solid lines are the median per capita effects calculated from 1000 samples of the posterior distribution of movement rates at each value of b . Uncertainty envelopes are bounded by the 0.025 and 0.975 quantiles of the resampling distributions. Due to overlapping uncertainty envelopes, colored dashed lines indicating the boundaries of the uncertainty envelope for line of corresponding color were included. Note that due to mixing among pools, a change in the recruitment rate of one pool will affect the per capita contribution of each of the other pools to the growth rate of the Dresden Island population.

account for the gaps in data: (1) the need for population estimates was mitigated by recognition of the direct conceptual link between per capita growth rates and the important management metric of harvesting efficacy; (2) to account for the unknown recruitment rates, estimates were generated over a range of values and resampled to provide a measure on uncertainty; and (3) finally, we used sensitivity analysis to parameterize the sensitivity and uncertainty of model predictions to the assumed parameter values.

In the Illinois River, the current goal is to prevent the spread of invasive carp to the Great Lakes from the Dresden Island Pool (Asian Carp Regional Coordinating Committee, 2010). Our results quantify and demonstrate the importance of matching harvest location to management goals. Specifically, near population equilibrium, the modeled system was most sensitive to movement from lower pools to the invasion front, and movements away from the pool representing the invasion front. As the population is moved farther from equilibrium by

increasing recruitment rates, removing individuals from the lower pools had an increasing impact compared with harvesting from the upriver pools. This result might be used to inform annual adjustments of the existing management strategy, depending on annual variation in recruitment. Portions of the downstream populations also were identified as an important driver of metapopulation dynamics in this system (Coulter, Brey, et al., 2018). The sensitivity and elasticity analyses support these conclusions across a wide range of parameter values, making this conclusion robust to uncertainty in model input parameters. It may seem most logical for managers to take control action at the invasion front when the goal is to reduce movement from this area, and indeed that strategy is supported for some parameter values. However, our results show that optimal management strategies depend on the time horizon of the management goals, and how the spatial arrangement and heterogeneity of the system drive or constrain demographic rates and movement patterns.

Local versus metapopulation management

This modeling effort has revealed that two important management goals, limiting the growth of the whole population and limiting the population growth rate at the invasion front, may require very different management actions. The difference between these two very different goals is the difference between short-term and long-term strategies. For short-term results, control/removal of individuals near the invasion front can be effective for reducing individuals and potential spread. However, managers might advocate for a long-term strategy of control to reduce source populations, limiting overall population growth and subsequent dispersal. Estimates of per capita effect on a target subpopulation represent the effect on the population in the next year, whereas the metapopulation growth rate estimates the long-term population growth rate in the whole river. We found that actions most effective at reducing the growth rate at the invasion front are not necessarily the same as those that reduce the growth rate of the metapopulation as a whole. This suggests that identifying optimal strategies will vary with the time frame of the analysis and will likely include dividing limited management resources among short-term and long-term goals. However, observed differences in long-term and short-term strategies from our analyses are not a general result but one that emerges from the analysis of this specific system, spatial context, and parameters. These nonintuitive results emphasize the valuable insights gained from using simple models in a system-specific context. Such applications can be useful to directly inform management, and to identify data gaps and inform more complicated, system-specific models.

Sink and source as a parameter-dependent spectrum

To date, theoretical treatments of developing strategies for efficient control of populations composed of spatially extended, heterogeneous subpopulations, such as those cited above, have found that, with caveats, concentrating control efforts on source populations is often most efficacious. However, those models focused on life histories in which the timescales of movement among patches, recruitment, culling, and censusing were equal. As a result, identifying source and sink patches was relatively straightforward. In the Illinois Waterway, these processes occur at different timescales, resulting in a much more sophisticated understanding of the net effects of one patch on another and on the metapopulation. For example, the largest proportional changes in the per capita contribution of the Lower Illinois River on Dresden Island Pool were associated with changes in the movement probability from Peoria Pool to Starved Rock Pool (ϕ_{34}).

This finding emphasized the importance of the specific control structures between Peoria Pool and Starved Rock Pool and would not have come out of an analysis that attempted to simply classify pools as sources or sinks.

From per capita to per effort

We focused on per capita contributions as an important metric to inform management efficacy. While this is likely the case, it assumes that the per capita catchability, defined as the probability of capture per individual per unit effort, is similar among pools. Combining results from this paper with information about variation in catchability among pools could make these results directly actionable by management agencies because it would provide an estimate of culling impact on the target subpopulation per unit effort. While we believe this is an important future direction to take this research, it is a substantial undertaking. Management methods often include multiple culling methods, the efficiency of which may vary by season as well as by pool. While some of these data exist for this system, there is not yet enough coverage of all pools for all common removal methods.

Caveats and extensions

While this analysis allows insight about the sensitivity of movement probabilities and the uncertainty associated with their contribution to vital rates, the current model is very simple. It does not, for example, incorporate individual variation that may influence reproductive potential (e.g., condition: Wootton, 1998; size: Lenaerts et al., 2021) and movements (Hoover et al., 2016; Radinger & Wolter, 2013). The current model does not incorporate nonlinearities in the demographic rates such as density-dependent recruitment and movement patterns. However, the relative simplicity of only looking at spatial dynamics assuming linear fish demographics benefits by creating a simpler to understand model that is less data-demanding and more readily allows comparisons and analysis not yet possible with more complex models. Thus, this analysis provides a baseline to which more complex models can be compared. For example, invasive carp exhibit demographic variability across their invasive range (Erickson et al., 2021; Lenaerts et al., 2021). Ongoing efforts are underway to combine population models (e.g., Tsehaye et al., 2013) with movement data (e.g., Coulter, Brey, et al., 2018) in a size-dependent spatially explicit invasive carp (SEICarP) model (Asian Carp Regional Coordinating Committee, 2018; Cupp et al., 2021). Comparisons of the outputs of models such as this to the current simpler linear

model could allow assessment of the importance of size on harvest and movement on management strategies.

Another important extension of this work lies in the direction of dealing with multispecies management. In the Illinois River, in addition to Bighead Carp, Silver Carp is also an invasive species of concern (Coulter, Brey, et al., 2018). Applying these analyses to data from Silver Carp is likely to be very informative. Comparing analogous sensitivities of the two populations has the potential to identify both synergistic and opposing management targets. For example, if a particular movement rate has a large negative sensitivity for one species but a positive one for the other, it suggests that management targeting this parameter would likely reduce the growth of one species but increase the other. Parameters that are highly sensitive in the same direction for each species would suggest that it is an especially efficient management target for limiting both species with a single effort.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data (Coulter et al., 2022) are available from South Dakota State University Open PRAIRIE: https://openprairie.sdstate.edu/nrm_datasets/3. The specific subset of these data and the code used to analyze it (Schoolmaster & Schoolmaster, 2022) are available from Zenodo: <https://doi.org/10.5281/zenodo.7032744>.

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