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Modelling bioenergetic and population-level impacts of invasive bigheaded carps (*Hypophthalmichthys* spp.) on native paddlefish (*Polyodon spathula*) in backwaters of the lower Mississippi River

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Abstract

1. While invasions of large rivers by exotic fish species are well documented, assessing actual or potential impacts on native species is a challenge. Rapid assessments may be possible through the application of a combination of bioenergetic and population dynamic models.
2. Paddlefish (*Polyodon spathula*) is a native species in the central USA with a history of population decline due to waterway development and overharvesting for roe. It is not known whether paddlefish are impacted by resource competition from invasive bigheaded carp populations, including silver (*Hypophthalmichthys molitrix*) and bighead carp (*Hypophthalmichthys nobilis*), which have expanded dramatically in the Mississippi River.
3. We used bioenergetic models to project the potential impact of invasive silver and bighead carp on zooplankton density and paddlefish somatic growth in backwater habitat. Bioenergetic outputs were translated to impacts on fecundity, becoming inputs for 50-year metapopulation simulations of backwater habitat connected to the main-stem Mississippi River by episodic flood events.
4. Competition with carp reduced growth and increased the risk of population decline for paddlefish. Impacts increased disproportionately with increased carp abundance and were further exacerbated in scenarios with increased diet overlap or decreased zooplankton abundance.
5. We also analysed paddlefish condition data collected at sites near the lower Mississippi River with varying histories of carp invasion. These data give credence to the bioenergetic model output; paddlefish had reduced body condition at sites with long-established, high-density carp populations.
6. We conclude that invasive bigheaded carps have great potential to reduce paddlefish growth, fecundity, and abundance. The pairing of bioenergetics and population models is likely to be broadly useful in assessing the risks posed by other invasive species.

KEYWORDS
Asian carp, bioenergetic model, invasive species, paddlefish, population viability analysis

1 | INTRODUCTION

As the number and frequency of invasions by exotic species increases, so does concern over their ecological impacts (Lodge et al., 2006; Nico & Fuller, 1999). Aquatic systems are common foci of invasions; non-native fish species threaten the stability and longevity of populations and ecosystems around the globe (Britton et al., 2007; Goren & Galil, 2005; Holeck et al., 2004). While invasive species have been placed only second to habitat degradation in their impact on imperilled native species (Wilcove, Rothstein, Dubow, Phillips, & Losos, 1998) and fish in particular (Miller, Williams, & Williams, 1989), empirical evidence clearly implicating invasive species in such impacts is relatively rare (Barney, Tekiela, Dollete, & Tomasek, 2013; Diederik, Assaf, & François, 2011; Gurevitch & Padilla, 2004). Even when data are available, interpretation can be obscured by the correlation between habitat degradation and species invasion (Light & Marchetti, 2007).

The challenge in assessing the potential impacts of invasive species is to accurately model complex dynamical interactions among the members of a community in response to the invasive species (Kamenova et al., 2017). Meeting this challenge requires mechanistic models. A variety of approaches combining physiological and population models has been successful in mechanistically generating expected responses to factors such as climate (Buckley, 2008; Crozier & Dwyer, 2006), population density (Friedenberg, Powell, & Ayres, 2007), and trophic interactions (Megrey et al., 2007). We demonstrate the value of such an approach for invasion ecology, coupling bioenergetic and population models to assess the potential for competitive effects of exotic fish on a native freshwater species of concern.

Bigheaded carps are a complex of invasive species that have become a nuisance to boaters and fishery managers in channels and tributaries of the Mississippi, Missouri, and Ohio Rivers. Bigheaded carps are thought to have escaped from aquaculture in the Mississippi River in the 1970s, but populations in the Mississippi River did not begin to increase substantially until after 1992 (Chick & Pegg, 2001). These planktivorous fish have exhibited rapid somatic growth, explosive population growth, and dramatic expansion of their non-native range; they appear to have the potential to impact native species through resource competition (Chick & Pegg, 2001; Irons, Sass, McClelland, & Stafford, 2007; Pegg, Chick, & Pracheil, 2009; Sampson, Chick, & Pegg, 2009).

One native species that may be threatened by bigheaded carps in the Mississippi River basin is the paddlefish (Acipenseriformes: Polyodontidae: *Polyodon spathula*; Pegg et al., 2009; Sampson et al., 2009; Schrank, Guy, & Fairchild, 2003). Among the most ancient species of freshwater fish, and related to sturgeon (Acipenseridae: *Acipenser* spp., *Scaphirhynchus* spp.), paddlefish populations were previously impacted by commercial harvest for their meat and valuable roe and by recreational trophy fishing motivated by large body size and unique morphology (Jennings & Zigler, 2009). Declines in abundance, first observed in the early 20th century, eventually prompted consideration for federal listing in the 1980s. Status review in 1992, prior to the establishment of large carp populations, concluded there was insufficient information for a Threatened classification and the species was considered Special Concern, a category no longer in use. More recently, paddlefish have been assessed as Vulnerable by the IUCN (IUCN, 2004) and the American Fisheries Society. Continued monitoring programmes have reported stable or increasing stocks in 17 of the 26 states in the paddlefish range, possibly in response to new management and regulatory practices that limit harvest (Bettoli, Kerns, & Scholten, 2009). Given the tenuous trajectory of paddlefish, the species serves as a model organism for examining potential negative impacts of bigheaded carps.

Among the possible factors impinging upon paddlefish population viability is the loss of backwater habitat in highly engineered navigable rivers (Graham, 1997). Bordering the main stem of the Mississippi River, where paddlefish feed and reproduce, are numerous backwater habitats that serve as nurseries for juveniles and feeding grounds for a portion of the adult paddlefish population. Being mostly lentic, these backwater habitats have high plankton productivity. Adult paddlefish in backwaters have historically been targeted by fishers for their substantially larger size (Stockard, 1907) and greater population density (Hussakof, 1911), suggesting a disproportionate contribution to total population recruitment. Episodic flooding of the main stem plays the important role of allowing intermittent exchanges of individuals between the two habitat types. However, floods have also facilitated invasion of backwaters by bigheaded carps (Pongruktham, Ochs, & Hoover, 2010; Varble, Hoover, George, Murphy, & Killgore, 2007). Between floods, backwater habitats are an isolated habitat where local competition both within and between species could affect juvenile survival and adult fecundity.

To better understand the potential for harm to paddlefish populations presented by exotic carp in backwaters of the lower Mississippi River, we quantified the strength and effect of resource competition using bioenergetic models. Three models, one for paddlefish and one for each of two invasive bigheaded carp species, bighead (*Hypophthalmichthys nobilis*) and silver carp (*Hypophthalmichthys molitrix*), were used to simulate somatic growth and prey consumption during the isolated periods between floods. Bioenergetic models have been used to model many aspects of fish ecology (Hartman & Kitchell, 2008), including environmental effects on growth and fecundity of large riverine species (Bevelhimer, 2002), bigheaded carp range expansion (Cooke & Hill, 2010), and age-structured species interactions (Tuomikoski, Rudershausen, Buckel, & Hightower, 2008). We coupled bioenergetic and demographic models to assess the potential for bigheaded carps to impact paddlefish population viability in the lower Mississippi River. We qualitatively validated model predictions through comparison with measurements of paddlefish at sites in Mississippi and Louisiana that differed in their history of bigheaded carp invasion.

Our study demonstrates the utility of combining bioenergetic and population modelling for assessing potential competition between native and exotic species. The bioenergetic approach provides a mechanistic method to integrate field and laboratory research and has been described previously as the *transfer function* between putative stressors and population impacts (Costa, 2012). The framework we present can be implemented with data from proxy species as needed for rapidly screening the risks posed by new invasions.

2 | METHODS

2.1 | Overview

We conducted a bioenergetic simulation to estimate the impact of competition for zooplankton prey between paddlefish and two invasive bigheaded carp species in Forest Home Chute (FHC), a backwater of the lower Mississippi River on the border between Louisiana and Mississippi. The bioenergetic simulations were coupled with a model of population dynamics by translating growth of adult paddlefish into fecundity. The population dynamic model projected the long-term impact of invasive carp on the viability of the paddlefish metapopulation occupying the backwater and adjacent main-stem river habitats and captured the effect of episodic flooding, which connects the two habitats after a period of isolation. The population model was stochastic and thereby captured probabilistic uncertainty about dynamics over time. Non-probabilistic uncertainty about the native-exotic interaction was captured through scenarios exploring prey density, carp abundance, and the degree of diet overlap between carp and paddlefish.

2.2 | Bioenergetic model

Bioenergetic simulations included six stage- and species-specific modules for juvenile and adult paddlefish, bighead carp, and silver carp. We used the framework of the Wisconsin model (Hanson, Johnson, Schindler, & Kitchell, 1997), accounting for metabolic requirements, prey consumption, and assimilation to project mass gained or lost in each module. The framework equates consumption and energy expenditures as a stoichiometric relationship:

$$\text{Consumption} = \text{Metabolism} + \text{Waste} + \text{Growth}, \qquad (1)$$

where metabolism is the cost of respiration, activity, and digestion; waste includes egestion and excretion (urine and faeces); and growth includes both somatic and gonadal growth. All rates are mass-specific with units of (g g^{-1} day^{-1}). We equated energy and mass using estimates of the energy density (kJ/g) of food, waste, and somatic and gonadal tissue. Although knowledge of the bioenergetics of bigheaded carps notably needs improvement (Cooke, 2016), sufficient information was available in the literature. Equations and parameter estimates used to compute each element of Equation 1 are in Table 1 for bigheaded carps and in Table 2 for paddlefish.

2.2.1 | Paddlefish bioenergetics

We defined juvenile paddlefish as females capable of filter feeding but incapable of reproducing (Rosen & Hales, 1981) and adults as females capable of reproducing. We excluded young of the year from the growth model because they have not yet developed gill rakers, feed mostly on aquatic insects rather than zooplankton (Rosen & Hales, 1981), and often have little diet overlap with silver and bighead carp (Hintz, MacVey, Asher, Porreca, & Garvey, 2017; Zhu, Li, & Yang, 2014). Males were not modelled, implying that male growth does not affect population dynamics (Morris & Doak, 2002).

We accounted for bioenergetic consequences of paddlefish behaviour by estimating the routine metabolic rate, or the energy used while swimming normally, using a temperature- and mass-specific parameterisation of paddlefish metabolism from Patterson, Mims, and Wright (2013). Waste as a proportion of consumption was based on white sturgeon (Bevelhimer, 2002). We calculated paddlefish growth to balance Equation 1. Hence, if expected energy gains through consumption exceeded metabolic requirements, individuals gained mass. If consumption was insufficient due to low zooplankton availability, individuals lost mass. We estimated growth of juveniles and adults using published age–length and length–mass relationships for paddlefish in Lake Pontchartrain, Louisiana (Figure 1a; Reed, Kelso, & Rutherford, 1992). Annual growth in mass was then converted to a daily rate. We assumed that all juvenile growth is somatic growth and all adult growth is gonadal. Conversion of energy budgets to growth assumed the energy density of paddlefish is equivalent to that of white sturgeon (*Acipenser transmontanus*), 4.39 kJ/g for somatic tissue and 9.20 kJ/g for gonadal tissue (Bevelhimer, 2002).

Paddlefish consumption was based on prey density and the average volume of water filtered each day. Zooplankton densities vary by several orders of magnitude across samples from the main stem and backwaters of the Mississippi River (Burdis & Hoxmeier, 2011). We therefore modified prey density with an aggregation parameter that doubled the effective density of prey, implying that paddlefish selectively feed in prey aggregations. We estimated filtration rate by modelling gape size as an ellipse and multiplying ellipse area by daily distance swum (Smith, Condrey, & Reed, 2009). We estimated juvenile gape size from adult and young of the year gape size data (Smith, 2004). Filtration rate was assumed to remain constant across varying temperatures and particle sizes. The daily distance swum was estimated using active (ram suspension feeding) and basal (equal parts ram ventilation and prey processing) swim speeds (Sanderson, Cech, & Cheer, 1994) converted to body length equivalents, then converted back to stage-specific average

TABLE 1 Components of the bioenergetic modules used in simulations: silver and bighead carp

Component	Equation	Parameters and references	Silver carp	Bighead carp
Consumption (g/g day^{-1})	$C = \text{CA} \times M^{CB} \times p \times V^{x} e^{X(1-V)}$	CA = intercept for maximum consumption CB = mass dependence coefficient (Wang et al., 1989)	CA = 0.369 CB = −0.225	CA = 0.369 CB = −0.225
	$V = (\text{CTM} - T) / (\text{CTM} - \text{CTO})$	CTM = maximum lethal temperature CTO = optimum temperature (Kolar et al., 2007)	CTM = 43 CTO = 29	CTM = 38 CTO = 26
	$X = Z^{2}\left[1 + (1 + 40Y)^{0.5}\right]^{2} / 400$	CQ = temperature dependence coefficient (tilapia, Hanson et al., 1997)	CQ = 2.5	CQ = 2.5
	$Z = (\text{CTM} - \text{CTO})\, ln\, (\text{CQ})$			
	$Y = 1/\left[Z + 2ln\,(CQ)\right]$			
Metabolism respiration (g/g day^{-1})	$R = \text{RA} \times M^{\text{RB}} e^{\text{RQ} \times T}$	RA = intercept of mass dependence function RB = mass dependence coefficient RQ = Q10 for low temperatures (Cooke & Hill, 2010; Hogue & Pegg, 2009)	RA = 0.00279 RB = −0.239 RQ = 0.076	RA = 0.00528 RB = −0.299 RQ = 0.048
Waste fecal waste (g/g day^{-1})	$\boldsymbol{F} = \text{FA} \times \boldsymbol{T}^{\text{FB}} \boldsymbol{e}^{\text{FG} \times \boldsymbol{p}} \boldsymbol{C}$	FA = intercept of the proportion of consumed energy egested and excreted FB = coefficient of temperature dependence FG = coefficient for ration dependence (Elliott, 1976)	FA = 0.212 FB = −0.222 FG = 0.631	FA = 0.212 FB = −0.222 FG = 0.631
Urinary waste (g/g day^{-1})	$\boldsymbol{U} = \text{UA} \times \boldsymbol{T}^{\text{UB}} \boldsymbol{e}^{\text{UG} \times \boldsymbol{p}} (\boldsymbol{C} - \boldsymbol{F})$	UA = intercept of the proportion of consumed energy egested and excreted UB = coefficient of temperature dependence UG = coefficient for ration dependence (Elliott, 1976)	UA = 0.031 UB = 0.58 UG = −0.299	UA = 0.031 UB = 0.58 UG = −0.299
Specific dynamic action	SDA	SDA = proportion of total consumption lost (Hanson et al., 1997)	0.1	0.1
Filtration rate (L/day)	$\text{FR} = \text{FRA} \times \boldsymbol{M}^{\text{FRB}} \times 24$	FRA = intercept for maximum filtration rate FRB = mass dependence coefficient (Smith, 1989)	FRA = 1.54 FRB = 0.713	FRA = 1.54 FRB = 0.713

Note: M is the mass of the fish (in g), T is temperature (in °C), which varies according to the day of the simulation in a sine function, and p is the theoretical proportion of maximum consumption.

TABLE 2 Components of the bioenergetic modules used in simulations: paddlefish

Component	Equation	Parameters and references	Paddlefish juvenile, adult
Metabolism			
Respiration (kJ/day)	$R = 0.001[\text{RA} \times T^{\text{RT}} M/1000)^{\text{RM}} \times 24 \times 13.59$	RA = respiration intercept RT = temperature dependent coefficient RM = mass-dependent coefficient (Patterson et al., 2013)	RA = 7.66 RT = 0.979 RM = 0.918
Waste			
Faecal waste (kJ/day)	$F = \theta_F C$	θ_F = faecal waste as a proportion of consumption (Bevelhimer, 2002)	θ_F = 0.15
Urinary waste (kJ/day)	$U = \theta_U C$	θ_U = urinary waste as a proportion of consumption (Bevelhimer, 2002)	θ_U = 0.05
Specific dynamic action	SDA	*SDA* = proportion of total consumption lost (Bevelhimer, 2002)	0.12
Filtration rate (L/day)	$\text{FR} = 0.25\pi \times \text{MSS} \times \text{MTB} \times 1000 \times 3600 \times 12\left[V_{\text{RSF}} + 0.5\left(V_{\text{RV}} + V_{\text{PP}}\right)\right]$	MSS = mouth width (m) MTB = mouth height (m) (Smith, 2004) V_{RSF} = ram suspension feeding velocity V_{RV} = ram ventilation velocity V_{PP} = prey processing velocity (Sanderson et al., 1994) converted to relative swim speed (m/s) using mean body lengths from Reed et al. (1992).	MSS = 0.093, 0.119 MTB = 0.099, 0.127 V_{RSF} = 1.001, 1.477 V_{RV} = 0.616, 0.908 V_{PP} = 0.650, 0.959

Note: M is the mass of the fish (in g), T is temperature (in °C), which varies according to the day of the simulation in a sine function, p is the proportion of maximum consumption, C is the specific consumption rate (kJ/day).

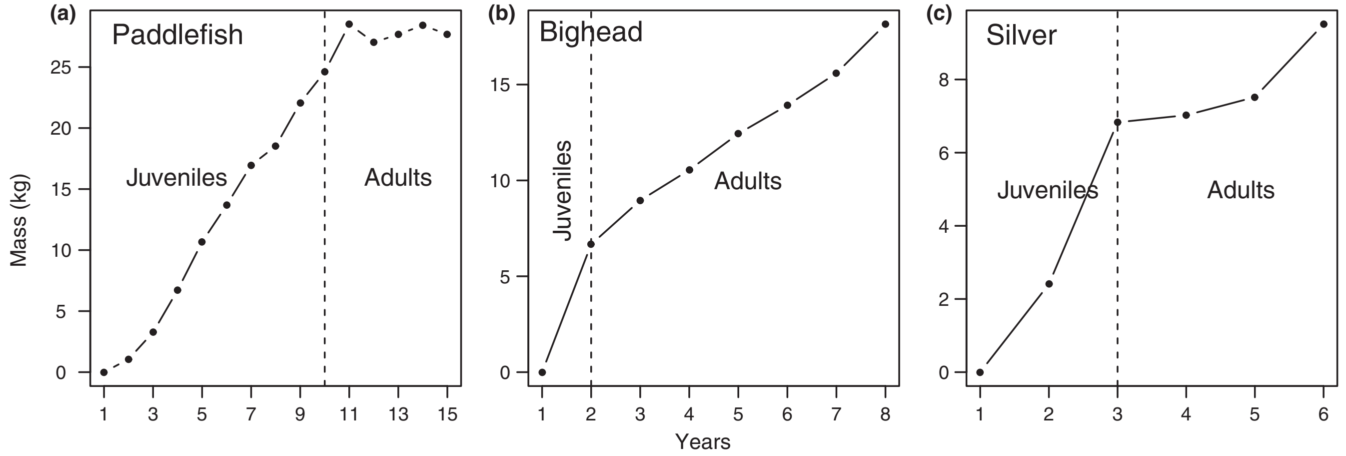

FIGURE 1 Modelled annual growth of (a) paddlefish, (b) bighead carp, and (c) silver carp. Life stages (juvenile and adult) were assigned by binning ages with similar growth rates. Length data for paddlefish from Reed et al. (1992) and for silver and bighead carp from J.J.H. (unpublished)

speeds using the weighted mean lengths of juvenile and adult paddlefish in Lake Pontchartrain, Louisiana (Reed et al., 1992). We assumed individuals spent, on average, 12 hr of every day in active foraging behaviour, interspersed with 12 hr of resting behaviour, with no diel pattern in feeding (Kuhajda, 2014; Rosen & Hales, 1981).

2.2.2 | Carp bioenergetics

Temperature- and mass-dependent consumption for bighead and silver carp were estimated using an allometric mass function developed for silver carp (Hanson et al., 1997; Kolar et al., 2007; Wang, Flickinger, Be, Liu, & Xu, 1989). Waste estimates for the two carp species were borrowed from brown trout (Elliott, 1976). We assumed that specific dynamic action (the cost of metabolising food) was 10% of total consumption (Hanson et al., 1997).

Daily growth for the two carp species was a linear constant calculated from annual condition data for carp measured in FHC (Figure 1b,c). Life stage mass thresholds were estimated from annual growth, where juvenile carp are defined by exhibiting rapid somatic growth and adults by slower somatic growth (Figure 1).

We assumed that carp filtration rates were static across varying prey densities and particle sizes and that filtration rate was mass-specific (Anderson, Chapman, Wynne, Masagounder, & Paukert, 2015; Smith, 1989). Carp are known to eat a combination of zooplankton and phytoplankton. In backwaters of the Illinois River, carp consume primarily rotifers and paddlefish consume larger-bodied zooplankton (Sampson et al., 2009). Plankton samples from FHC have indicated high rotifer density and a near absence of larger crustacean zooplankton species (Ochs, Pongruktham, Killgore, & Hoover, 2019). However, carp consumed most of the available zooplankton in a food web in the Illinois River, which could outweigh any trophic partitioning (Freedman, Butler, & Wahl, 2012). Uncertainty in the degree of diet overlap in backwaters of the Mississippi River was addressed by varying the degree of diet overlap, *z*, defined as the proportion of carp diet comprising zooplankton that could otherwise be utilised by paddlefish.

2.3 | Bioenergetic simulations

Bioenergetic simulations involving the six integrated modules were run for 3 years (1,095 days) to estimate the impact of bigheaded carps on the potential fecundity of paddlefish in FHC. Bioenergetic simulations, implemented in R version 3.5.2 (R Core Team, 2018), simulated interspecific competition by assuming carp pre-empt paddlefish resources from the total resource pool. The total resource pool (mg) was the product of the volume of FHC and prey density. We estimated FHC volume to be about 2 million m^3 based on measurements of satellite imagery of the waterway (14 km length × 50 m width × 3 m average depth). Per capita consumption rates estimated in the species- and stage-specific bioenergetic modules were applied to abundance to obtain total consumption. After decrementing the resource pool for carp consumption, the remaining biomass was converted back into prey density (mg/L) to serve as an input for paddlefish bioenergetics. Energy (kJ/day) available for each life stage was calculated from the product of prey density, prey energy density, and stage-specific filtration rate (L/day). A deficit of energy for metabolic maintenance translated to a loss of mass; a surplus yielded growth. Mass outputs for each daily time step became the inputs for the following day. Maturation took place when juveniles of any species surpassed the mass threshold of their stage. Upon maturation, juvenile abundance was transferred to the adult class. The functional response of fecundity to mass determined adult potential fecundity. Paddlefish and carp abundance declined with an annual mortality rate of 20 and 60%, respectively (Donabauer, Stoeckel, & Quinn, 2009; Williamson, 2004).

Temperature, which affects the calculation of consumption, metabolism, and waste (Hanson et al., 1997), was modelled through the year as a sine function with a midpoint of 21.75°C and an amplitude of ±7.55°C, encompassing previously reported medians and ranges in FHC (Ochs et al., 2019; Pongruktham et al., 2010; Varble et al., 2007).

We assumed that there was no diel or seasonal mitigation of competition between carps and paddlefish beyond the effects of temperature on bioenergetic rates. Paddlefish are negatively buoyant, obligate ram ventilators, and constantly moving (Kuhajda, 2014; Mims & Shelton, 2015) and therefore cannot exhibit torpor, although they can modify their swimming behavior and speed based on environmental conditions (Hoover et al., 2019). In the lower Mississippi River basin, they swim actively and feed intensively throughout the year (Cage, 2015; George, Hoover, Killgore, & Lancaster, 1995) and thus are in constant competition with sympatric bigheaded carps for food.

Bioenergetic simulations addressed scenarios of prey density, carp abundance, and diet overlap between carp and paddlefish. We considered two prey density scenarios, high with mean of 0.4 mg/L and low with a mean of 0.3 mg/L, to capture the spectrum of prey densities observed at various locations within the Mississippi watershed (Burdis & Hoxmeier, 2011; Moore & Cotner, 1998). At both high and low mean prey density, seasonal variation around the mean was modelled as a sine function with an amplitude of ±0.2 mg/L. These values for prey density are realistic based on the mean mass of common rotifer species in the system (Theilacker & Kimball, 1984) and zooplankton samples from FHC (Ochs et al., 2019).

We considered three competition scenarios, including a control with no carp to isolate paddlefish intraspecific competition, as well as medium and high carp abundance. The maximum count of silver carp in FHC during electrofishing surveys was around 200 individuals; bighead carp populations were roughly one third as common (Jan Jeffrey Hoover, unpublished). For the medium and high carp abundance scenarios, we inflated these counts assuming a detection rate of 30 and 10%, respectively. Based on catch data from oxbow lakes in Alabama, we assumed adult abundance was 75% that of juveniles for both carp species (Hoxmeier & Devries, 1997). Table 3 summarises the initial abundance of all three species in each competition scenario.

We explored diet overlap ranging from none (z = 0) to nearly perfect competition (z = 0.9). These scenarios addressed uncertainty about the proportion of carp diet that is zooplankton in backwaters of the Mississippi River.

Paddlefish fecundity was estimated for each of the 3 years of the bioenergetics simulation using a body mass and fecundity relationship for paddlefish developed by Lein and DeVries (1998),

$$F = 31656.6 \times M - 205121, \qquad (2)$$

where F is fecundity and M is mass (kg). Fecundity was calculated from the bioenergetic projection of mass at the end of each year (at day 365, 730, and 1,095). Relative fecundity, used to modify the population dynamic model, was obtained by comparing projected fecundity estimates to fecundity at initial mass.

TABLE 3 Initial abundances of juvenile and adult silver carp, bighead carp, and paddlefish used in different competition scenarios in bioenergetic simulations, estimated from electrofishing data in Forest Home Chute

Species/Stage	No carp	Medium carp abundance	High carp abundance
Silver carp juveniles	0	893	2,679
Silver carp adults	0	670	2,010
Bighead carp juveniles	0	266	798
Bighead carp adults	0	200	600
Paddlefish juveniles	198	198	198
Paddlefish adults	148	148	148

2.4 | Population simulations

We used estimates of relative fecundity from the bioenergetic simulations to modify the adult fecundity parameter in a stochastic, stage-based population model implemented in RAMAS Metapop 6.0 (Akçakaya & Root, 2013). The population model thereby translated the mechanistic impact of resource competition into changes in projected paddlefish population size. We simulated the population trajectory of paddlefish for a 50-year period in main stem and backwater paddlefish populations, the former with standard paddlefish vital rates and the latter with no spawning (Table 4).

The population model included an annual probability of flooding, set at 60% based on gage data and the controlling elevation of FHC (J.J.H., unpublished). Flood events triggered a complete migration of paddlefish from the backwater to the main stem and enough reciprocal migration to return the backwater populations to their carrying capacities, mimicking dispersal during flood pulses evidenced by radio tagging data for bighead and silver carp by DeGrandchamp, Garvey, and Colombo (2008). Floods occurred at random with constant annual probability, creating an exponential distribution in the length of the period of isolation between floods with a mean of 1.7 years.

TABLE 4 Parameters used in population dynamic simulations for both paddlefish subpopulations (main stem and backwater) in all scenarios

Parameter	Main stem	Backwater
Juvenile survival	0.3	0.3
Juvenile to adult transition rate	0.3	0.3
Adult fecundity	0.5	0.00001
Adult survival	0.8	0.8
Juvenile initial abundance	542	115
Adult initial abundance	758	231

Differences in fecundity of backwater adults relating to their isolation or dispersal to the main stem were generated by varying carp population density, diet overlap, and prey density. Under each scenario, the corresponding bioenergetic model projected mean juvenile and adult mass for 1, 2, and 3 years of isolation from the main stem. Adult mass at the end of each year determined mean relative fecundity (Table S1). If isolation continued beyond 3 years, the third-year backwater fecundity in the sequence repeated. Flood events reset the sequence to its initial value, reflecting an influx of individuals from the main stem, where we assumed paddlefish growth was not affected by carp.

The baseline population model represented conditions in FHC before carp invasion: high mean prey density and no carp competition. (For ease of reference, we refer to 50% diet overlap as baseline, as well.) The baseline scenario produced continued growth of adults entering from the main-stem habitat, reflecting historical observations of high condition in backwaters (Stockard, 1907). The paddlefish population was also assumed to be stable in the absence of commercial and recreational fishing. To obtain a stable baseline population, we adjusted adult fecundity in the main-stem habitat iteratively until the total average population trajectory increased by <5% over 50 years. We then used this fecundity as the baseline in all other scenarios. Survival and fecundity varied annually, drawn from a lognormal distribution with a coefficient of variation of 10%.

We extrapolated initial paddlefish abundance in backwater habitat from a density estimate of 4.94 fish/ha, derived from Quinn (2009), and the area of FHC (*c.* 70 ha). Initial abundance in the main-stem habitat was based on the same paddlefish density and an area equivalent to a corresponding stretch of the lower Mississippi River, using a 3.7:1 ratio of main stem to backwater area (Baker, Killgore, & Kasul, 1991). The initial age distributions in each habitat were adjusted using *burn-in* runs under baseline conditions to obtain abundances that remained static over 50 years. After the burn-in runs, the population comprised 542 juveniles and 758 adults in the main stem, and 115 juveniles and 231 adults in the backwater. All scenarios used these initial abundances.

2.5 | Paddlefish length and weight

Paddlefish were caught, measured, and weighed from five locations in or adjacent to the Lower Mississippi River Basin. Fish were typically collected using brief sets (<2 hr) of monofilament gillnets and occasionally by other techniques. Fish size was measured on a curved Plexiglas fish board to the nearest mm as eye-to-fork length: the linear distance from the anterior orbit to the shortest caudal rays. Weight was measured to the nearest 0.05 kg using an Open Country model DS-150SK top-loaded digital scale (Two Rivers, WI, USA).

Two locations, Moon Lake, in Arkansas and Mississippi, an oxbow lake remote from the main channel Mississippi River (34.410850 N, −90.548812 W), and the Pearl River, Louisiana, at Lock and Dam #1 (30.45633 N, −89.77902 W), were sampled in 2013–2014 (*n* = 46) and 2010 (*n* = 37) respectively. Fish from the Pearl River (a coastal river adjacent to the Mississippi basin) were collected by hand following an anoxia-caused fish kill. Both locations had low bigheaded carp density (carp numbers and biomass ≪ paddlefish numbers and biomass) and only a recent history (<5 years) of invasion.

Three locations, the Bonnet Carré Floodway, below the diversion structure at Norco LA (30.00411 N, −90.43355 W), Lake George MS, a backwater of the Yazoo River (32.734536 N, −90.616632 W), and FHC MS (32.463134 N, −91.042884 W), a backwater of the lower Mississippi River, were sampled in 2011 (*n* = 15), 2013 (*n* = 15), and 2016 (*n* = 24) respectively. Some fish from the Bonnet Carré were collected by electrofishing. All three locations had high carp abundance (carp numbers and biomass ≫ paddlefish numbers and biomass) and a history of invasion exceeding 10 years.

We analysed mass (g) as a function of body length (eye–fork length, in mm). Both measurements were log-transformed for analysis comparing linear length–weight regressions between high- and low-density carp environments, with sampling location as a random effect within carp density group. Models were fit in R using the package *lme4* (Bates, Mächler, Bolker, & Walker, 2015) and mixed-effects ANCOVA hypothesis tests were performed using the package *afex*, (Singmann, Bolker, Westfall, & Aust, 2018); all hypothesis tests used Type III sums of squares, and degrees of freedom were calculated using the Kenward–Roger approximation.

3 | RESULTS

Our bioenergetic and population simulations indicated that bigheaded carps could substantially reduce both the somatic growth and population trajectory of both juvenile and adult paddlefish. Competition with bigheaded carps impacted paddlefish growth in all scenarios, although the contribution of carp to paddlefish population risk increased substantially when carp were at high abundance.

3.1 | Bioenergetic simulations

The magnitude of the impact of carp on paddlefish growth was sensitive to the degree of overlap in carp and paddlefish diet and the density of prey available (Figure 2). The baseline (no resource limitation) daily metabolic activity of paddlefish, bighead carp, and silver carp at juvenile and adult stages is summarised in Table 5. If we assumed that carp are predominantly zooplanktivorous (corresponding to a diet overlap near 1.0), paddlefish mass after 3 years declined by approximately 28–79% depending on the abundance of carp and prey level (Figure 2). The absolute response of final paddlefish mass to carp competition was similar at low (Figure 2a) and high (Figure 2b) prey levels. Under medium carp abundance, paddlefish growth declined linearly with diet overlap, although the impact was relatively

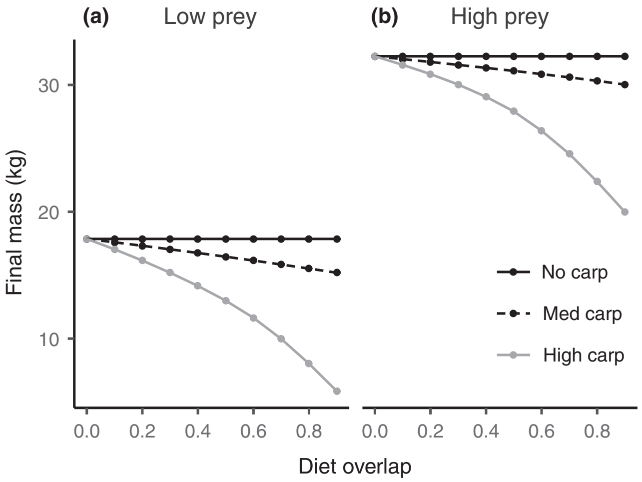

FIGURE 2 Projected paddlefish mass after 3 years given the proportion of zooplankton in the carp diet (referred to as diet overlap). Series represent bioenergetic outcomes under a low prey regime (a), and a high prey regime (b) at each of three levels of competition with carp: none (solid black line), medium (dashed black line), and high (solid grey line)

small. Under high carp abundance, the impact of competition was more pronounced and increased disproportionately with increasing diet overlap (Figure 2).

The bioenergetic consequences of intra- and interspecific competition in our model were mediated through the impact of consumption on prey density (Figure 3). In isolation, the impact of paddlefish on zooplankton density peaked at about a 0.1 mg/L reduction in the first summer of backwater isolation, with smaller impacts during winter and transitional seasons (Figure 3a). With the assumption of a 50% diet overlap between bigheaded carps and paddlefish ($z = 0.5$), paddlefish had a greater gross impact on their prey base than did carp in the medium competition scenario (Figure 3b). However, in the high competition scenario, the gross impacts of bigheaded carps on prey density were greater than that of paddlefish (Figure 3c). In all cases, attrition of the fish populations via a constant natural mortality rate (under the assumption of no recruitment in backwaters) led to slight increases in prey density over time, as evidenced by the increase in the height of the summer prey density peaks visible in Figure 3.

With low prey density, paddlefish experienced a net loss of mass over 3 years in all scenarios (Figure 4a–c). In all cases, this loss manifested as a sudden decline in mass in the first year followed by a more gradual trend. With no carp or medium carp abundance, the second and third years showed continued paddlefish mass loss punctuated with seasonal trends of moderate growth (Figure 4a,b). With high carp abundance, paddlefish exhibited net growth after the first-year loss (Figure 4c,f). While the amount of mass lost in the first

TABLE 5 Bioenergetic outputs (kJ/day) by species and life stage assuming no resource limitation

Species (age, weight)	Metabolism (kJ/day)	Growth (kJ/day)	Waste (kJ/day)	Total consumption (kJ/day)
Silver carp				
(<3 years, 0.3 kg)	420.94	48.65	282.44	752.04
(≥3 years, 0.85 kg)	382.56	17.71	256.24	656.51
Bighead carp				
(<2 years, 3.3 kg)	309.18	63.91	434.55	807.65
(≥2 years, 13.3 kg)	264.16	17.14	365.16	646.46
Paddlefish				
(2–10 years, 13.1 kg)	581.86	36.20	290.85	908.91
(≥10 years, 27.9 kg)	1,000.33	103.69	503.93	1574.77

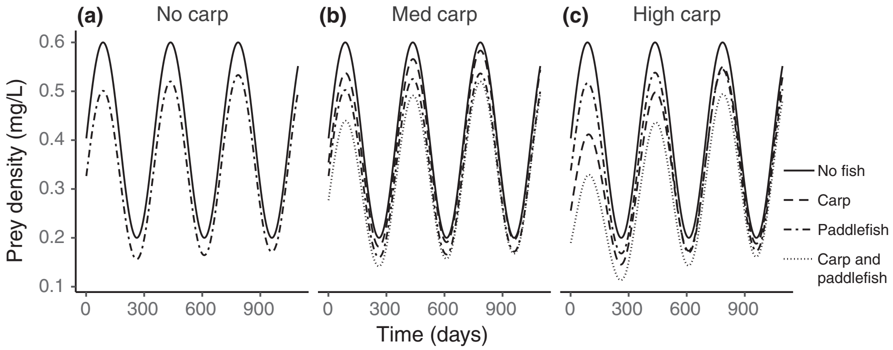

FIGURE 3 Projected impact of paddlefish and carp on resource availability (zooplankton density in mg/L) at high prey density over a 3-year period. Resource availability modelled at three levels of competition: (a) none, (b) medium, and (c) high. Depletion of prey at levels prior to consumption (solid curve), after silver and bighead consumption (dashed curve), after paddlefish consumption (dash–dotted curve), and the sum of all fish consumption (dotted curve)

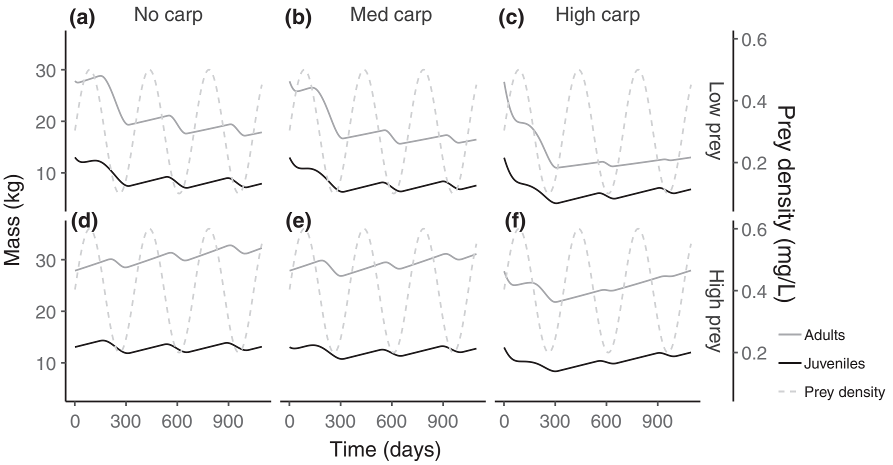

FIGURE 4 Projected effects of carp competition on adult (grey) and juvenile (black) paddlefish mass over a 3 year period at two different prey density ranges, 0.1–0.5 mg/L (a–c) and 0.2–0.6 mg/L (d–f). Bioenergetic simulations were run under three competition scenarios: no carp (a, d), medium carp abundance (b, e), and high carp abundance (c, f)

year was sensitive to the presence of carp, the subsequent rate of growth was not. In all cases, the growth of adult and juvenile paddlefish was proportionally equivalent.

With high prey density, paddlefish exhibited net gains in mass over 3 years in all scenarios (Figure 4d,e,f). However, high carp abundance caused a loss of mass in the first year. For adults, this loss was not recovered until the third year of the bioenergetic simulation (Figure 4f).

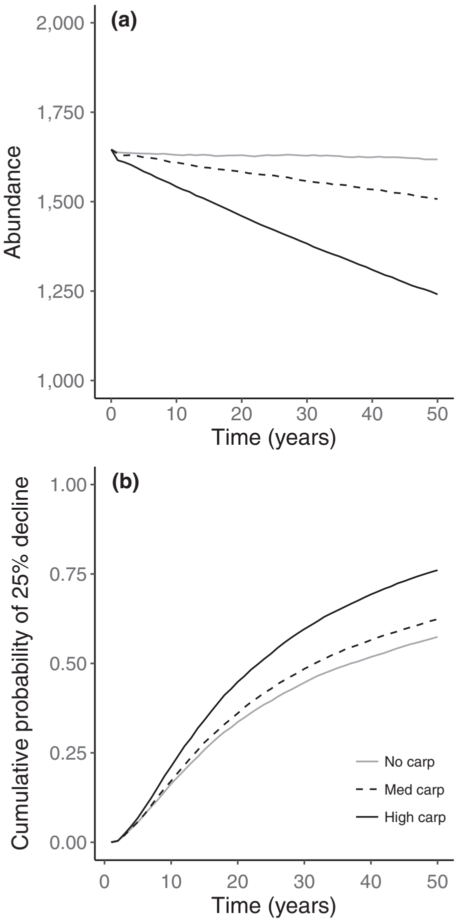

FIGURE 5 The impact of Asian carp on paddlefish population dynamics. Panels depict (a) paddlefish population trajectories (female juveniles and adults), and (b) the risk of a 25% decline in abundance over 50 years for scenarios of varying carp abundance

3.2 | Population simulations

Under the assumptions of mass-specific fecundity and no reproduction in backwater habitat, the impacts of intra- and interspecific competition on paddlefish growth translated to reduced recruitment and increased risk of population decline. Under low prey density scenarios, fecundity was greatly reduced even when there were no carp, with relative fecundities of 0.62, 0.55, and 0.53 over the 3-year period. Meanwhile, the baseline high prey density scenario yielded increased size and therefore fecundity relative to main-stem residents, with relative fecundity reaching 1.06, 1.13, and 1.21 over 3 years of isolation, consistent with historical observations of large backwater individuals (Stockard, 1907). Even with high prey availability, competition with carp had the potential to impact paddlefish fecundity. For instance, with high prey, high carp, and 50% diet overlap, relative fecundity was 0.74, 0.86, and 1.00 over 3 years.

Population model scenarios indicated potential impacts of bigheaded carps on the paddlefish population's expected size and its risk of decline (Figure 5a). Starting from an initial abundance of 1,646 juvenile and adult paddlefish, mean paddlefish abundance in competition with bigheaded carps at medium abundance, 50% diet overlap, and high prey density decreased over the 50-year projection to 1,507 (*SD* = 658). When bigheaded carps were at high abundance, mean paddlefish abundance decreased to 1,241 (*SD* = 541; Figure 5a). As for mass, bigheaded carps had a sizeable negative effect only at high abundance. Regardless of carp abundance, low prey density led to severe decreases in paddlefish abundance over 50 years (Figure S1a–c). Diet overlap did exacerbate the population decline of paddlefish, though only under high prey density (Figure S1d–f).

Mean trajectories fail to communicate small-probability risks to the population. We therefore compared the probability of a 25% decline over the 50-year simulation (Figure 5b). While abundance in the absence of carp was projected to, on average, increase under the high prey scenario (Figure 5a), environmental variability and demographic stochasticity generated a probability of 0.57 that the population would decline by at least 25%. The median time to a 25% decline in this baseline scenario was 37 years. The introduction of carp at medium abundance and medium diet overlap slightly increased the probability of decline to 0.62 and shortened the median time to decline by 5 years. Carp at high abundance and medium diet overlap led to a more pronounced increase in the risk of decline, to a probability of 0.76, and shortened the median time to decline by 14 years. Hence, the marginal impact of carp was a 5–19% increase from baseline levels of decline risk. Under low prey density scenarios, the risk of a 25% decline was extremely high even in the absence of carp, 0.92 after 50 years (Figure S2a–c). Thus, competition with invasive carp had a lower marginal impact on paddlefish population viability already stressed by low prey availability in the backwater. Increasing diet overlap increased decline risk in all scenarios with carp, although its effect was only large when the density of both carp and prey were high (Figure S2d–f).

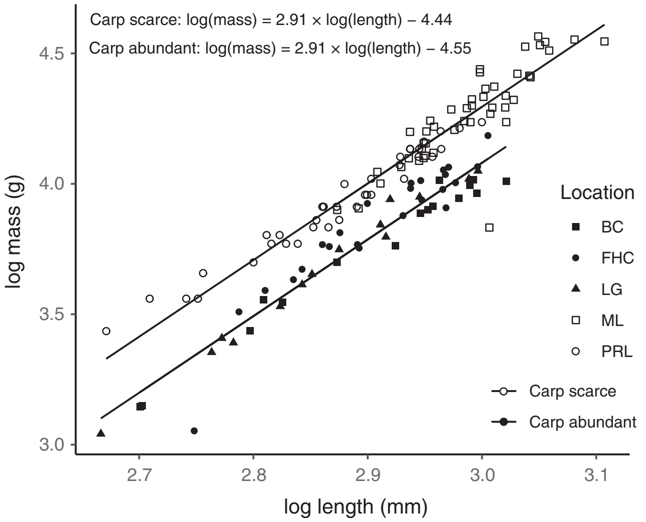

FIGURE 6 Paddlefish weight as a function of length (measured as eye-to-fork length) measured in five sites in the Lower Mississippi River between 2011 and 2016. Asian carp were scarce in two sites, Moon Lake (ML) and Pearl River (PRL), and were abundant in the other three sites, Bonnet Carré Floodway (BC), Lake George (LG), and Forest Home Chute (FHC). Both continuous variables were log scaled. Regression lines were fit as an ANCOVA of the difference between sites with abundant and scarce carp, controlling for the effect of length

3.3 | Paddlefish length and weight

Measurements of paddlefish length and weight at five sites in southern Mississippi indicated that a high density of carp or long history of invasion impact paddlefish growth. A linear mixed model regression of log mass as a function of log length and carp density (low-carp or high-carp) with site as a random effect indicated there was no significant difference in the log-log-linear slope of mass with length and we therefore removed the interaction term from the model. The simplified comparison of growth suggested paddlefish from the three sites with abundant bigheaded carps had reduced weight at length compared with those from the two sites where carp were scarce ($F_{1,\ 123.51}$ = 1,106, $p \ll 0.001$, Figure 6). Converted back from log space into the form of a power function, mass = $a \times \text{length}^{b}$, the exponent, b, was 2.91, a small deviation from the expected value of 3 if paddlefish were simple cubes. The intercept, a, decreased from 3.62×10^{-5} at low-carp locations to 2.18×10^{-5} at locations with high carp density, indicating high carp density was associated with a 40% decrease in paddlefish mass at length ($F_{1,\ 2.72}$ = 57.62, p = 0.007).

4 | DISCUSSION

Our bioenergetic simulations demonstrated that invasive bigheaded carps have the potential to reduce the growth of both adult and juvenile paddlefish in the backwaters of the lower Mississippi River. Negative impacts on paddlefish abundance were much greater when bigheaded carps were highly abundant; a medium abundance of bigheaded carps in the backwater led to only modest impacts. Field observations strongly supported the predicted potential for reduced paddlefish condition because of resource competition with bigheaded carps. Paddlefish at study sites with a large and long-established carp population had lower mass at length than those in water bodies where carp were still rare. This finding is particularly notable because one of the high-carp locations, FHC, was a backwater. Rather than being robust like the backwater specimens reported by Stockard (1907), individuals collected at FHC had condition similar to paddlefish found in the main-stem river. Our study adds to a growing body of research strongly suggesting impacts of bigheaded carps on native species (Irons et al., 2007; Sampson et al., 2009; Schrank et al., 2003).

Careful studies documenting causality between invasive species and loss or decline of native populations are of great importance to basic and applied questions in ecology. A growing number of examples illustrate population-level impacts of invasives. Introduced fishes directly reduced populations' native desert fish species in Southern Nevada (Deacon, Hubbs, & Zahuranec, 1964) and were implicated in the extinctions of 27 out of 40 North American fishes (Miller et al., 1989). Well-documented terrestrial examples include the impacts of brown tree snakes (*Boiga irregularis*) in Guam (Wiles, Bart, Beck, & Aguon, 2003), Burmese pythons (*Python molurus bivittatus*) in the Florida Everglades (Dove, Snow, Rochford, & Mazzotti, 2011), and cane toads (*Bufo marinus*) throughout Australia (Doody et al., 2009; Shine, 2010).

While the potential for invasions to have population-level impacts on native species is supported both theoretically and empirically, this potential should not be taken for granted. Direct evidence of population-level impacts on native species is often lacking

(Gurevitch & Padilla, 2004). In many cases, such as the apparent dominance of introduced Mozambique tilapia (*Tilapia mossambica*) over native fishes (Eldredge, 2000), concern is based primarily on anecdotes rather than empirical studies or modelling exercises to assess its likelihood.

Bioenergetic modelling of interspecific competition provides a widely useful means of mechanistically exploring the potential for invasive species to impact native populations. Correlational approaches to assessing impacts from survey data, as with our field study, can suffer from confounding factors. While such issues may be circumvented through careful consideration (e.g. Light & Marchetti, 2007), modelling specific effects mechanistically facilitates the use of independent field and laboratory data that can bolster the interpretation of correlational studies. Bioenergetic models suffer from having a large number of parameters. However, where parameter estimates are unavailable for a focal species, information from proxy species can be used, a practice which allows assessment even for poorly studied populations. It may be useful to separate sources of uncertainty into intraspecific and interspecific factors, as the former are likely to comprise the imprecision of existing knowledge while the latter are more likely to represent a lack of knowledge (Ferson, 1996).

Intraspecific factors in our study included paddlefish metabolic rate, age at maturity, and fecundity. While the paddlefish metabolic rates used in our model were based on the measurement of individuals moving in still water (Patterson et al., 2013), which is consistent with the largely lentic nature of backwater habitat, a recent study of paddlefish metabolism in moving water found lower metabolic rates and a negative relationship between the rate of flow and the cost of movement (Cage, 2015). Similarly, the age of maturity used in our model was based on Louisiana populations in which all females matured by age 10 years (Reed et al., 1992); ages at maturity have been documented as young as 6–7 and as old as 14 years in some populations outside the lower Mississippi Basin (Mims & Shelton, 2015). Survival probably also differs across locations and through time. For instance, fishing pressure varies temporally and some populations have only been recently exploited commercially for caviar (e.g. Lucas, 2014). Greater metabolic efficiency or earlier maturation for paddlefish would reduce the impacts of competition with bigheaded carps in backwaters by lowering intraspecific competition for resources. Non-intuitively, a reduction in paddlefish survival would also reduce the marginal effect of carp by decreasing paddlefish abundance and therefore intraspecific competition between floods.

Uncertainty about factors affecting the potential strength of interspecific competition in our study, including carp population density, prey density, and diet overlap, was captured though the use of non-probabilistic scenarios. Notably, even a small overlap in diet in our model led to a decrease in paddlefish mass. The amount of diet overlap between paddlefish and bigheaded carps is difficult to resolve. Sampson et al. (2009) found relatively little overlap while Schrank et al. (2003) found a greater potential for competition. Stable isotope analysis found bigheaded carps had less trophic overlap with paddlefish than with native facultative planktivorous fishes (Freedman et al., 2012). However, FHC is nearly bereft of larger-bodied zooplankton (Ochs et al., 2019), suggesting that carp and paddlefish must directly compete for rotifers. Silver carp have been found to consume more phytoplankton than bighead carp in their native range (Yao, Huang, Xie, & Xu, 2016), potentially reducing direct competition for resources but exerting indirect pressure on paddlefish via the survival and growth of silver carp at low zooplankton densities. Geographic and seasonal variation in the zooplankton assemblage is also likely to lead to variation in the strength of competition between the species.

Invasive species may alter the benefit of potential paddlefish conservation actions. For instance, we found that competition with carp increases intraspecific paddlefish competition. As a result, protection from fishing may have less benefit in invaded backwaters. Another example is flooding, which provides the opportunity for backwater paddlefish to disperse to the main stem and spawn and is an important source of resources for the backwater ecosystem. Artificially increasing flood frequency through barrier removal would have both costs and benefits in the absence of carp, as is generally true for fish in intermittent habitats (Fullerton et al., 2010). The period of isolation provides ideal conditions for growth, as suggested by the relatively high condition of adult paddlefish (Stockard, 1907). Coho salmon utilising intermittently connected tributaries also showed higher smolt size and survival (Ebersole et al., 2006). The presence of carp in the main stem changes the calculus of managing flood frequency. The bioenergetic model projected that the impact of carp on paddlefish growth generally decreases with the time between flooding, largely because the carp have a higher attrition rate. Increased flood frequency would maintain a higher average density of bigheaded carps in the backwater, increasing their impact on paddlefish growth.

It is important to note that interspecific dynamics occur in a community setting and are poorly understood even under controlled conditions (Wilbur, 1972). In the interest of parsimony, we limited our investigation to direct competition between bigheaded carps and paddlefish. In mesocosm experiments, silver carp had strong indirect effects on both the zooplankton assemblage and phytoplankton levels (Domaizon & Devaux, 1999). Thus, it is possible that carp could have more complex effects on the backwater environment that would modify the impacts we estimated.

Although imprecise, the assessments of impact in this study are probably conservative. Bioenergetic models are conservative tools when applied to the assessment of possible interspecific impacts. Chipps and Wahl (2008) found that 82% of bioenergetic models overestimated consumption. The authors attributed this error to several sources including consumption-dependent error, seasonal variation in metabolic rate, abiotic factors such as dissolved oxygen and salinity, and impacts of prey composition and abundance on fish activity rates. Such errors are likely when modelling bigheaded carps, which have highly plastic behaviours and diets (Cooke, 2016). Additionally, the ratio of main stem to backwater habitat we used (Baker et al., 1991) could be an underestimate. A higher ratio would diminish the influence of backwater dynamics on the paddlefish population as a whole. At a more general level, our results are probably conservative because they omit any effects of bigheaded carps in the main stem and any possible upward trend in carp abundance over time.

Our omission of climate change from our modelling framework is an additional conservative factor. While paddlefish and bigheaded carps are eurythermal, occupying water temperatures of 4–30°C (Crance, 1987; Jennings, 1988; Leuven et al., 2011), paddlefish spawn at cooler temperatures (Crance, 1987; Deters, Chapman, & McElroy, 2013; Jennings, 1988). Streams and rivers are warming in the USA by up to 0.077°C per year (Kaushal et al., 2010). If the Mississippi River warms at that rate, a decline of paddlefish spawning relative to that of bigheaded carps can be expected well within the 50-year horizon of our projections, aggravating the impact of the introduced species.

Our study provides a starting point in the study of impacts of invasive bigheaded carps on the growth and population trajectory of native paddlefish in the backwaters of the Mississippi River. Our results substantiate the broader concern that bigheaded carps impact the condition and abundance of native fishes through resource competition. Although our modelling highlights the need for a better understanding of the effects of both carp and paddlefish on their resource base and of the characteristics of that resource base in backwater habitats, its concurrence with empirical patterns of paddlefish body condition also demonstrates the utility of even a simplified mechanistic modelling framework for substantiating the plausibility of native population responses to introduced species.

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CONFLICT OF INTEREST

The authors of this paper have no conflicts of interest to disclose.

DATA AVAILABILITY STATEMENT

No shared data from this study are available. The condition data used in this paper are available from the corresponding author upon reasonable request.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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