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A food web modeling assessment of Asian Carp impacts in the Middle and Upper Mississippi River, USA

Nicholas W. Kramer [a,*], Quinton E. Phelps [b,1], Clay L. Pierce [c], Michael E. Colvin [d]

[a] Southeast Missouri State University, Department of Biology, 1 University Plaza, Cape Girardeau, MO 63701, United States of America
[b] Missouri Department of Conservation, Big Rivers and Wetlands Field Station, 3815 E. Jackson Blvd, Jackson, MO 63755, United States of America
[c] U.S. Geological Survey, Iowa Cooperative Fish and Wildlife Research Unit, Iowa State University, 339 Science II, Ames, IA 50011, United States of America
[d] Mississippi State University, Department of Wildlife, Fisheries and Aquaculture, Mississippi State, MS 39762, United States of America

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ABSTRACT

The invasion of non-native fishes has caused a great detriment to many of our native fishes. Since the introduction of invasive carps, such as Silver, Bighead, Common and Grass Carp, managers and researcher have been struggling to remove these species while also hypothesizing the detriment of further invasion. This study developed a food web model of four locations on the Mississippi River and used those models to assess the impacts of two scenarios: carp removal and carp invasion. In the Middle Mississippi River where these invasive carps are already present, the models found that it would take a sustained exploitation of up to 30% of initial biomass over an extended period to remove Grass Carp and up to 90% removal of initial biomass to remove Silver and Bighead Carp. In the locations where Silver, Bighead, and Grass Carp are not yet established (i.e., Pools 4,8, and 13) the invasion of these species could cause declines from 10 to 30% in initial biomass of native fishes as well as already established nonnative invasive species.

1. Introduction

Throughout history, numerous introductions of non-native aquatic organisms have occurred (Fuller et al., 1999; Rahel, 2000; Sultana and Hashim, 2016). These can be intentional or unintentional, beneficial or harmful. Copp et al. (2005), in their tally of non-native fish by country, report that 92 of 185 non-native fish in the United States have been intentionally introduced outside of their native range. Four detrimental non-native freshwater fish introductions of the Mississippi River, Common Carp, Grass Carp, Silver Carp, and Bighead Carp, have all been introduced intentionally (DeKay, 1842; Guillory and Gasaway, 1978; Henderson, 1976). Many studies have addressed the negative effects of carps (Forester and Lawrence, 1978; Miller and Crowl, 2006; Irons et al., 2007; Dibble and Kovalenko, 2009; Sampson et al., 2009; Kloskowski, 2011). As a result, focus in the literature has included methods of carp eradication and the effort required (Ricker and Gottschalk, 1941; Rose and Moen, 1953; Weber et al., 2011; Colvin et al., 2012a, 2012b; Seibert et al., 2015). One recent approach used the spawning potential ratio (SPR) to identify the most efficient level of exploitation to successfully reduce invasive carps (Weber et al., 2011; Seibert et al., 2015). The SPR is the proportion of mature eggs produced at a certain exploitation level to the amount of eggs that theoretically would be produced with no exploitation (Slipke et al., 2002). Historically, SPR modeling has been used to make management decisions focused on protecting fishes from overfishing (Goodyear, 1993; Quist et al., 2002; Quist et al., 2010). Another recent approach (Colvin et al., 2012a, 2012b) uses biomass dynamics modeling and the ecotrophic coefficient to estimate levels of harvest necessary to achieve various levels of control. Regardless of how SPR, biomass dynamics, or ecotrophic coefficient modeling are used, the input and the results generated provide insight into only one species or a group of similar taxonomy.

Ecosystem-based fisheries management has been implemented in marine fisheries in recent decades to reduce the negative impacts of species-centric fisheries management and regulation on endangered or threatened species (Slocombe, 1993; Pikitch et al., 2004). Freshwater researchers have also applied this approach when studying the effects of non-native species on native fishes (Irons et al., 2007; Sampson et al., 2009). Recent publications have developed ecosystem-based models to predict the impact of non-native fishes on systems in which they have not been introduced but could be in the future (Cooke and Hill, 2010; Zhang et al., 2016). One method used to illustrate the intricacies of large aquatic systems and measure effects of disturbances

* Corresponding author at: Kansas Department of Wildlife, Park, and Tourism, 5441 West Lake Road, Ozawkie, KS 66512, United States of America.
E-mail addresses: nick.kramer@ks.gov (N.W. Kramer), quinton.phelps@mail.wvu.edu (Q.E. Phelps), cpierce@iastate.edu (C.L. Pierce), michael.colvin@msstate.edu (M.E. Colvin).
[1] Present Address: Missouri State University, Biology, 901 S. National Ave., Springfield, MO 65897.

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(e.g., non-native species) on these systems is the implementation of food web models. Models such as Ecopath with Ecosim have been used by Zhang et al. (2016) and Arias-González et al. (2011) to predict the impacts of non-native Silver and Bighead Carp on Lake Erie and Indo-Pacific Lionfish in the Caribbean Sea, respectively. Asian Carp (i.e., Grass, Silver and Bighead Carp) and their impacts or predicted impacts of have been a major focus of research on numerous systems throughout the Midwestern United States. However, most of this focus is centered on the Laurentian Great Lakes and the possibility of Asian Carp invasion in these systems (Langseth et al., 2012; Zhang et al., 2016); relatively little research focus has been devoted to an equally important system, the Upper Mississippi River (Delong, 2010; Freedman et al., 2012).

The Upper Mississippi River System flows nearly 2200 km from Lake Itasca, Minnesota to the confluence of the Ohio River at Cairo, Illinois. Throughout its course, the river flows past 27 lock and dams between Minneapolis, Minnesota and St. Louis, Missouri. Lock and Dam 19, constructed in 1913, was the first lock and dam constructed on the Mississippi River and the second largest dam in the country at the time (Jahn and Anderson, 1986). The dam itself was constructed in a manner that greatly limited upriver fish migration (Coker, 1929). Today, this dam acts as the largest barrier to upstream movement of Asian Carp in the Mississippi River. Upstream movement of fishes is only possible through utilization of the lock chamber (Coker, 1929). Telemetered Asian Carp have been observed using the lock chamber in Keokuk to pass from Pool 20 to Pool 19 (Sara Tripp, Missouri Department of Conservation, personal communication). Continued passage of these non-native fish has upstream river managers concerned about the effects of these fish on the native fishes of the Upper Mississippi River pools (Phelps et al., 2017).

The goal of this study was to use a food web modeling approach to explore the impacts and consequences of Asian Carp invasion in portions of the Middle and Upper Mississippi River. Specific objectives were to (1) quantify the amount of effort necessary to effectively remove invasive carps from the Middle Mississippi River, (2) determine the impacts of Asian carp on native fishes in that system, and (3) determine what effects the invasion of Asian carps will have on native fishes in Pools 4, 8, and 13 of the Upper Mississippi River.

2. Methods

2.1. Study site

The study areas used to develop our models were Pools 4, 8, and 13 of the Upper Mississippi River as well as a stretch of the Middle Mississippi River (MMR) (rkm 80–20) near Cape Girardeau, Missouri, USA. Each of these locations was chosen because of the presence of a Long Term Resource Monitoring (LTRM) monitoring station. The LTRM element of the Upper Mississippi River Environmental Monitoring Program has been collecting standardized fish, water quality, and vegetation data since 1993. The standardization of data between these stations allowed for uniformity when developing the models in this study.

2.2. Ecopath with Ecosim

Ecopath with Ecosim (EwE) is a food web modeling software suite available for free download (www.ecopath.org) and commonly used to construct mass-balance trophic models (Christensen and Walters, 2004; Colleter et al., 2015). While primarily used to model marine ecosystems, published models of freshwater systems are becoming more prevalent (e.g., Colvin et al., 2015; Zhang et al., 2016). All models in this study were constructed in EwE version 6.4.4.12634. The following paragraphs describe only the methods used in this study to derive the input parameters; a full description of equations and processes used in the software can be found in Christensen et al. (2008).

2.3. Ecopath inputs

Ecopath models were generated for each of our four study areas. Biomass values for fish groups were determined using the Long Term Resource Monitoring data for the respective field station. Species with similar taxonomy and similar diets were grouped to reduce redundancy and simplify the model. For each fish group, the mean for five years of data (2010–2014) was calculated and converted to metric tons. These values were then divided by the sum of all fish groups biomass and used as our input. Essentially, the initial biomass input was equivalent to the percentage of biomass that group occupied in the system. Not all of the same fish groups were used in each of the study sites due to differences in catch rates by reach or absence from the system. As noted above, Pools 4, 8, and 13 do not contain Silver, Bighead, or Grass Carp at a level detectable by our data set and thus, we could not generate Ecopath models with their relative biomass included. Therefore, these three carps were “introduced” into the Pool 4, 8, and 13 Ecopath models using the biomass values from the MMR model.

Biomass values for the plankton groups were determined using a combination of LTRM data and literature values. Zooplankton estimates were compiled from Chick et al. (2010) and combined with Chlorophyll a values for each of the field stations represented in the models. Benthic invertebrate biomass information was modified from Corti et al. (1996). No estimates of detritus biomass in the model systems was easily accessible in the literature so the input value chosen was derived from estimates of other freshwater models derived in Ecopath (Colvin et al., 2015; Zhang et al., 2016). In the Upper Mississippi Systems, vegetation biomass information was modified from Dewey et al. (1997).

Production values in Ecopath are entered as production/biomass; this value is equivalent to the instantaneous mortality of a fish group. For the fish groups it was assumed that fishing mortality was low and thus P/B values were determined using instantaneous natural mortality values. To do this maximum age for each fish group was determined using readily available aging structures or values from literature. For groups with multiple species, a weighted average of maximum age was used based upon the composition of each species within the group. The Hoenig (1983) method was then used to convert t_{max} to instantaneous natural mortality values. For non-fish groups (i.e., plankton, invertebrates, & plants) production was determined from values derived in previous models of Midwestern freshwater systems (Colvin et al., 2015; Zhang et al., 2016).

Annual consumption for fish groups was calculated using an empirical estimator developed by Liao et al. (2005). These values were then divided by our initial biomass values to determine the Q/B input values. Diet compositions for all fish groups were estimated using published peer-reviewed literature and in some cases were adjusted based upon unpublished field observations. For fishery landings, it was assumed that low fishing pressure occurred and as a result each commercially harvested fish was assigned a landing value of 1% of their initial biomass.

After all initial values were entered additional manipulation of input variables was required to obtain balance within the model. Langseth et al. (2014) showed that the methodology used in the mass-balancing process does not largely affect the output of the model. Our methodology followed Colvin et al. (2015) in that we first identified groups where ecotrophic efficiency values were >1. The inputs of these groups were adjusted by modifying the diet compositions of predators of this group, adjusting P/B and Q/B values or adjusting biomass values.

2.4. Ecosim: Middle Mississippi River carp removal

The first and second objectives of this study required the quantification of the amount of effort needed to remove invasive carps from the system and the impact of such a removal on native fishes. To do this fishing effort was modified for each of the four invasive carps in the MMR model. This was easily achieved due to the 1% fishery landing values; to model an n-percent increase, the fishing effort value was simply increased to n. Harvest of invasive carps was increased in increments of 5% starting at 5% harvest of initial biomass and simulated for 50 years. To account for decreases in biomass of fish groups feeding heavily on invasive carps, due to their opportunistic nature, the switching behavior of our predatory fish groups (e.g., Lepisostids and Moronids) was adjusted. The "switching power parameter" is a user-supplied power parameter representing how strongly the predator responds to changes in prey availability (Christensen et al., 2008). This value ranges from 0 to 2 with a value of 0 representing that the predator will not switch prey sources and a value of 2 signifying that the predator will switch prey sources very rapidly when prey increases or decreases.

2.5. Ecosim: Upper Mississippi River carp invasion

The third objective was to simulate an invasion of carps into the Upper Mississippi River and determine the effect on the biomass of existing fishes. Three sets of invasive carp invasions were simulated in these upper pools: just Grass Carp, just Silver and Bighead Carp, and all three carps. Langseth et al.'s (2012) "method 3" was used to incorporate the invasive groups into the already balanced Ecopath models for each of the Upper Mississippi systems. In this method, the invasive groups are introduced into the model at recently observed levels and then biomass values are immediately reduced by increasing fishing effort until the desired year of invasion. In the simulations of Pool 4, 8, and 13 the values of invasive carp biomass from the MMR were used. Once incorporated into the model the invasive groups were immediately "fished out" by applying an amount of fishing mortality which caused the applied groups to be removed from the model. The model was allowed to re-balance by obtaining constant values before returning the applied fishing mortality back to default values. The difference between the re-balanced biomass values and the post invasion biomass values were then used when drawing conclusions regarding the invasion of our carp groups. As with the MMR simulations, "switching power parameter" was again adjusted. Additionally, for these simulations a mediation forcing function was applied to select groups. The mediation functions in Ecosim can be used to either simulate facilitation or protection (Christensen et al., 2008). These simulations were modified so certain groups (i.e., sunfish, crappie, and small fishes) were "protected" by aquatic vegetation from predation. Applying this mediation function to the simulations of the upper pools of the Mississippi River allowed for the determination of the effect Grass Carp would have on native fishes via habitat consumption.

3. Results

The models of Pools 4, 8 and 13 and the Middle Mississippi River each consisted of 31 fish groups, and one group each for plankton, benthic invertebrates, and detritus. Model parameters (i.e., biomass, production-biomass ratios, consumption-biomass ratios, ecotrophic efficiency, production-consumption ratios, and trophic levels) for all groups can be seen in Table 1. In all river locations, the Common Carp group had the most biomass of all fish groups. The only other species that was within the top third of biomass values for all locations was Channel Catfish. Smallmouth Buffalo, Redhorse spp., Freshwater Drum, Bowfin, Sunfish, Black Bass spp., and Gar spp. were also found in the top third of relative biomass for at least three of the four locations. Trophic levels for each fish group varied from 2.000 for Silver Carp to 3.833 for the Chestnut Lamprey group in Pool 13. Mean trophic level for the pools was highest in pool 13 (mean = 3.06, SE = 0.10) and lowest in the Middle Mississippi River (mean = 2.82, SE = 0.09). Mean ecotrophic efficiency ranged from 0.46 (SE = 0.07) in the Middle Mississippi River to 0.72 (SE = 0.07) in Pool 12 indicating that nearly half to three quarters of available fish biomass was being utilized in our models.

3.1. Middle Mississippi River carp removal

The simulations of increased harvest indicated that biomass of Grass Carp reached 0 t/km^2 with sustained harvest of 30% of initial biomass and Common Carp followed closely after, reaching 0 t/km^2 at 40% sustained exploitation of initial biomass. Silver and Bighead Carp required more effort for removal, not reaching 0 t/km^2 until a simulated sustained removal of 95% of initial biomass (Fig. 1). For all carp species, at the aforementioned exploitation levels, relative biomass was reduced by 75% in the first 34 months of sustained harvest, another 60 months to increase to 90% removal and the remaining 10% reduction not occurring until 44 years after removal was initiated. Upon removal of invasive carps, all model groups showed increases in biomass ranging from 2% to 166% (mean = 51%, SE = 12%; Fig. 2). The largest increases were observed in groups that had high invertebrate diet composition (e.g., Blue Sucker, Shovelnose Sturgeon, and American Eel). The least increasing groups (i.e., Moronids and Lepisostids) had a high proportion of invasive carps in their diets.

3.2. Upper Mississippi River carp invasion

In all of our invasion simulations Silver and Bighead Carp were able to reach biomass levels of established areas (i.e., Middle Mississippi River) shortly after 20 years of introduction. Grass Carp took longer to reach established biomass levels with populations not reaching levels equivalent to the MMR model until 40 years post-introduction. When all three carps invaded the pools simultaneously every group other than the invading groups exhibited decreases in relative biomass (Pool 4 mean = -22.7 ± 0.84%; Pool 8 mean = -21.1 ± 0.74%; Pool 13 mean = -20.3 ± 0.75%; see Fig. 3). In Pool 4 the largest decrease in relative biomass occurred in the Bigmouth Buffalo group (−30.6%) followed closely by Shovelnose Sturgeon (−30.0%). Pools 8 and 13 both had the largest decrease occur with the Shovelnose Sturgeon group (−29.6% and − 30.3%, respectively). The least affected fish group in all three pools was the Moronids; however, decreases in this group still ranged from −14.2% in Pool 13 to −16.5% in Pool 4. Aquatic vegetation in this invasion scenario was decreased by −12.7%, −12.7%, and −15.3% in Pools 4, 8, and 13, respectively.

When only Grass Carp invaded the Upper Mississippi River pools, relative biomass of aquatic vegetation exhibited declines ranging from −15.3% in Pool 4 to −18.0% in Pool 13. In this invasion scenario, most fish groups still exhibited declines in relative biomass (see Fig. 3). Groups that had the "protective" mediating factor applied (i.e., crappie, sunfish, and small fish) had the highest decreases among fish groups in this scenario. Crappie biomass exhibited the largest decline with a mean change of -4.3 ± 0.60% across the three modeled pools. Sunfish and the small fish groups showed declines of -4.1 ± 0.06% and -3.3 ± 0.11%, respectively.

The scenario in which only Silver and Bighead Carp invaded the pools yielded results similar to that of the combined invasion. However, in this scenario there was no observed effect on aquatic vegetation (see Fig. 3). Relative biomass of our plankton groups decreased by −19.3% in Pool 4, −19.2% in Pool 8, and −19.1% in Pool 13 following the invasion. The groups with the largest decline in relative biomass following the Silver and Bighead Carp invasion were Shovelnose Sturgeon (-30.0 ± 0.23%), Lampreys (-29.3 ± 1.14%), Bigmouth Buffalo (-29.0 ± 0.95%), and Paddlefish (-28.3 ± 0.12%). The least influenced fish group in this invasion scenario was again the Moronids with declines in this group ranging from −13.9% in Pool 13 to −16.1% in Pool 8.

4. Discussion

The models and simulations generated in this study produced estimates of the effort required to remove invasive carps from an established system as well as the impacts of such a removal effort on remaining fishes. Simulated removal of 30%, 40%, and 95% of the initial

Table 1
Model groups for all EwE models developed in this study and their parameter values. Abbreviations in the column headers are as follows: B = biomass (t/km2), P/B = annual production-biomass ratio, Q/B = annual consumption-biomass ratio, EE = ecotrophic efficiency (i.e., proportion of production used in system), P/Q = annual production-consumption ratio, and TL = trophic level. Pool 4, 8, and 13 balanced models represent the relative average biomass for the most commonly sampled fish in the LTRM dataset including Silver, Bighead and Grass Carp at levels observed in an established area of the Mississippi River. The Middle Mississippi River balanced model represents the relative average biomass for the most commonly sampled fish in the LTRM dataset.

Group name	Scientific name	Relative B	P/B	Q/B	EE	P/Q	TL
Middle Mississippi River							
American Eel	*Anguilla rostrata*	0.052	0.096	3.541	0.030	0.027	3.162
Bighead Carp	*Hypophthalmichthys nobilis*	13.930	0.375	3.466	0.970	0.108	2.011
Bigmouth Buffalo	*Ictiobus cyprinellus*	1.794	0.209	3.493	0.048	0.060	2.049
Black Bass	*Micropterus* spp.	0.270	0.174	3.519	0.003	0.049	3.343
Black Buffalo	*Ictiobus niger*	8.001	0.173	3.474	0.728	0.050	2.632
Blue Catfish	*Ictaluris furcatus*	2.396	0.199	3.489	0.960	0.057	3.238
Blue Sucker	*Cycleptus elongatus*	0.433	0.323	3.512	0.001	0.092	3.053
Bowfin	*Amia calva*	0.377	0.139	3.514	0.508	0.040	3.441
Bullheads	*Ameiurus* spp.	0.807	0.468	3.507	0.847	0.133	3.063
Carpsucker	*Carpoides* spp.	3.049	0.421	3.486	0.067	0.121	2.263
Channel Catfish	*Ictaluris punctatis*	13.755	0.173	3.466	0.410	0.050	2.658
Chesnut Lamprey	*Ichthyomyzon castaneus*	0.001	0.527	3.592	0.000	0.147	3.770
Common Carp	*Cyprinus carpio*	38.587	0.125	3.453	0.805	0.036	2.737
Crappies	*Pomoxis* spp.	0.186	0.323	3.524	0.461	0.092	3.335
Flathead Catfish	*Pylodictis olivaris*	3.769	0.209	3.483	0.141	0.060	3.258
Freshwater Drum	*Aplodinotus grunniens*	8.778	0.391	3.472	0.986	0.113	2.758
Gar	*Lepisosteus* spp.	5.596	0.174	3.478	0.058	0.050	3.353
Grass Carp	*Ctenopharyngodon idella*	1.552	0.144	3.495	0.070	0.041	2.737
Hiodonts	*Hiodon* spp.	0.050	0.421	3.541	0.002	0.119	3.094
Moronids	*Morone* spp.	0.627	0.355	3.508	0.993	0.101	3.157
Paddlefish	*Polyodon spathula*	1.043	0.075	3.501	0.136	0.021	2.013
Redhorse	*Moxostoma* spp.	0.040	0.468	3.544	0.010	0.132	2.691
Sauger	*Sander canadensis*	0.022	0.232	3.552	0.029	0.065	3.361
Shad	*Dorosoma* spp.	11.930	0.531	3.468	0.999	0.153	2.011
Shovelnose Sturgeon	*Scaphirhynchus platorynchus*	1.107	0.096	3.500	0.001	0.027	3.000
Silver Carp	*Hypophthalmichthys molitrix*	22.596	0.394	3.460	0.933	0.114	2.000
Skipjack Herring	*Alosa chrysochloris*	0.129	1.593	3.528	0.695	0.451	3.134
Small Fishes	All darters, minnows, shiners, chubs, and madtoms	2.950	1.979	3.487	0.897	0.568	2.895
Smallmouth Buffalo	*Ictiobus bubalus*	24.711	0.279	3.459	0.553	0.081	2.063
Sunfish	*Lepomis* spp., *Ambloplites rupestris*, and *Centrarchus macropterus*	4.760	0.703	3.480	0.877	0.202	2.786
Western Mosquitofish	*Gambusia affinis*	1.650	1.420	3.494	0.985	0.406	2.409
Invertebrates		60.000	5.939	9.716	0.664	0.611	2.053
Plankton		12.000	92.378	0.000	0.204		1.000
Detritus		250.000			0.546		1.000
Pool 4							
Bighead Carp	*Hypophthalmichthys nobilis*	13.930	0.375	3.466	0.012	0.108	2.011
Bigmouth Buffalo	*Ictiobus cyprinellus*	1.039	0.209	3.576	0.325	0.058	2.049
Black Bass	*Micropterus* spp.	4.396	0.174	3.559	0.261	0.049	3.258
Bowfin	*Amia calva*	5.612	0.139	3.533	0.560	0.039	3.321
Bullheads	*Ameiurus* spp.	1.413	0.518	3.502	0.915	0.148	3.063
Carpsuckers	*Carpoides* spp.	1.587	0.446	3.534	0.629	0.126	2.263
Channel Catfish	*Ictaluris punctatis*	13.428	0.223	3.641	0.838	0.061	2.617
Common Carp	*Cyprinus carpio*	23.788	0.225	3.539	0.918	0.064	2.737
Crappie	*Pomoxis* spp.	1.915	0.323	3.549	0.844	0.091	3.185
Flathead Catfish	*Pylodictis olivaris*	7.763	0.209	3.544	0.134	0.059	3.300
Freshwater Drum	*Aplodinotus grunniens*	6.366	0.491	3.524	0.833	0.139	2.758
Gar	*Lepisosteus* spp.	0.389	0.174	3.554	0.005	0.049	3.352
Gizzard Shad	*Dorosoma cepedianum*	3.122	0.681	3.575	0.976	0.190	3.000
Grass Carp	*Ctenopharyngodon idella*	1.552	0.144	3.495	0.014	0.041	2.211
Hiodonts	*Hiodon* spp.	0.020	0.421	3.537	0.005	0.119	3.103
Lake Sturgeon	*Acipenser fulvescens*	0.165	0.144	3.495	0.183	0.041	2.737
Lamprey	*Lampetra* spp. and *Ichthyomyzon* spp.	0.002	0.527	3.551	0.000	0.148	3.762
Moronids	*Morone* spp.	2.467	0.405	3.536	0.846	0.115	3.361
Northern Pike	*Esox lucius*	1.118	0.139	3.566	0.645	0.039	3.577
Paddlefish	*Polyodon spathula*	0.300	0.075	3.544	0.021	0.021	2.013
Redhorse	*Moxostoma* spp.	14.138	0.468	3.566	0.594	0.131	2.691
Sanders	*Sander* spp.	1.154	0.232	3.547	0.269	0.065	3.239
Shovelnose Sturgeon	*Scaphirhynchus platorynchus*	0.712	0.096	3.665	0.109	0.026	2.011
Silver Carp	*Hypophthalmichthys molitrix*	22.596	0.394	3.460	0.012	0.114	2.000
Small Fish	All darters, minnows, shiners, chubs, and madtoms	3.498	2.479	3.529	0.962	0.702	2.895
Smallmouth Buffalo	*Ictiobus bubalus*	11.439	0.279	3.528	0.999	0.079	2.063
Suckers	*Catostomus* spp.	0.863	0.423	3.532	0.430	0.120	3.053
Sunfish	*Lepomis* spp. and *Ambloplites rupestris*	4.796	0.703	3.556	0.962	0.198	2.776
Yellow Perch	*Perca flavescens*	3.051	0.482	3.552	0.997	0.136	3.079
Benthic invertebrates		65.000	5.939	9.716	0.696	0.611	2.053
Plankton		12.000	92.378	0.000	0.160		1.000
Aquatic vegetation		35.000	1.200	0.000	0.084		1.000
Detritus		250.000			0.506		1.000
Pool 8							

Table 1 (*continued*)

Group name	Scientific name	Relative B	P/B	Q/B	EE	P/Q	TL
Bighead Carp	*Hypophthalmichthys nobilis*	13.930	0.375	3.466	0.020	0.108	2.011
Bigmouth Buffalo	*Ictiobus cyprinellus*	2.291	0.209	3.576	0.528	0.058	2.049
Black Bass	*Micropterus* spp.	8.267	0.174	3.559	0.858	0.049	3.209
Bowfin	*Amia calva*	8.230	0.139	3.533	0.648	0.039	3.303
Bullheads	*Ameiurus* spp.	1.749	0.518	3.502	0.998	0.148	3.063
Carpsuckers	*Carpoides* spp.	3.198	0.446	3.534	0.870	0.126	2.263
Channel Catfish	*Ictaluris punctatis*	8.075	0.223	3.641	0.993	0.061	2.596
Common Carp	*Cyprinus carpio*	21.430	0.225	3.539	0.993	0.064	2.737
Crappie	*Pomoxis* spp.	3.445	0.323	3.549	0.997	0.091	3.119
Flathead Catfish	*Pylodictis olivaris*	4.490	0.209	3.544	0.374	0.059	3.205
Freshwater Drum	*Aplodinotus grunniens*	3.978	0.491	3.524	0.714	0.139	2.758
Gar	*Lepisosteus* spp.	5.597	0.174	3.554	0.001	0.049	3.228
Gizzard Shad	*Dorosoma cepedianum*	3.922	0.681	3.575	0.990	0.190	3.000
Grass Carp	*Ctenopharyngodon idella*	1.552	0.144	3.495	0.025	0.041	2.211
Hiodonts	*Hiodon* spp.	0.038	0.421	3.537	0.004	0.119	3.095
Lake Sturgeon	*Acipenser fulvescens*	0.141	0.144	3.495	0.813	0.041	2.737
Lamprey	*Lampetra* spp. and *Ichthyomyzon* spp.	0.004	0.527	3.551	0.000	0.148	3.723
Moronids	*Morone* spp.	2.756	0.405	3.536	0.972	0.115	3.305
Northern Pike	*Esox lucius*	4.476	0.139	3.566	0.644	0.039	3.502
Paddlefish	*Polyodon spathula*	0.300	0.075	3.544	0.031	0.021	2.013
Redhorse	*Moxostoma* spp.	18.597	0.468	3.566	0.617	0.131	2.691
Sanders	*Sander* spp.	1.249	0.232	3.547	0.993	0.065	3.229
Shovelnose Sturgeon	*Scaphirhynchus platorynchus*	0.432	0.096	3.665	0.117	0.026	2.011
Silver Carp	*Hypophthalmichthys molitrix*	22.596	0.394	3.460	0.019	0.114	2.000
Small Fish	All darters, minnows, shiners, chubs, and madtoms	4.078	2.479	3.529	0.976	0.702	2.895
Smallmouth Buffalo	*Ictiobus bubalus*	5.644	0.279	3.528	0.823	0.079	2.063
Suckers	*Catostomus* spp.	0.879	0.423	3.532	0.793	0.120	3.053
Sunfish	*Lepomis* spp. and *Ambloplites rupestris*	8.185	0.703	3.556	0.994	0.198	2.776
Yellow Perch	*Perca flavescens*	2.275	0.482	3.552	0.955	0.136	3.079
Benthic invertebrates		65.000	5.939	9.716	0.786	0.611	2.053
Plankton		12.000	92.378	0.000	0.167		1.000
Aquatic vegetation		35.000	1.200	0.000	0.084		1.000
Detritus		250.000			0.503		1.000
Pool 13							
Bighead Carp	*Hypophthalmichthys nobilis*	13.930	0.375	3.466	0.018	0.108	2.011
Bigmouth Buffalo	*Ictiobus cyprinellus*	1.558	0.209	3.576	0.998	0.058	2.049
Black Bass	*Micropterus* spp.	7.337	0.174	3.559	0.426	0.049	3.304
Black Buffalo	*Ictiobus niger*	1.740	0.213	3.543	0.877	0.060	2.632
Bowfin	*Amia calva*	5.668	0.139	3.533	0.647	0.039	3.423
Bullheads	*Ameiurus* spp.	1.239	0.518	3.502	0.998	0.148	3.063
Carpsuckers	*Carpoides* spp.	2.737	0.446	3.534	0.998	0.126	2.263
Channel Catfish	*Ictaluris punctatis*	8.788	0.223	3.641	0.998	0.061	2.628
Chestnut Lamprey	*Ichthyomyzon castaneus*	0.002	0.527	3.551	0.000	0.148	3.833
Common Carp	*Cyprinus carpio*	38.573	0.225	3.539	0.998	0.064	2.737
Crappie	*Pomoxis* spp.	2.715	0.323	3.549	0.998	0.091	3.327
Flathead Catfish	*Pylodictis olivaris*	1.976	0.209	3.544	0.507	0.059	3.371
Freshwater Drum	*Aplodinotus grunniens*	12.864	0.441	3.524	0.998	0.125	2.758
Gar	*Lepisosteus* spp.	7.210	0.174	3.554	0.000	0.049	3.406
Gizzard Shad	*Dorosoma cepedianum*	13.635	0.681	3.575	0.998	0.190	3.000
Grass Carp	*Ctenopharyngodon idella*	1.552	0.144	3.495	0.049	0.041	2.105
Hiodonts	*Hiodon* spp.	0.000	0.421	3.537	0.391	0.119	3.118
Moronids	*Morone* spp.	1.827	0.405	3.536	0.998	0.115	3.468
Northern Pike	*Esox lucius*	3.051	0.139	3.566	0.643	0.039	3.608
Paddlefish	*Polyodon spathula*	1.043	0.075	3.544	0.004	0.021	2.013
Redhorse	*Moxostoma* spp.	5.575	0.468	3.566	0.942	0.131	2.691
Sanders	*Sander* spp.	2.657	0.096	3.665	0.001	0.026	2.011
Shovelnose Sturgeon	*Scaphirhynchus platorynchus*	3.724	2.479	3.529	0.998	0.702	2.895
Silver Carp	*Hypophthalmichthys molitrix*	22.596	0.394	3.460	0.933	0.114	2.000
Small Fish	All darters, minnows, shiners, chubs, and madtoms	15.991	0.279	3.528	0.998	0.079	2.063
Smallmouth Buffalo	*Ictiobus bubalus*	1.000	0.423	3.532	0.618	0.120	3.053
Suckers	*Catostomus* spp.	12.182	0.703	3.556	0.998	0.198	2.793
Sunfish	*Lepomis* spp. and *Ambloplites rupestris*	2.497	0.482	3.552	0.998	0.136	3.116
Yellow Perch	*Perca flavescens*	1.428	0.232	3.547	0.592	0.065	3.300
Benthic invertebrates		65.000	5.939	9.716	0.925	0.611	2.053
Plankton		12.000	92.378	0.000	0.180		1.000
Aquatic vegetation		35.000	1.200	0.000	0.103		1.000
Detritus		250.000			0.558		1.000

biomass of Grass, Common, and Silver and Bighead Carp, respectively, was shown as the minimum amount of exploitation required to eradicate these non-native fishes from the Middle Mississippi River. These values are similar to values found in other studies on invasive carps using species-centric modeling approaches. Weber et al. (2011) found that exploitation levels of 40% were the most efficient in removal of Common Carp in three natural lakes in South Dakota, whereas Colvin et al. (2012b) reported that >76% of annual production needed to be removed annually to reduce overall biomass of the same species in Clear Lake, Iowa. Similarly, Wolf's (2017) SPR modeling on Common Carp and Grass Carp in the Middle Mississippi River suggests that exploitation rates of 35% and 30% are capable of overfishing, and thus

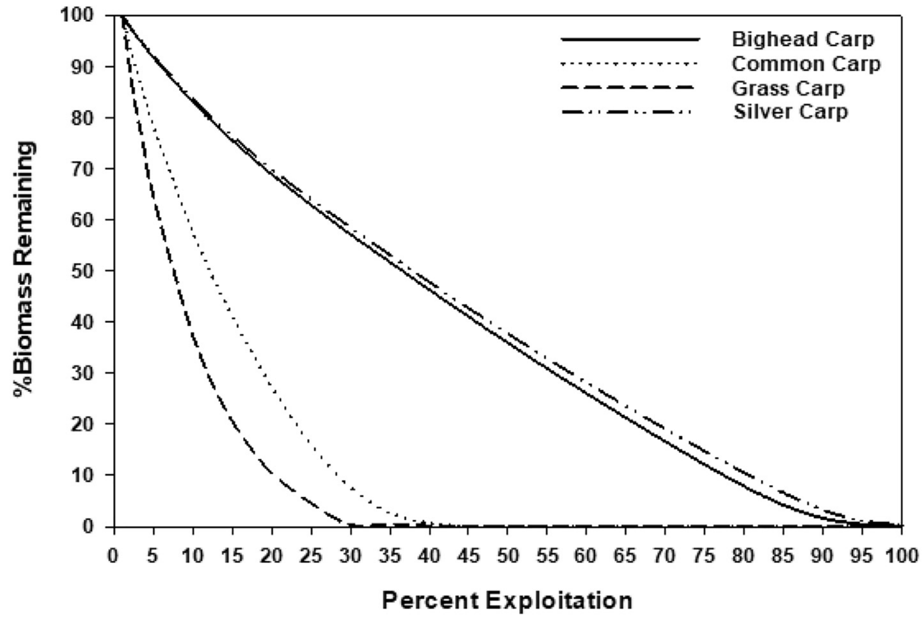

Fig. 1. The amount of exploitation required to decrease biomass of Common, Grass, Silver and Bighead Carp in the Middle Mississippi River.

eradicating, Common Carp and Grass Carp populations, respectively. Our estimate of the amount of exploitation required to overfish Silver Carp was higher than that predicted by Seibert et al. (2015) for the Middle Mississippi River (about 70%). The differences between our simulation results and those reported by Seibert et al. (2015) may be due to the weighting of the production values in our Ecopath models to account for a high amount of age-0 Silver Carp in the system. Tsehaye et al. (2013) also report that at Silver and Bighead Carp may become overfished at an exploitation rate of 70%, however the error associated with their prediction indicates relative biomass of these non-native fish could range from 75% to 0%. Furthermore, their prediction of relative biomass resulting from a 90% exploitation rate indicates the possibility of overfishing with lower associated error, which is more agreeable with the results of our simulation. While the estimates of exploitation required to remove these carps are congruent with other studies, ours is the only study which provides inference into the effects of such a removal on other fishes.

While the aforementioned studies have not provided insight into the effects of carp removal on other fishes, other studies predict impacts of a carp invasion. The models developed by Zhang et al. (2016) showed that Silver and Bighead Carp took about 20 years to establish a stable population in Lake Erie, the same duration observed in our models. Additionally, they found that most simulations projected biomass decreases <25% for most piscivorous and planktivorous groups while suggesting Silver and Bighead Carp would have minor effects on benthic invertebrates, phytoplankton, and bacteria. Our Pool 4, 8, and 13 models and simulations indicated decreases of nearly all groups, including benthic invertebrates, following an invasion of Silver and Bighead Carp. However, we simulated over twice the amount of carp biomass as Zhang et al. (2016) used when drawing those conclusions. In simulations in which Zhang et al. (2016) increased Silver and Bighead Carp biomass to levels more similar to our simulations (>20 t/km^2), results agreed with studies conducted in areas of high Silver and Bighead Carp densities (Freedman et al., 2012; Garvey et al., 2012) and expert predictions compiled by Wittmann et al. (2015), as well as the simulation results generated in this study.

As noted above, the models and simulations developed in this study have generated results similar to those from other modeling exercises whether it is spawning potential ratio modeling (Weber et al., 2011; Seibert et al., 2015; Wolf, 2017), ecotrophic coefficient modeling (Colvin et al., 2012b), age-structured dynamic simulation model (Tsehaye et al., 2013), or food web-based mass-balance models

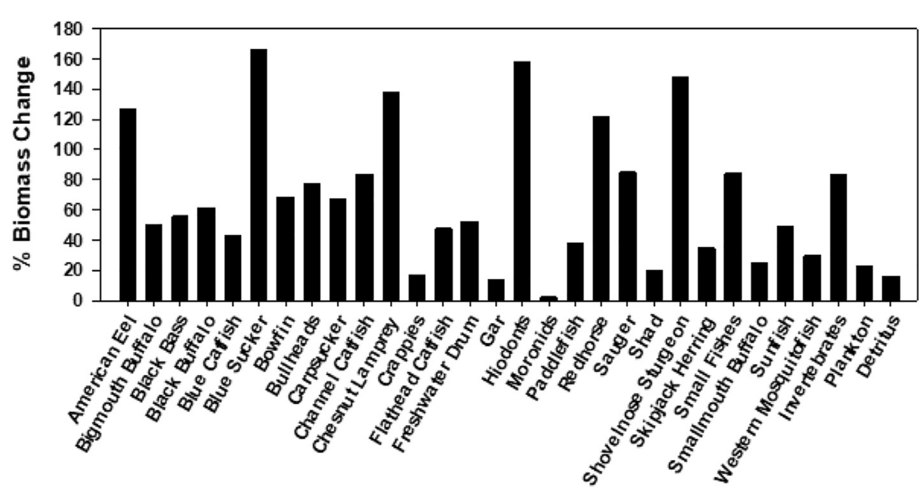

Fig. 2. Relative change in biomass of model groups following the simulated removal of Common, Grass, Silver and Bighead Carp in the Middle Mississippi River.

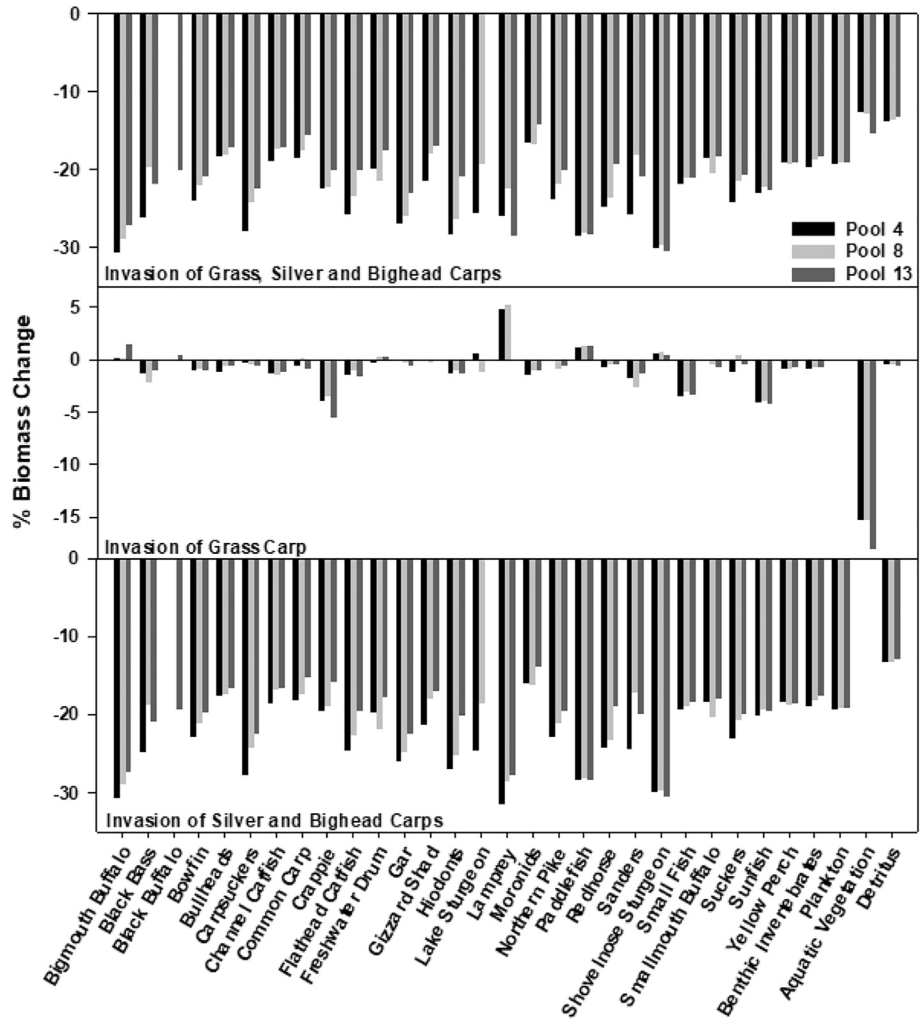

Fig. 3. Relative change in biomass of model groups following the simulated invasion of Grass, Silver, and Bighead Carp in Pools 4, 8, and 13 of the Mississippi River. Separate simulations were completed for all three carps invading, just Grass Carp invading, and just Silver and Bighead Carp invading.

(Zhang et al., 2016) as well as field observations (Freedman et al., 2012). While generating similar results, food-web modeling, specifically EwE, allows the user to study the effects of alterations (e.g., invasive species) at the food-web level, rather than a single species. Additionally, the EwE software suite allows users to define their food-web with as many or as few groups as they wish, essentially allowing the user to determine the level of complexity the model possesses as well as the possible insight the model outputs could generate. While our model contained 34 groups, the size and complexity of each base model is relatively low partly due to insufficient data to split groups apart across age groups or further separate lower trophic groups (i.e., plankton, benthic invertebrates).

While the models developed in this study did allow us to predict the impacts of invasive species removal and introduction within close proximity to previous studies listed above, the Ecopath with Ecosim approach is not without flaws. A common weak point in Ecopath models are the input values themselves. Most studies may wish to gather the required data first hand however, time or funding may prevent that from occurring forcing the model inputs to be derived from literature reviews and data mining. This data more-often-than-not is either outdated or from other systems and may not accurately represent the species or groups present in a model. Essington (2007) evaluated the sensitivity of Ecopath to imprecise data inputs and found that precision of biomass and ecotrophic efficiency inputs are roughly equivalent to the precision of input data, specifically biomass and production values. The models and simulations presented in this manuscript relied heavily on outside data, unpublished field observations, and calculations/conversions to satisfy the input requirements of Ecopath which may lead to imprecision. However, a known value is required to determine the precision and accuracy of an estimate and for many of the input values there are no readily available known values with which to compare in this system. Instead, this study compared the results of simulations to values derived in other studies and found similar results. Heymans et al. (2016) states that correct use of ecosystem models relies on the ability to understand uncertainty in input data and the ability to assess the confidence in the model outputs. The authors understand the uncertainty of the inputs used in this study and the imprecision that may lead to but are fully confident in the model outputs and the precision at which they agree with results from modeling completed on invasive carps in other studies on the Mississippi River.

To successfully incorporate ecological considerations into fisheries management, we do not need an exhaustive understanding of ecological processes but rather an investment in the data required to illustrate the important ecological processes in existing models (Link, 2002). The sustainability of our freshwater ecosystems and the individual populations residing within are reliant upon the implementation of management objectives and regulations founded on science not from a species-centric approach, but rather at the ecosystem level. Additionally, Cury et al. (2005) state that fisheries science is “deeply skewed towards biology using scarce data of poor quality” and the results have produced impractical and poorly implemented policy advice. The consequence has been collapses of many important fisheries throughout the world (Pauly et al., 2002). If real insight into effective fisheries management is to be achieved, then it is imperative that food web-based approaches such as this study built upon EwE are utilized. EwE food web modeling is a big step in the direction of modeling the whole ecosystem. However, Heymans et al. (2016) EwE models should not be used as the only tool for ecosystem based management but rather one of a suite of tools. This study and the models created within have developed estimates of harvest and reductions that are similar to those found in other studies and models and thus, work to further strengthen the findings in those studies.

As demonstrated in this study, the implementation of an ecosystem-based approach to non-native species management in freshwater systems may provide valuable insight into the predicted impact to an existing fishery, as well as the amount of exploitation required to eradicate an established population. An ecosystem approach allows exploration of the linkages throughout the system which may not be apparent using a species-centric approach. Thus, future implementation of food-web models such as those developed in this study may provide valuable insight into freshwater ecosystems and the food web interactions therein.

Declaration of competing interest

No potential conflict of interest is present at the time of submitting this article for review.

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