

Reduced condition factor of two native fish species coincident with invasion of non-native Asian carps in the Illinois River, U.S.A. Is this evidence for competition and reduced fitness?

K. S. IRONS*†, G. G. SASS*, M. A. MCCLELLAND*
AND J. D. STAFFORD‡

**Illinois River Biological Station, Illinois Natural History Survey, 704 N. Schrader Avenue, Havana, IL 62644, U.S.A.* and ‡*Forbes Biological Station, Illinois Natural History Survey, P. O. Box 590, Havana, IL 62644, U.S.A.*

Non-native, Asian carps bighead *Hypophthalmichthys nobilis* and silver *Hypophthalmichthys molitrix* have been present in the Illinois River since the early 1990s. The Long-Term Resource Monitoring Program (LTRMP) has been collecting bighead and silver carps in routine monitoring of the La Grange Reach, Illinois River, since 1995 and 1998, respectively. Despite variable recruitment, Asian carps abundance and biomass have increased since 2000, as evidenced by commercial landings, and Asian carps now dominate the fish community on La Grange Reach. Previous research suggests dietary overlap among bighead and silver carps and two native Illinois River fishes, gizzard shad *Dorosoma cepedianum* and bigmouth buffalo *Ictiobus cyprinellus*. Total length and mass data from c. 5000 fishes were used to test for changes in gizzard shad and bigmouth buffalo body condition after Asian carps establishment and investigate potential competitive interactions and changes in fitness. Analyses revealed significant declines in body condition of gizzard shad (–7%) and bigmouth buffalo (–5%) following the Asian carps invasion from 2000 to 2006. Segmented regression analyses showed no significant change in the rate of decline in gizzard shad condition after 2000, whereas the rate of decline in bigmouth buffalo condition increased significantly after 2000. Statistically significant differences in gizzard shad condition after Asian carps establishment (2000–2006) was observed, whereas condition of bigmouth buffalo was significantly lower in all years following Asian carps establishment as compared to 2000. Declines in gizzard shad and bigmouth buffalo condition were significantly correlated with increased commercial harvest of Asian carps and poorly correlated with other abiotic and biotic factors (e.g. temperature, chlorophyll *a* and discharge) that may influence fish body condition. These results may suggest that Asian carps are influencing native planktivore body condition, and future research should focus on determining whether food is limited in the Illinois River for native planktivores and other fish species.

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Key words: bighead carp; bigmouth buffalo; body condition; gizzard shad; non-native; silver carp.

†Author to whom correspondence should be addressed. Tel.: +1 309 543 6000; fax: +1 309 543 2105; email: kirons@uiuc.edu

INTRODUCTION

Non-native carps, bighead *Hypophthalmichthys nobilis* (Richardson) and silver *Hypophthalmichthys molitrix* (Valenciennes) have increased in abundance and biomass in several Mississippi and Illinois rivers reaches of the Upper Mississippi River System (UMRS). Originally brought to the U.S. for aquaculture, bighead and silver carps escaped confinement, established feral populations and moved upstream in the UMRS. Since the mid 1990s, the Long-Term Resource Monitoring Program (LTRMP) has been able to document this expansion (Tucker *et al.*, 1996; Chick & Pegg, 2001). Two long-term monitoring programmes on the Illinois River collect basic information from fishes, *e.g.* total length (L_T), mass (M) and relative abundance, as part of standardized monitoring. Therefore, a large body of long-term information exists in regards to the overall fish communities and Asian carps in the UMRS.

For the purpose of this study, Asian carps are defined as bighead and silver carps, exclusive of other Asian carps such as grass carp *Ctenopharyngodon idella* (Valenciennes) and black carp *Mylopharyngodon piceus* (Richardson), which have also been found in the U.S. Asian carps are filter feeders, feeding upon zooplankton, phytoplankton and organic particles suspended in the water column. Filtering efficiencies vary by species, with bighead carp filtering organisms to 20 μm and silver carp filtering down to 10 μm (Jennings, 1988; Smith, 1989; Vörös, 1997). Due to their large adult maximum sizes (>35 kg) and ability to filter efficiently, Asian carps may disproportionately deplete plankton and alter zooplankton community composition of inhabited systems (Berg, 1964; Spataru & Gophen, 1985; Burke *et al.*, 1986; Xie & Yang, 2000; Lu *et al.*, 2002; Xie, 2003). Additionally, evidence suggests that global introductions of Asian carps have led to decreased fish species diversity and abundances of desirable fishes in commercial catches (Spataru & Gophen, 1985; Sugunan, 1997; Petr, 2002). For example, Asian carps have had negative effects on native filter-feeding fishes in Thailand (de Iongh & Van Zon, 1993). Due to the biology and life histories of Asian carps, concern exists that additional negative impacts to native filter feeding fishes of the U.S. may be realized, *e.g.* paddlefish *Polyodon spathula* (Walbaum), bigmouth buffalo *Ictiobus cyprinellus* (Valenciennes) and gizzard shad *Dorosoma cepedianum* (LeSueur) (Schrank *et al.*, 2003; Sampson, 2005). Changes in native fish abundances in the U.S. as a consequence of competition with these new invaders, however, has not been documented or evaluated.

The objective of this study was to test for changes in body condition of two native filter-feeding fish species, gizzard shad and bigmouth buffalo, before and after the invasion of Asian carps in the La Grange Reach, Illinois River (hereafter referred to as La Grange Reach). Additional abiotic and biotic factors that may influence fish condition were also tested to determine co-varying influences on gizzard shad and bigmouth buffalo body condition. Two long-term fish monitoring data sets on La Grange Reach were used to test for changes in body condition. Specifically, these data provided: (1) trends in abundance of Asian carps on La Grange Reach and (2) trends in body condition for planktivorous gizzard shad and bigmouth buffalo through the assessment of relative mass (M_r). Decreases in M_r of planktivorous fishes over time may suggest increased competition for food resources among native fishes and

Asian carps, which could have negative implications for the long-term fitness of affected species.

MATERIALS AND METHODS

STUDY AREA

The 129 km long La Grange Reach is located between La Grange Lock and Dam (L&D) and Peoria L&D on the Illinois River, U.S., and is about midway between the Mississippi River and Lake Michigan (Fig. 1). The Illinois River is a major tributary of the Mississippi River, draining nearly two-thirds of the state of Illinois. Fish monitoring on La Grange Reach is performed by the Illinois River Biological Station, Illinois Natural History Survey (INHS).

LTRMP AND LTEF DATA COLLECTION

The fish community of La Grange Reach has been monitored by the LTRMP from 1990 to the present, with *c.* 500 random collections each year from 15 June to 31 October. Long-term Illinois River Fish Population Monitoring (LTEF) has occurred since 1957, with *c.* 27 collections each year from 21 August to 7 October.

The LTRMP is part of the Environmental Management Program on the UMRS, which is funded through the U.S. Army Corps of Engineers, Rock Island District. Programme management of the LTRMP is conducted by the U.S. Geological Survey, Upper Midwest Environmental Sciences Center, LaCrosse, Wisconsin, and implemented in collaboration with the natural resource agencies of the five UMRS states

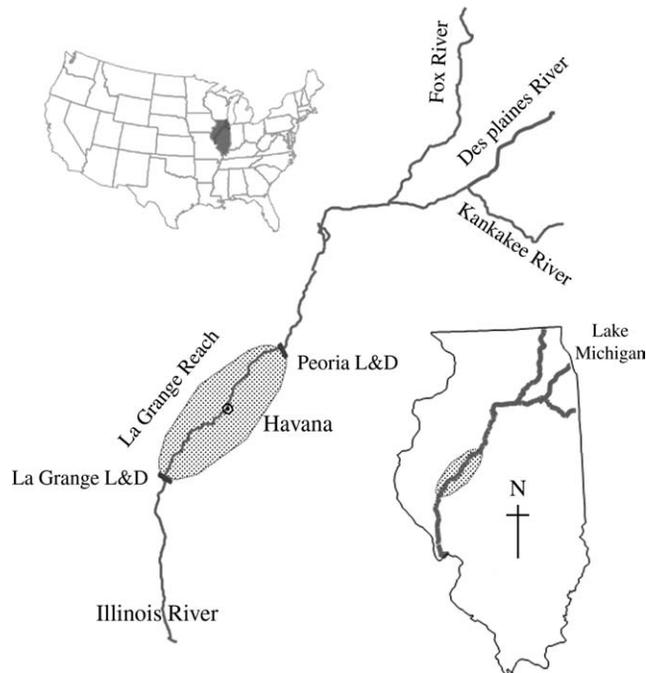


FIG. 1. Map of Illinois River, Illinois, U.S.A. The 129 km long La Grange Reach, Illinois River is located between La Grange Lock and Dam (L&D) and Peoria L&D.

of Illinois, Iowa, Minnesota, Missouri and Wisconsin. The LTRMP fish collection methodology included a multiple gear approach (netting and electrofishing) to monitor the general fish community of the UMRS through time (Gutreuter *et al.*, 1995). The L_T were recorded for all fishes captured, while M were also recorded for selected species captured only during autumn sampling (15 September to 31 October) annually. Only data from La Grange Reach were used in this synthesis, and LTRMP fish component effort remained relatively consistent through time. Methodology, protocols and modifications to the LTRMP can be found in Gutreuter *et al.* (1995), Ickes & Burkhardt (2002) and Ickes *et al.* (2005). Additional details regarding monitoring methods and timeline can be found at: http://www.umesc.usgs.gov/reports_publications/ltrmp/fish/2005/samplinghistory.html

The LTEF fish collection methodology also monitored fish populations through time and was supported by the Federal Aid in Sportfish Restoration Program (F-101-R; Koel & Sparks, 2002). The LTEF monitored La Grange Reach as one of five Illinois River reaches sampled from 21 August to 7 October annually since 1959. Within La Grange Reach, six fixed sites were sampled annually for *c.* 1 h each using AC electrofishing gears. Only data from La Grange Reach were used in this synthesis, and LTEF effort remained consistent through time. The L_T and M were recorded for all fishes captured. Further details of the LTEF can be found in Koel & Sparks (2002).

ASIAN CARP CATCHES

Simple linear regression was used to test for a relationship between total catch [numbers and biomass (kg)] of bighead and silver carps collected by all gears (dependent variable) and time (1990–2006; independent variable). Similarly, a relationship between total Asian carps and commercial harvest time during 1990–2005 was tested for. Annual total commercial catch of Asian carps from the Illinois River was provided by the Illinois Department of Natural Resources as unproofed, draft-quality data pending final quality assurance measures; however, these data may be assumed reliable and general trends should not change significantly (R. Maher, pers. comm.). A null hypothesis of no change in Asian carp catch over time was used at the $\alpha = 0.05$ level.

Not all fishes collected by the LTRMP were weighed; therefore, M and L_T relationships were developed for Asian carps on La Grange Reach from a sub-set of fish weighed each autumn. These relationships were used to estimate total annual catch in biomass based on recorded L_T . All M and L_T were \log_{10} transformed to establish linearity among the variables. On the La Grange Reach, the M (g) and L_T (mm) the relationship for bighead carp was given by: $\log_{10} M = 2.952\log_{10} L_T - 4.838$ (F -test, d.f. = 1,71, $P < 0.001$) and for silver carp was given by: $\log_{10} M = 3.122\log_{10} L_T - 5.294$ (F -test, d.f. = 1,450, $P < 0.001$).

GIZZARD SHAD AND BIGMOUTH BUFFALO BODY CONDITION

La Grange Reach mass and total length relationships

To examine body condition of gizzard shad and bigmouth buffalo before and after Asian carps establishment, species-specific M and L_T relationships were developed for La Grange Reach. To develop standards, all records were used where actual M values exist from the LTRMP data in 1990–1999 and all records where actual masses were recorded from individual fish in the LTEF during 1983–1999 (Table I). Years were included in the analysis when a minimum of three fish per species were collected. The M and data for gizzard shad and bigmouth buffalo in 2000–2006 were excluded from the development of the standards because Asian carps became established in 2000.

La Grange Reach-specific M and L_T relationships were established for gizzard shad and bigmouth buffalo by \log_{10} transforming M and L_T to establish linearity among the variables. Linear regression was used to test for a statistical relationship between M and L_T with the null hypothesis of no change in M with increasing L_T ($\alpha = 0.05$).

TABLE I. Total and annual number of *Dorosoma cepedianum* and *Ictiobus cyprinellus* weighed and measured from La Grange Reach, Illinois River from the Long-Term Illinois River Fish Population Monitoring Program (LTEF) and the Long-Term Resource Monitoring Program (LTRMP) from 1983 to 2006

Year	<i>Dorosoma cepedianum</i>		<i>Ictiobus cyprinellus</i>	
	LTEF	LTRMP	LTEF	LTRMP
1983	37	—	6	—
1984	25	—	3	—
1985	7	—	—	—
1986	—	—	—	—
1987	—	—	—	—
1988	—	—	—	—
1989	20	—	30	—
1990	—	234	12	7
1991	17	93	15	231
1992	24	—	26	2
1993	—	—	—	—
1994	78	—	53	2
1995	19	—	24	4
1996	11	—	28	20
1997	20	—	31	97
1998	17	—	18	104
1999	21	—	7	96
2000	32	—	10	66
2001	59	—	26	230
2002	10	196	5	165
2003	18	176	7	142
2004	134	328	6	183
2005	43	788	6	86
2006	87	679	2	74
Total	680	2494	315	1510

As far as is known, no standard mass (M_S) equation existed for bigmouth buffalo (Anderson & Neumann, 1996). The published M_S equation for gizzard shad was not used because the minimum L_T required for the model (180 mm) typically exceeded the sizes of the catches (Anderson & Gutreuter, 1983). Further, the purpose of this study was to specifically assess gizzard shad and bigmouth buffalo body condition within La Grange Reach and not across all sampled populations of each species. Average body condition (50th percentile) within the La Grange Reach was of specific interest. Hrabik *et al.* (1998) and Sass *et al.* (2004) used similar methodologies for examining fish species without a M_S and L_T relationship or for regional species-specific body condition analyses, respectively.

On La Grange Reach, the M_S and L_T relationship for gizzard shad in 1983–1999 was given by: $\log_{10} M = 2.9516 \log_{10} L_T - 4.9038$ (F -test, d.f. = 1,703, $P < 0.001$). The minimum size of gizzard shad applicable to this model was 69 mm. The gizzard shad M and L_T relationship on La Grange Reach was similar to that reported by Anderson & Gutreuter (1983) ($\log_{10} M = 3.17 \log_{10} L_T - 5.376$).

On La Grange Reach, the M_S and L_T relationship for bigmouth buffalo in 1983–1999 was given by: $\log_{10} M = 3.2054 \log_{10} L_T - 5.3256$ (F -test, d.f. = 1,821, $P < 0.001$). The minimum size of bigmouth buffalo applicable to this model was 125 mm.

From these developed standards, relative mass (M_r) for gizzard shad and bigmouth buffalo was calculated as: $M_r = MM_S^{-1}$.

La Grange Reach condition analysis

From these developed standards, M_r were calculated for each gizzard shad and bigmouth buffalo captured and weighed in 1983–2006 from LTRMP and LTEF. To test for differences in mean M_r among time periods and species (pre-Asian carps, 1983–1999; post-Asian carps, 2000–2006), a single factor ANOVA was used, with the null hypothesis of no difference in mean M_r among time periods for each species ($\alpha = 0.05$). In addition, segmented regression models were used to test for changes in slope of the mean M_r for each species among time periods (Draper & Smith, 1998). The year 2000 was used as the breakpoint in the segmented regression models because Asian carps became established on La Grange Reach in this year (Draper & Smith, 1998). The segmented regression model of: $Y = \beta_0 + \beta_1 X_1 + \beta_2 X_2 + \varepsilon$ was used, where $b_0 =$ value of Y at point of intersection, $X_1 = X_2 = 0$, $b_1 =$ slope of first trend line, and $b_2 =$ slope of second trend line. Dummy variables were coded for X_1 and X_2 based on the time interval prior to or after the year 2000 and all terms were calculated simultaneously by least squares. Dummy variable X_1 and X_2 were both set to zero at year 2000; X_1 is stepped back for the first line, X_2 is stepped forward for the second line and both variables are otherwise zero (Draper & Smith, 1998). The segmented regression models were tested for statistical significance using ANOVA at the $\alpha = 0.05$ level.

Post-Asian carps

If a significant change or breakpoint in gizzard shad or bigmouth buffalo condition was observed in 2000, a general linear model was used to further examine condition of gizzard shad and bigmouth buffalo following Asian carps establishment. Annual (2000–2006) M and L_T relationships were developed for both species from all records where actual masses exist. Relationships between \log_{10} transformed M (dependent variable) and \log_{10} transformed L_T (independent variable) for gizzard shad and bigmouth buffalo were analysed using general linear models in PROC MIXED, SAS v9.2a (Singer, 1998; SAS, 1999). Sampling year was included as a fixed-effect in the models, and estimated individual year effects using the CLASS statement in the MIXED procedure. When a significant fixed effect was detected ($P < 0.05$), the relationship was compared among years *via* least-squares means contrasts, by specifying the PDIF option in the LSMEANS statement. Multiple comparisons were accounted for by correcting the *a priori* type I error rate ($\alpha = 0.05$) using a Bonferroni correction ($\alpha = 0.05/21 = 0.0024$).

TRENDS OF RELATIVE FISH ABUNDANCE

Simple linear regression was used to test for a relationship between mean catch per unit effort (CPUE; fish per electrofishing run) of gizzard shad, bigmouth buffalo and predators for day electrofishing (dependent variable) during 1994–2006 (independent variable). The analyses assumed that autumn (September to October) LTRMP day electrofishing catches were reflective of ambient fish abundances. The null hypothesis of no change in catch over time was used at the $\alpha = 0.05$ level.

Predators were defined as an amalgam of shortnose gar *Lepisosteus platostomus* Rafinesque, channel catfish *Ictalurus punctatus* (Rafinesque), flathead catfish *Pylodictis olivaris* (Rafinesque), white bass *Morone chrysops* (Rafinesque) and largemouth bass *Micropterus salmoides* (Lacepède) from autumn LTRMP day electrofishing only. These fishes represented the majority of piscivorous fishes within LTRMP catches on La Grange Reach.

Annual commercial harvest of Asian carps (independent variable) was also regressed upon mean annual gizzard shad and bigmouth buffalo body condition (dependent variable). Commercial harvest of Asian carps was \ln transformed to satisfy the assumptions of linear regression. The null hypothesis of no change in gizzard shad or bigmouth buffalo condition with commercial harvest of Asian carps was used at $\alpha = 0.05$ level.

ALTERNATIVE PREDICTORS OF BODY CONDITION

Multiple regression was used to test for additional abiotic and biotic factors that may influence gizzard shad and bigmouth buffalo condition over time. Nineteen different predictor variables were regressed on mean annual gizzard shad and bigmouth buffalo body condition. The 19 predictors included year, mean water temperature, mean pH, mean turbidity, mean conductivity, mean chlorophyll *a*, mean silica, mean suspended solids, mean total phosphorus, mean total nitrogen, minimum water temperature, maximum water temperature, variation of water temperature, mean discharge, minimum discharge, maximum discharge, variance in discharge and mean predator CPUE. All mean predictors were averages from August to October LTRMP sampling. Discharge values were collected by the U.S. Army Corps of Engineers (Soballe & Fischer, 2004). Best sub-set regression was used to determine inclusion of predictor variables for full model consideration ($\alpha = 0.05$). Due to the number of variables, a Bonferroni correction was applied to α based on the number of predictors considered for the full model. Maximum r^2 value, maximum adjusted r^2 value and Mallows C_p statistic were used to determine the best model (Draper & Smith, 1998). Mallows C_p statistic was given by: $C_p = X_p s^{-2} - (n - 2p)$, where X_p is the residual sum of squares from a model containing p parameters, p is the number of parameters in the model including β_0 , and s^2 is the residual mean square from the largest equation postulated containing all the parameters and is presumed to be a reliable unbiased estimate of the error variance σ^2 . Adequate models are considered when C_p is similar in value to p . All interactions of selected predictor variables were dropped from model consideration if p exceeded 0.05.

RESULTS

ASIAN CARP CATCHES

Bighead and silver carps catches increased on La Grange Reach from 1990 to 2006 (Fig. 2). Increases in catch of silver carp were statistically significant and best characterized by a linear model ($P < 0.001$), whereas bighead carp catches did not change over time using a linear model [Fig. 2(a)]. Bighead carp were first observed in 1995 and catches peaked in 2000 with 1142 individuals captured. Silver carp were first observed in 1998 with catches peaking in 2004 at 580 fish. Since 1999, bighead carp catches have peaked in 2000 and declined to < 100 individuals (2005–2006) using LTRMP gears. Catches of silver carp have also increased since 1999, peaked and then declined to just > 300 fish per year using LTRMP gears.

Using the developed M and L_T relationships for Asian carps, bighead and silver carps biomass increased on La Grange Reach during 1990–2006 [Fig. 2(b)]. Silver carp increases in biomass over time were best characterized by an exponential model, with peak biomass of > 630 kg of silver carp in 2005. Bighead carp biomass did not change over time in La Grange Reach according to LTRMP gears. Commercial harvest records from the Illinois River showed a significant exponential increase in annual Asian carps harvested during 1990–2005 (Fig. 3).

GIZZARD SHAD AND BIGMOUTH BUFFALO CONDITION

La Grange Reach condition analysis

Mean M_T of gizzard shad and bigmouth buffalo declined significantly after Asian carp establishment in 2000. Mean M_T of gizzard shad declined from

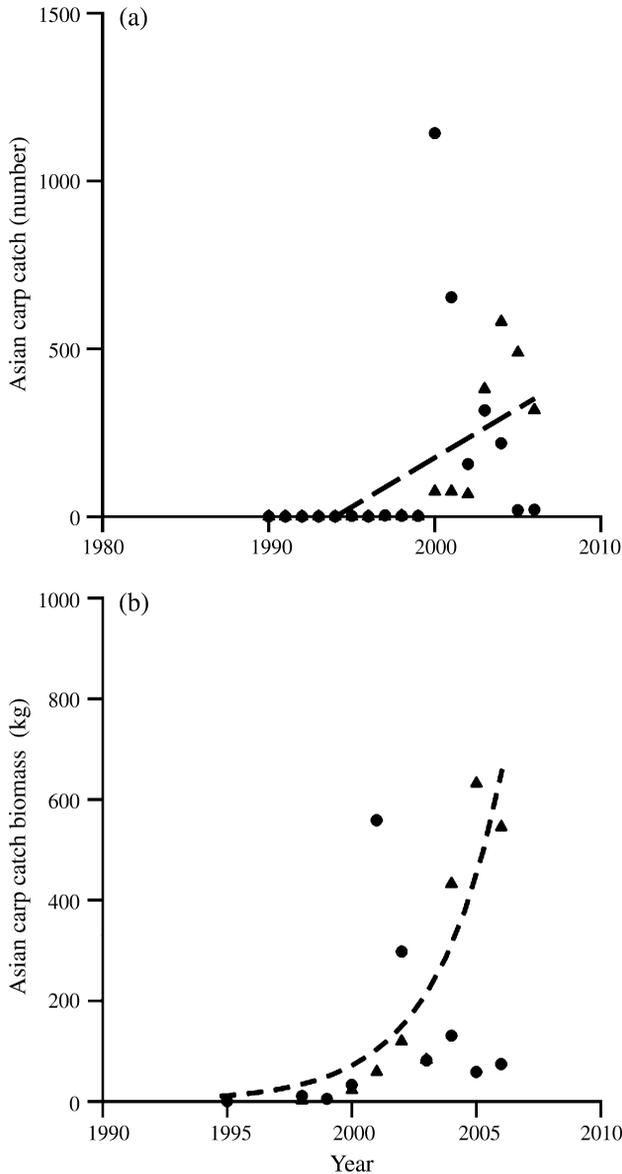


FIG. 2. Trends in (a) total annual catch (number) and (b) total annual estimated biomass of bighead (●) and silver (▲) carps catches in La Grange Reach, Illinois River, 1990–2006. The curves were fitted for silver carp (a) numbers ($y = 29.728x - 58\,481.676$; $r^2 = 0.55$) and (b) biomass over time ($y = 7.561e^{0.372x}$; $r^2 = 0.82$).

1.00 to 0.93 (−7%) among time periods (F -test, d.f. = 1,3172, $P < 0.001$; Fig. 4). Mean M_r of bigmouth buffalo also declined from 1.00 to 0.95 (−5%) among pre-Asian carps (1983–1999) and post-Asian carps (2000–2006) time periods on La Grange Reach, respectively (F -test, d.f. = 1,1823, $P < 0.001$; Fig. 4).

Segmented regression models suggested greater negative slopes of the best-fit line for mean M_r of gizzard shad and bigmouth buffalo after 2000 compared to

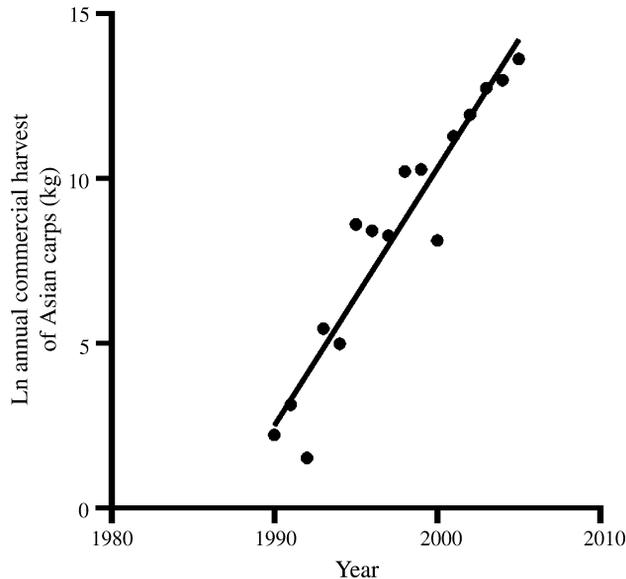


FIG. 3. Ln transformed annual commercial harvest of Asian carps (bighead and silver carps combined) from the Illinois River as reported to Illinois Department of Natural Resources (unproofed data). The curve was fitted by: $y = 0.7798x - 1549.2$ ($r^2 = 0.90$).

1983–1999. Bigmouth buffalo mean M_T rate of change declined significantly post-Asian carp establishment [F -test, d.f. = 2,16, $P < 0.001$; Fig. 4(b)]. No significant changes were detected in the segmented regression analysis for gizzard shad after 2000; however, a greater negative slope was observed [Fig. 4(a)].

Post-Asian carps

Results of general linear models indicated M and L_T relationships for gizzard shad and bigmouth buffalo on La Grange Reach declined significantly over time. A significant M and L_T relationship existed for gizzard shad from 2000 to 2006 [$\log_{10} M = 2.9468 \log_{10} L_T - 4.9307$; $n = 2550$, $P < 0.001$]. Differences of least squares means (DLSM) showed significant increases in condition of gizzard shad among 2002 and 2004, 2005 and 2006, as well as between 2003 and 2004, 2005 and 2006 ($P < 0.01$). Both 2002 and 2003 gizzard shad body condition was significantly less than 2001 ($P < 0.01$). Likewise, a significant M and L_T relationship existed for bigmouth buffalo from 2000 to 2006 [$\log_{10} M = 3.1253 L_T - 5.1401$; $n = 1008$; $P < 0.001$]. The DLSM showed significant declines in body condition of bigmouth buffalo among 2000 and all subsequent years [2001, 2002, 2003, 2004, 2005 and 2006 ($P < 0.001$)].

TRENDS OF RELATIVE FISH ABUNDANCE

Gizzard shad CPUE did not change over time [F -test, d.f. = 1,11, $P > 0.05$; Fig. 5(a)]. Bigmouth buffalo CPUE significantly decreased over time on La Grange Reach [F -test, d.f. = 1,11, $P < 0.01$; Fig. 5(b)]. Predator CPUE (y) also

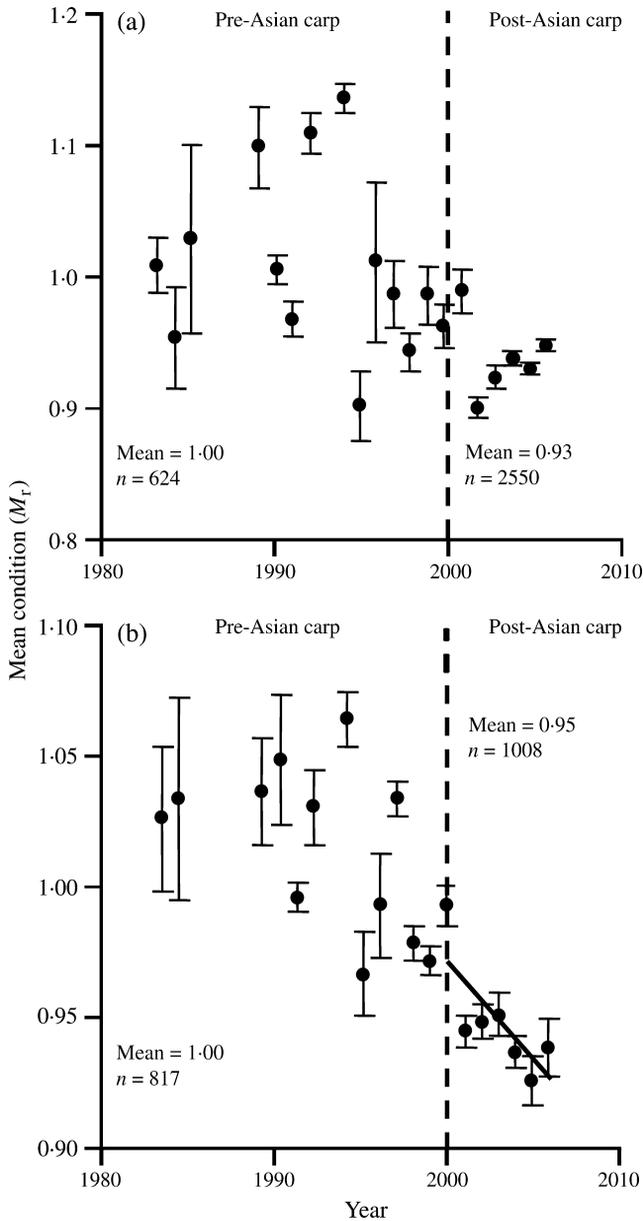


FIG. 4. Means \pm S.E. and trends in autumn (August to October) relative mass (M_r) of (a) gizzard shad and (b) bigmouth buffalo from La Grange Reach, Illinois River from the Long-Term Illinois River Fish Population Monitoring Program (LTFE) and the Long-Term Resource Monitoring Program (LTRMP) during pre- (1983–1999) and post-Asian carps establishment (2000–2006). Statistical differences (ANOVA, $P < 0.001$) in mean M_r were detected among pre- and post-periods. The curve in (b) post-Asian carp was fitted by: $y = 0.984 - 0.004x_1 - 0.01x_2$.

significantly declined over time (year; x) on La Grange Reach ($y = -1.9783x + 31.41$; F -test, d.f. = 1,11, $P < 0.001$).

Gizzard shad and bigmouth buffalo body condition (y) was inversely correlated with ln transformed commercial harvest (x ; kg) of Asian carps. Gizzard shad and bigmouth buffalo body condition declined significantly with increases in commercial harvest of Asian carps (gizzard shad $y = 1.075 - 0.011\ln x$; F -test, d.f. = 1,13, $P < 0.01$; bigmouth buffalo $y = 1.063 - 0.009\ln x$; F -test, d.f. = 1,13, $P < 0.001$). Ln transformed Asian carp commercial harvest

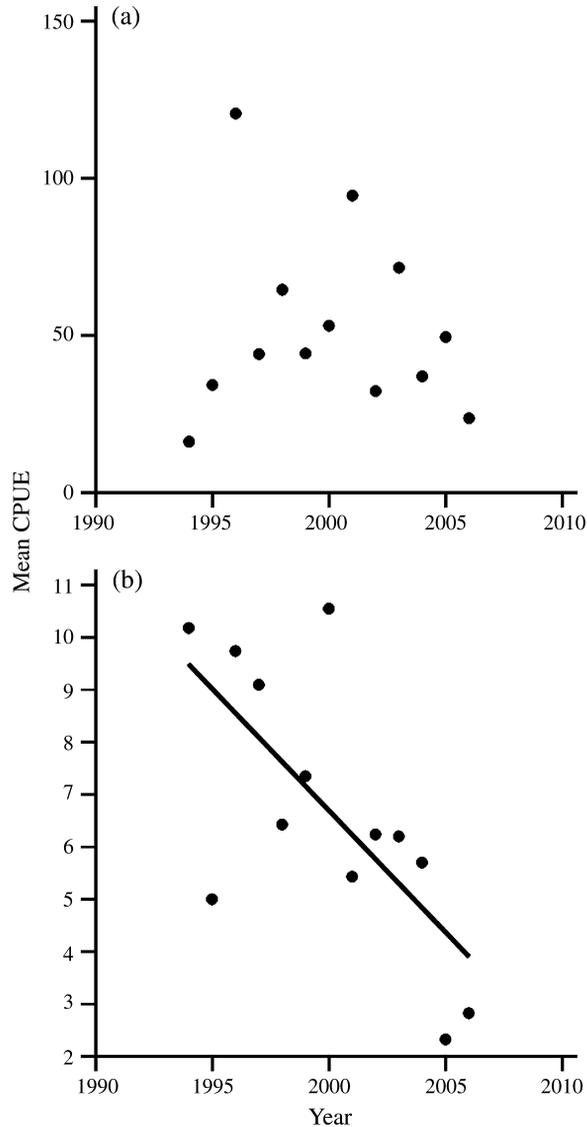


FIG. 5. Mean catch per unit effort (CPUE) of (a) gizzard shad and (b) bigmouth buffalo from La Grange Reach, Illinois River autumn electrofishing from the Long-Term Resource Monitoring Program from 1994 to 2006. (b) The curve was fitted by: $y = -0.4651x + 9.9528$ ($r^2 = 0.43$).

explained 41 and 70% of the variability in gizzard shad and bigmouth buffalo body condition, respectively.

ALTERNATIVE PREDICTORS OF BODY CONDITION

No additional abiotic or biotic predictor variables explained a statistically significant amount of variation in mean gizzard shad or bigmouth buffalo body condition after the Bonferonni corrected α was applied, except for a year effect, which is consistent with the analyses described above. Gizzard shad body condition (y) declined significantly from 1983 to 2006 (x , year) (gizzard shad $y = 9.849 - 0.004x$; F -test, d.f. = 1,18, $P < 0.05$). Bigmouth buffalo body condition declined significantly from 1983 to 2006 (bigmouth buffalo $y = 11.166 - 0.005x$; F -test, d.f. = 1,17, $P < 0.001$).

DISCUSSION

Increases in the numbers and biomass of Asian carps on La Grange Reach, Illinois River, are consistent with other successfully invading exotic species population dynamics. In general, exotic species abundances and biomass often peak quickly following establishment and later cycle about a level commensurate with the carrying capacity of the system (Roughgarden, 1998). Significant linear and exponential increases in silver carp numbers and biomass were observed over time, respectively. The observed trend in silver carp abundances and statistically stable abundances in bighead carp were probably underestimates of true population abundances and biomass due to inefficiencies of LTRMP sampling gears. LTRMP gears are biased towards smaller fishes and bighead and silver carps are elusive and often avoid LTRMP gears. For example, the great jumping ability of silver carp makes capture by electrofishing difficult, whereas trammel nets (the most effective gear for catching bighead carp) are no longer used in LTRMP protocols. Commercial fishers using trammel nets routinely catch >11 360 kg of bighead and silver carps per day on La Grange Reach. Commercial fishers reporting of annual catches, combined with low market prices and no evidence of catch declines, further support continued increases of Asian carps numbers and biomass within La Grange Reach. Based on LTRMP trends in silver carp and overall commercial landings of Asian carps, the present results suggest that Asian carps numbers and biomass are at high levels on La Grange Reach, Illinois River, which may have negative effects on native filter feeding fishes.

Indeed, gizzard shad and bigmouth buffalo body condition declined significantly after the invasion of Asian carps in La Grange Reach. Further, the rate of decline in condition after 2000 was greater for both species compared to the pre-invasion time period. Although results of the analysis of condition (post-establishment) for gizzard shad was less conclusive, bigmouth buffalo M and L_T relationships declined significantly in each year following the Asian carps invasion. In contrast, condition of gizzard shad increased in recent years. This observation is probably due to 2002 showing the lowest overall body condition for gizzard shad in the time series and the greater statistical power to detect effects due to increases in sample sizes in recent years. Nevertheless, condition

of gizzard shad in 2002 was the lowest on record for La Grange Reach and overall body condition of gizzard shad was significantly less following the Asian carps invasion.

Alternative abiotic and biotic variables known to influence fish condition did not explain significant variation in gizzard shad or bigmouth buffalo condition. For example, water quality (*e.g.* turbidity and conductivity), annual river conditions (*e.g.* temperature and discharge), predator–prey interactions (predator CPUE) and primary productivity (*e.g.* chlorophyll *a* and total P) indicated no co-varying trends that would account for reduced condition. Density-dependent processes also did not appear responsible for the observed declines in gizzard shad and bigmouth buffalo condition. Given trends in abundance of gizzard shad and bigmouth buffalo over time, stable or increased condition would have been expected if density-dependent processes were occurring in each species, respectively. Besides a year effect, gizzard shad and bigmouth buffalo condition was only negatively correlated to commercial landings of Asian carps in the Illinois River. Although there is no evidence to support direct competition (*e.g.* food limitation in the Illinois River) among native planktivores and Asian carps, these results suggest that Asian carps have negatively affected gizzard shad and bigmouth buffalo growth in La Grange Reach.

The results of this study provide multiple lines of evidence to suggest negative effects of Asian carps on native filter feeding bigmouth buffalo and gizzard shad on La Grange Reach, as reflected by declines in body condition. Interspecific competitive effects of Asian carps on native food webs are generally observed through direct competition with native planktivores for limiting plankton resources (Lu *et al.*, 2002). The high abundances and extreme filtering efficiencies of Asian carps may make them competitively superior to native filter feeding fishes on La Grange Reach. For example, Schrank *et al.* (2003) reported that age 0 year bighead carp were competitively superior to native age 0 year paddlefish in mesocosm experiments. Unfortunately, paddlefish are rarely collected in La Grange Reach ($n = 6$, LTRMP 1990–2006) and could not be included in this study.

Because of similarities in diet composition among Asian carps and native planktivores (*e.g.* paddlefish, gizzard shad and bigmouth buffalo), interspecific competition among species is likely (Sampson, 2005). Gizzard shad and bigmouth buffalo are planktivorous; however, both have the tendency of feeding at or near the bottom of the water column as evidenced by occasional detritus found in the gut (Becker, 1983; Pflieger, 1997). These findings may suggest that bigmouth buffalo on La Grange Reach are competitively inferior to both gizzard shad and Asian carps if plankton resources are limited in the Illinois River. Bigmouth buffalo exhibited more pronounced and frequent declines in condition following Asian carp establishment. Gizzard shad also appear to be competitively inferior to the Asian carps but may display less pronounced effects on body condition due to diet plasticity (*i.e.* the potential to incorporate detritus in their diet more readily). Ultimately, declines in body condition may decrease potential fitness and the long-term sustainability of gizzard shad, bigmouth buffalo and other native riverine fishes. For example, decreases in condition may lead to declines in fecundity because egg production generally scales exponentially with mass (Murphy & Willis, 1996). Decreases in condition have

been linked with poor annual year class strength in gizzard shad (Willis, 1987). Furthermore, a 5% decline in gizzard shad condition has been shown to reduce fecundity 1–5% (Kilambi & Baglin, 1969). Reduced condition may also lead to poorer health and increase susceptibility to diseases (Anderson & Neumann, 1996). Therefore, the observed and continued declines in condition of gizzard shad and bigmouth buffalo may not only imply interspecific competition for food resources with Asian carps but also the potential for long-term decreases in fitness and associated reproductive potential if direct competition is occurring and plankton resources are limited.

This study presents preliminary evidence of ecosystem-scale, negative effects of feral bighead and silver carps on native fish species in the U.S. Because these negative effects are strongly linked to Asian carps densities and biomass, population reduction is paramount. Population reductions may occur naturally over time as Asian carps approach carrying capacities of invaded systems; however, proactive management through a better understanding of the Asian carps biology as invaders, development of additional markets for Asian carps consumption and technologies to reduce spread (*e.g.* sound-bubble and electric barriers) should be explored. Future research should also provide accurate estimates of Asian carp abundances, test for plankton limitation in Asian carps invaded systems and examine potential mechanistic competitive interactions among Asian carps and fish species that rely on plankton resources solely or at particular life stages.

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