Strong Reductions in Bigheaded Carp Size at Age Accompany Increasing Population Densities

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ABSTRACT

Since their arrival in the 1990s, invasive bighead carp (*Hypophthalmichthys nobilis*) and silver carp (*Hypophthalmichthys molitrix*) have attained exceptional population densities and growth rates in the Illinois River. Standardized monitoring encompassing the duration of the invasion provides a rare opportunity to examine changes in the size distribution of age-0 and adult (age-3+) cohorts as biomass expanded dramatically. Biomass of bigheaded carps sampled expanded 150-fold, from just over 3,000 kg in 2000 to over 490,000 kg in 2013. Over the period of invasion, size distributions within both age-0 and adult cohorts have consistently fallen as population densities increased, strongly implying constraints on individual growth rates. Between 2000 and 2014, the mode of total lengths of age-0 bigheaded carps fell by 67%, whereas the 50th and 75th percentiles of adult silver carp lengths declined by 25%. Declines in zooplankton abundance and native planktivore condition suggest density-dependent competition for food likely has driven the decline in the size at age for both age groups. The trends observed in this study may provide useful information on how size distributions can vary across densities, particularly during the exponential growth phase of invasions.

INTRODUCTION

Invasive species can sometimes reach exceptional population densities. At high densities, competition among individuals can limit food resources, causing decreased individual growth rates and reduced body condition, in some cases leading to population crashes (Elton 1958; Simberloff and Gibbons 2004; Cooling et al. 2012). Studying the dynamics of invasive species may provide useful information for targeted management of their populations. However, there are relatively few long-term records of the arrival, establishment, and rapid expansion of a large population of invasive fish with which to explore density related constraints on population dynamics (Garcia-Berthou 2007; but see Trexler et al. 2000 and Bøhn et al. 2008).

Bighead carp (*Hypophthalmichthys nobilis*) and silver carp (*H. molitrix*; hereafter referred to collectively as bigheaded carps) are examples of invasive species that have spread rapidly across the Mississippi River Basin, setting off a cascade of interactions (Jennings 1988; Chick and Pegg 2001; Lu et al. 2002; Sampson et al. 2009). Bigheaded carps arrived in the Illinois River, a highly productive tributary to the Mississippi River, in the mid-1990s and subsequently achieved among the highest recorded population densities anywhere in the global range of either species (McClelland et al.2012; Sass et al. 2010; MacNamara et al. 2016). One of the keys to the success of bigheaded carps as invasive fishes is their ability to switch between zooplankton, phytoplankton, and detritus as food resources, and the rapid increase of bigheaded carp populations has dramatically reduced zooplankton abundance in the Illinois River (Sass et al. 2014).

Studies in the Illinois River during the period of bigheaded carps invasion have documented rapid and significant changes in the fish assemblage structure, consistent with the idea that bigheaded carps are competing with native species (Solomon et al. 2016). Specifically, the bigheaded carps invasion coincided with declining condition of co-occurring native planktivores like gizzard shad (*Dorosoma cepedianum*) and bigmouth buffalo (*Ictiobus cyprinellus*) (Irons et al. 2007; Pendleton et al. 2017). Alternatively, studies from the Wabash River, where populations of bigheaded carps are substantially lower, suggest native planktivores have declined for reasons unrelated to competition with bigheaded carps (Pyron et al. 2017). However, silver carp captured in 2011 in the Illinois River displayed reduced growth and length-at-age relative to silver carp in the Wabash River, potentially due to the higher density of silver carp in the Illinois River (Stuck et al. 2015). Despite documented interspecific effects, few studies have looked at whether competition between silver carp and bighead carp, or within the same species, may also affect their populations.

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The population increase of bigheaded carps in the Illinois River is remarkably high even compared to other aquatic invasive species in the Midwestern U.S. A recent estimate considered the intrinsic rate of increase for silver carp to be several times that of rainbow smelt (*Osmerus mordax*) or rusty crayfish (*Orconectes rusticus*) (Sass et al. 2010). The explosive population growth of bigheaded carps may have led to greater competition, and therefore reduced growth. Reductions in both zooplankton abundance and body condition of native planktivorous fishes are consistent with the idea of increased competition after bigheaded carp arrival. We tracked changes in the population size structure using a standardized monitoring program to test whether bigheaded carps have experienced reductions in size distributions, potentially from congeneric competition (i.e., competition within the genus *Hypophthalmichthys*). The data from the monitoring program allowed us to estimate changes in the size distribution for bigheaded carps from the initial appearance of reproducing individuals to the point at which they have become one of the most abundant species captured. Our objective was to use 15 years of data from a standardized monitoring program to assess how the size structure of the age-0 bigheaded carps and adult (age-3+) silver carp population changed in concert with increasing densities. We use changes in the size distribution to make inferences about growth rates of bigheaded carps in different age classes.

METHODS

Study Area and Sampling. The La Grange Reach of the Illinois River, part of the lower Illinois River, flows through a broad floodplain inherited from a pre-glacial path of the Mississippi River (Figure 1). This 125 km reach stretches from the La Grange Lock and Dam (river km 129) to the Peoria Lock and Dam (river km 254) and is a mosaic of main channel, side channel, and backwater (both contiguous and semi-contiguous) habitats. Throughout the reach, there are varying degrees of connected and semi connected flood-
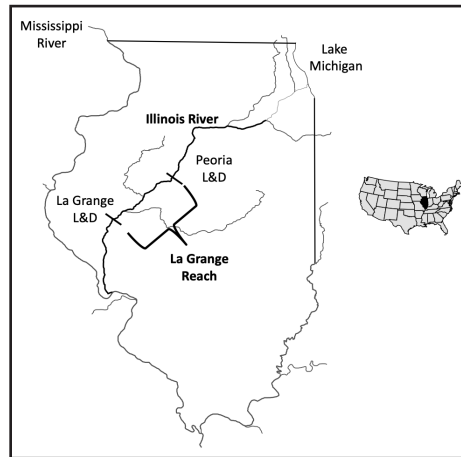

Figure 1. Map of the La Grange Reach of the Illinois River.

plain habitats.

The U.S. Army Corps of Engineers' Upper Mississippi River Restoration Program Long Term Resource Monitoring element (LTRM) has been using standardized methods and effort to sample the La Grange Reach since 1993. Implemented by a partnership of the U.S. Army Corps of Engineers, the United States Geological Survey and the five Upper Mississippi River states (Illinois, Iowa, Minnesota, Missouri, and Wisconsin), the LTRM monitors the fish community using a stratified random sampling design to encompass major riverine habitat strata (i.e. main channel, side channels, and backwaters).

To sample the overall fish community based on species-habitat relationships, LTRM sampling used multiple gears (day electrofishing, trawling, and netting using fyke, mini-fyke, and hoop nets; Ickes et al. 2014; Ratcliff et al. 2014). The combination of gear types used by the LTRM provided coverage of all ages of bigheaded carps, including age-0. Stratified random sampling on the La Grange Reach was supplemented by fixed site sampling at the Peoria Lock and Dam tailwater zone (river km 254) and in Bath Chute, a side channel at river km 182. Samples were collected from June 15th to October 31st of each year in three sequential periods of equal duration, with

effort distributed equally across the field season and consistently by gear type, facilitating comparisons of size distributions over time (Table 1). Total lengths (TL) of fish were measured for all fish during all three sampling periods. In 2005 and 2006, sampling did not occur during the first one-third of the sampling season for reasons unrelated to river conditions, but this is the only meaningful change that has occurred. Additional details of the LTRM protocols can be found in Gutreuter et al. (1995) and Ratcliff et al. (2014). All data used in the analysis are available for download through the U.S. Geological Survey's Long Term Resource Monitoring Element (LTRM 2016). All data used in this analysis are available in an online data depository (see Supporting Information).

Data Analysis. To provide an estimate of how competition for food has increased from 2000 to 2014, we calculated the biomass of bigheaded carps sampled across all gears in LTRM sampling. The amount of effort across this time was essentially constant, with the exception of a reduction of effort by one-third in 2005 and 2006 (Table 1).

The standardization of the sampling program allows for a straightforward evaluation of population size structure (Gutreuter et al. 1995; Ratcliff et al. 2014). We did not examine the size structure of bigheaded carps prior to 2000 because the first evidence of successful spawning in the La Grange Reach occurred in 2000. Only nine bigheaded carps were captured in LTRM sampling prior to 2000. Previous research on bigheaded carps in the La Grange Reach of the Illinois River highlighted a trend of strongly episodic recruitment: more than 99.9% of all age-0 bigheaded carps from 2000-2014 occurred in four cohorts: 2000, 2004, 2007-2008, and 2014 (Gibson-Reinemer et al. 2017). We used this pattern of a population dominated by cohorts produced several years apart as the basis for further exploration of trends in bigheaded carps size distributions over time.

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We conducted two separate analyses of bigheaded carps size distributions. In the first, we examined age-0 bigheaded carps, which included both bighead carp and silver carp. In the La Grange Reach of the Illinois River, a recent study estimated a hybridization rate of 39% for silver carp and bighead carp, and hybrids cannot be distinguished on the basis of morphology (Lamer et al. 2015). Therefore, we did not attempt to distinguish between the two species in the age-0 analysis, but we used field identification of silver carp for the analysis of adult fish. As adult bighead carp are known to grow to larger adult sizes than silver carp, omitting bighead carp from the analysis reduces the possibility that changes in the abundance of bighead carp would introduce a bias in the analysis of size distributions over time.

Age-0 analysis. We used known information on bigheaded carps size-at-age and the extensive field sampling of the LTRM to identify age-0 fish. Previous research identified a size limit of 200 mm TL as a threshold for assigning age-0 based on length (Chick et al. 2013). Although estimates of fish age through otoliths or other structures would have been ideal, we are unaware of any dataset containing such information for bigheaded carps across the 15 years of our study period. Instead, we used length-frequency analysis to identify age-0 fish. The length-frequency method has been used to assign ages to fish for over a century, but it is generally used to make distinctions among only a few age-classes when species are fast-growing (Isely and Grabowski 2007), which the conditions in this study met. For the age-0 analysis, we chose to use the modal length, as this is a common metric for length-frequency analysis (Busacker et al. 1990, Shoup and Michaletz 2017).

Several features of the study design and bigheaded carps biology enabled us to use the length-frequency method with confidence. First, bigheaded carps grow quickly, commonly achieving lengths of 200 mm within several months of hatching (Irons et al. 2011;

Table 1. Distribution of sampling effort across and within years for the sampling gears used by LTRM sampling that are most effective at capturing bigheaded carp in the La Grange Reach of the Illinois River from 2000 to 2014. The number of day electrofishing samples, mini fyke nets samples, and fyke net samples in each period of each year are listed. P1, P2, and P3 refer to period 1, period 2, and period 3 of LTRM sampling, respectively.

Year	Day electrofishing			Mini fyke nets			Fyke nets		
	P1	P2	P3	P1	P2	P3	P1	P2	P3
2000	41	42	42	29	29	30	14	13	14
2001	42	42	42	30	30	30	14	14	14
2002	42	42	42	30	30	30	14	14	14
2003	40	40	40	28	28	28	12	12	12
2004	40	40	40	28	28	28	12	12	12
2005	0	40	40	0	28	28	0	12	12
2006	0	40	40	0	28	28	0	12	12
2007	40	40	40	28	28	28	12	12	12
2008	39	40	40	28	27	28	12	12	12
2009	40	40	40	28	28	28	12	12	12
2010	40	40	40	28	28	28	12	12	12
2011	40	40	40	28	28	28	12	12	12
2012	40	41	40	28	28	28	12	12	12
2013	40	40	39	28	28	28	12	12	12
2014	40	40	40	28	28	28	12	12	12

Chick et al. 2013). As such, age-1 fish are distinctively larger than young age-0 fish, creating a large size gap between age-0 fish and older age classes. Second, bigheaded carps can be captured at lengths of 10 mm using mini-fyke nets (and less commonly, day electrofishing) in LTRM sampling. The LTRM sampling also extended across four-and-a-half months of the growing season, so we were able to track the appearance of small (typically 30 mm TL or shorter) bigheaded carps as they grew over the course of the summer. Third, previous research on bigheaded carps on the La Grange Reach of the Illinois River showed that, in the four cohorts producing the vast majority of age-0 bigheaded carps, recruitment was clustered in short, discrete spawning events (Gibson-Reinemer et al. 2017). The large cohorts of bigheaded carps are linked to large floods that occur during warm months, creating conditions favorable for spawning and larval survival (Gibson-Reinemer et al. 2017). Catches of at least 1,000 age-0 fish occurred in only four years: 2000, 2007, 2008, and 2014. We excluded analysis of age-0 carp in 2007 because

most of these fish were the result of a spawning event that occurred in September, approximately three months later than in other years. The years 2000, 2008, and 2014 contained 94% of all age-0 bigheaded carps captured between 2000 and 2014. Therefore, we used fish lengths to identify age-0 fish in only three years (2000, 2008, and 2014) under conditions that reduced the possibility of mistakenly including older age classes (Table 2). Size distributions of bigheaded carps in the La Grange Reach also have previously been used to identify distinct year classes on the basis of length-frequency analysis (Irons et al. 2011).

To estimate how the size structure of bigheaded carps changed with increasing density and biomass of potential congeneric competitors, we examined the size distributions of age-0 bigheaded carps at the end of the growing season in 2000, 2008, and 2014. We used data from mini-fyke nets and electrofishing to reduce the gear bias associated with any single gear. For instance, in the LTRM sampling, mini-fyke nets tended to be more effective at capturing smaller age-0 fish, whereas

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Table 2. Descriptions of the abundance of different cohorts used to estimate the size structure of adult (age-3+) bigheaded carp sampled by the LTRM in the La Grange Reach of the Illinois River, as well as the numbers of age-0 bigheaded carp sampled in the years following large cohorts.

Cohort	Number of age-0 fish in cohort	Year sampled	Age-0 fish collected in intervening years
2000	1,057	2003	57 (2001-02)
2003-04	874	2007	48 (2005-06)
2007-08	93,500	2011	54 (2009-10)
2007-08	93,500	2014	783 (2011-13)

day electrofishing tended to be more effective at capturing large age-0 fish; by combining these two gears, we reduced the gear bias associated with any single gear. As our analysis was based on estimating changes in size structure, not catch per unit effort (CPUE), combining mini-fyke nets and day electrofishing samples reduced size bias associated with a single gear without introducing problems associated with combining gears for CPUE estimates.

In each of the years 2000, 2008, and 2014, we selected one week of LTRM sampling that best combined two criteria: providing a reasonably large sample size (>30 individuals) and occurring within a comparable time frame across years (between weeks 39 and 42 of the year). We quantified differences in size across years using Kolmogrov-Smirnov comparisons in R (ks.test; R Core Development Team 2017).

To control for the possibility that differences in age-0 sizes were caused by different hatch dates or different water temperatures across years, we examined both of these factors. Small bigheaded carps (typically 20 mm TL) were captured in 2000, 2008, and 2014, and we used a growth equation derived from silver carp on a nearby section of the Mississippi River to estimate their hatch date. Hatch dates calculations were based on mean length at emergence (6 mm TL) and a daily growth rate of 2.24 mm, from growth estimates for age-0 silver carp validated by daily otolith circuli (Michael Wolf, Minnesota Department of Natural Resources, personal communication). To examine whether water temperatures varied meaningfully across years, we calculated mean weekly water temperatures from June through October in 2000, 2008, and 2014. Water temperatures were collected in LTRM sampling us-

ing a stratified random sampling design (Ratcliff et al. 2014).

Age 3+ analysis. To identify cohorts of age-3+ silver carp, we relied on the length frequency analysis and patterns of recruitment in previous years. For these adult fish, we used only silver carp to avoid any differences in adult size between species from confounding our analysis. In this part of the analysis, we assessed changes in all fish age-3 or older. We pooled data across gears and plotted total lengths of fish across years to examine trends in the size structure and apparent recruitment across years. We selected three sampling years in which we could distinguish age-3+ fish from younger cohorts with confidence: 2003 (the 2000 cohort), 2007 (the 2003-2004 cohort), and 2011 (the 2007-2008 cohort). There was a relatively large number of age-0 fish captured in both 2003 and 2004, so we combined the two for the purposes of age assignment and conservatively assigned all fish from these two years to 2004. This procedure was conservative in the sense that it could have underestimated the age of fish (e.g., by mistaking an age-4 fish for an age-3 fish), thereby underestimating reductions in size distribution over time rather than overestimating the reduction in size. A similar pattern occurred in 2007 and 2008, and we also conservatively assigned all fish from this cohort to the 2008 year class.

To establish confidence in age-3+ assignments, we examined how many age-0 fish were captured in the two years after a cohort's emergence. For instance, in the 2000 cohort, we compared the number of age-0 fish in 2000 to the number captured in 2001 and 2002, accounting for survey effort between years (Table 1). When the cumulative number of age-0 fish produced in the two years after a cohort was

minimal relative to the cohort (<10%), we concluded recruitment in the intervening years was not contributing substantially to our analysis.

To compare the size distributions of age-3+ silver carp over time, we used the 2000 cohort (sampled in 2003), 2004 cohort (sampled in 2007), and 2008 cohort (sampled in 2011). We also examined the size of silver carp captured in 2014, which we identified as primarily composed of fish from the 2008 cohort. We were reasonable confident that adult silver carp sampled in 2014 were at least six years old because the cumulative number of age-0 fish captured between 2009 and 2013 was two orders of magnitude lower than the number of age-0 fish produced in 2007-2008. We included all silver carp over 300 mm TL to eliminate the possibility that younger cohorts might confound the analysis. As with age-0 fish, the standard level of sampling effort in 2003, 2007, 2011, and 2014 (Table 1), as well as the fact that we are not measuring CPUE, provided a way to reduce gear-related size bias to estimate population size structure.

RESULTS

In 2000, 1,216 bigheaded carps were captured, including the first instance of hundreds of small (≤ 30 mm TL) bigheaded carps recorded in the La Grange Reach. From 2000 to 2014, LTRM sampling collected 202,538 bigheaded carps, which tended to occur in noticeable cohorts (Figure 2). Of the 195,127 age-0 bigheaded carps captured across 15 years, 193,277 (>99%) occurred in three cohorts (2000, 2007-2008, and 2014; Table 3). Within years in which strong recruitment occurred, we could track the emergence and growth of age-0 bigheaded carps across weeks and reliably distinguish them from older age-classes (Figure 3). The two years immediately following the cohorts of 2000, 2003-2004, and 2007-2008 never had more than 5.5% of the abundance of age-0 fish collected in the stronger year classes.

Estimated hatch dates were nearly identical across years: day 186 in 2000, day 182 in 2008, and day 186 in 2014.

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Weekly water temperatures were also similar across the three years, and stayed within the optimal range for age-0 silver carp growth (26 °C – 30 °C; Kolar et al. 2005) for most of the growing season (Figure 4).

There were strong interannual differences in the size distribution of age-0 bigheaded carps at the end of their first growing season (Figure 5). The reductions in size distribution occurred as the biomass of bigheaded carps sampled under standard methods increased from approximately 3,000 kg in 2000 to approximately 490,000 kg by 2013 (all data used in the analysis are available in supplementary data files). The mode of total length for age-0 fish at the end of the growing season decreased from 200 mm in 2000 to 100 mm in 2008 to

60 mm in 2014. The size distributions of age-0 were significantly different between 2000 and 2008 (D=0.7025, p < 2.2x10^{-16}) and between 2008 and 2014 (D=1, p < 2.2x10^{-16}), with modal total lengths in each successive year smaller than the previous.

Reductions in the size distribution of age-3+ fish were also substantial (Table 4). Between 2003 and 2011, the total length of age-3+ silver carp in the 50th percentile decreased by 25% from 640 to 480 mm, and fish in the 90th percentile decreased by 25% from 710 to 520 mm. In addition, the 50th percentile of putative age-6+ fish in 2014 was smaller (550 mm) than the 50th percentile for age-3+ fish in 2003 and 2007 (640 and 590 mm, respectively).
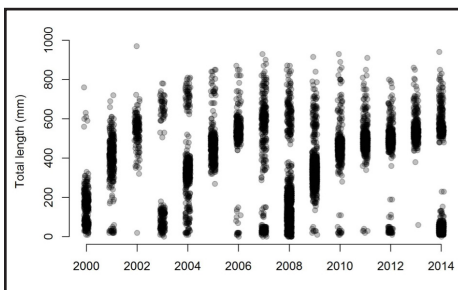

Figure 4. Mean weekly water temperature in the La Grange Reach of the Illinois River in 2000, 2008, and 2014.

Figure 2. Total lengths of individual bigheaded carp sampled on the La Grange Reach of the Illinois River from 2000 to 2014. Each symbol indicates an individual fish. The x-axis has been jittered to avoid overplotting. The source of the data in this figure is the same as in Gibson-Reinemer et al. (2017).

Table 3. Number of age-0 bigheaded carp captured in sampling from 2000-2014 using electrofishing and mini-fyke nets.

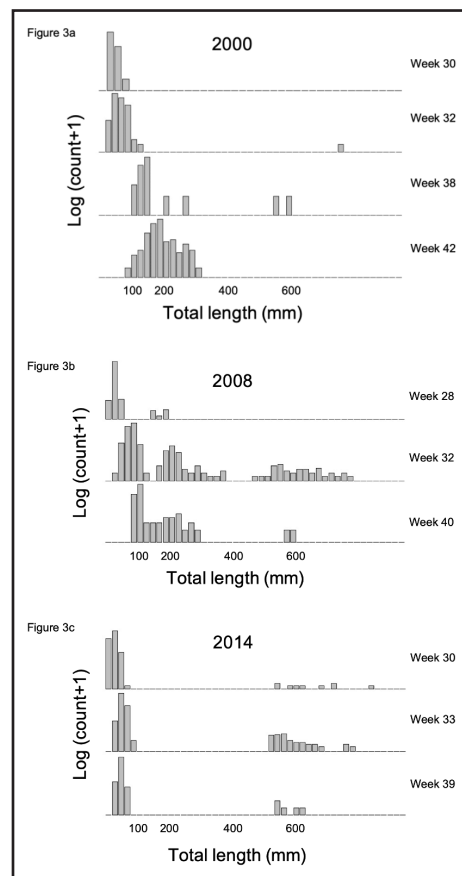| Year	Number Captured
2000	1,086
2001	56
2002	1
2003	647
2004	227
2005	0
2006	48
2007	10,706
2008	82,794
2009	43
2010	21
2011	24
2012	782
2013	1
2014	98,691

Figure 3. Length-frequency histograms of the size distributions of bigheaded carp collected in different weeks of 2000 (a), 2008 (b), and 2014 (c). Counts of fish in each group have been log-transformed to enhance the visibility of large size classes, which are less abundant.
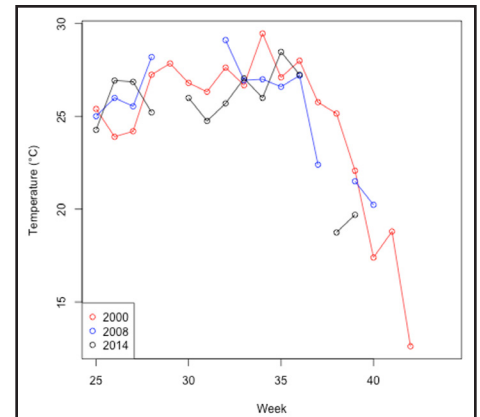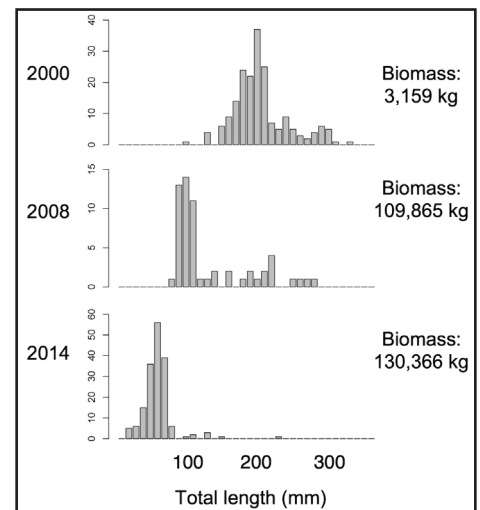

Figure 5. Length-frequency histograms of the size distribution of age-0 bigheaded carp collected during a one-week period at the end of the growing season in 2000 (n = 190 fish captured in week 42), 2008 (n = 59 fish captured in week 40), and 2014 (n = 171 fish captured in the week 39).

DISCUSSION

The standardization of the LTRM sampling program and fortuitous spacing of dominant year classes of bigheaded carps provided nearly ideal conditions for examining how increasing congeneric densities may have affected growth. The three cohorts we analyzed for age-0 size-at-age were hatched within 4 calendar days and experienced optimal growing temperatures, holding temperature and the length of the growing season essentially constant across years; however, congeneric

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Table 4. Total length (mm) percentiles of adult silver carp (over 300 mm) captured in 2003, 2007, 2011, and 2014 in the La Grange reach of the Illinois River. The 2003, 2007, and 2011 fish are likely dominated by age-3+ individuals. The 2014 fish are estimated to be predominantly age-6+ from the

Estimated age	Year sampled	50th percentile	75th percentile	90th percentile	95th percentile
3+	2003	640	661	710	721
3+	2008	590	630	660	709
3+	2011	480	500	520	550
6+	2014	550	580	650	690

biomass increased 100-fold during the same interval. Additionally, plankton samples collected before and after bigheaded carps establishment showed a decrease of 90% to 96% in preferred zooplankton densities following the establishment of bigheaded carps (Sass et al. 2014, DeBoer et al. 2018). In other reaches of the Illinois River, bigheaded carps appear to show increased relative weight in response to increasing harvest, suggesting they are being released from congeneric competition (Coulter et al. 2018). Together, these results provide evidence that size-at-age of bigheaded carps have declined substantially as a result of increased congeneric competition.

Temperature is commonly the single most important factor regulating the growth of fish (Neuheimer and Taggart 2007). In this study, temperatures varied little across years and remained within a range that is optimal for growth in bigheaded carps. In contrast, the density of congeneric competitors increased dramatically across the study years and the most valuable prey for bigheaded carps decreased substantially. Under these conditions, temperature is unlikely to be responsible for differences in size distributions of age-0 fish. Non-thermal factors affecting growth rates of age-0 fish are sometimes only apparent when temperatures are suitably warm (e.g., Mills et al. 1989), and this appears to have been the case in the present study. Changes in the physical structure of the river channel, such as increased sedimentation (Fritts et al. 2017), have been occurring over the study period and may have contributed to the change in size distribution of bigheaded carps. However, the years in which recruitment was high had large floods, greatly expanding shallow, nutrient-rich areas for larval and juvenile fishes and providing similar habitat conditions across the years of the study.

This study presents a rare opportunity to examine the influence of congeneric density on size at age because congeneric densities varied so widely while temperatures were so similar. Although the data we analyzed was from invasive species, the relative influence of congeneric competition should allow comparisons to a wide range of temperate, freshwater fishes. Therefore, the magnitude of the reductions in size at age may be useful in predicting ecological outcomes for other invasive species, as well as changes that occur in native species experiencing changes in biomass (e.g., from climate change).

While the size distribution of a year class can vary from year to year, we observed a steady directional change over time that accompanied sharply rising congeneric biomass. The mode of total lengths of age-0 bigheaded carps at the end of the growing season fell by 67% between 2000 and 2014. In comparison, age-0 striped bass *Morone saxatalis* lengths fell by 35.2% when densities increased approximately 25-fold (Martino and Houde 2012). Typically, reductions in growth during the first year caused by competition are more modest for freshwater fish that are largely planktivorous (Michaeletz 1998, Mills et al. 1989). The relatively large reduction in age-0 size distributions was likely caused because the dramatic increase in biomass documented for bigheaded carps in the La Grange Reach was unusual. The higher population densities of silver carp in the Illinois River was suggested as a likely cause of their reduced size relative to silver carp in the Wabash River (Stuck et al. 2015), which is consistent with the decline in size distributions over time in the present study.

Although some of the variation in age-0 lengths can be attributable to the fact that they were sampled in different weeks in different years, this can only account for a small portion of the difference among years. Our samples of age-0 fish collected in week 42 in 2000, week 40 in 2008, and week 39 in 2014. It is implausible to suspect a 60 mm fish captured in September of 2014 would attain a length of 200 mm (the mode of age-0 fish in 2000) if it was sampled three weeks later. Similarly, the disparities in age-0 lengths cannot be attributed to differences in their emergence earlier in the year. Estimated hatch dates for bigheaded carps were similar across years in which age-0 size structure was assessed, with all three falling within a 4 day window (day 182 to186).

Because we could not distinguish between the 2007 and 2008 cohorts based on size, we combined them for the purposes of our analysis. However, it is possible that some of the larger putative age-0 fish in 2008 (the right tail of the 2008 histogram in Figure 4) are actually age-1 fish from 2007. The vast majority of age-0 fish captured in 2007 came after a flood in September, unusually late in the year. If a substantive number of what we identified as age-0 fish in 2008 were in fact age-1 fish from 2007, this would overestimate the size distribution of age-0 fish and therefore underestimate the reduction in size distributions. There was some evidence that bigheaded carps spawned again later in the summer of 2008, producing the individuals in the far left end of the histogram (Figure 4); however, the number fish caught using the same amount of effort was smaller, so these fish would not affect the modal size.

Since bigheaded carps began to reproduce in the La Grange Reach of the Illinois River in 2000, there is little evidence to suggest density-dependent mortality or interference with recruitment has constrained their abundance. The number of age-0 fish collected in standardized sampling in 2014 (98,691) was greater than the combined number of age-0 fish that had been captured in all previous years, suggesting the pop-

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ulation is continuing to grow. However, there is clear evidence that the high populations of bigheaded carps have reduced the size distributions of both juveniles (age-0) and adults (age-3+). The fact that bigheaded carps abundance appears to keep increasing despite reduced size of individuals suggests congeneric competition has not reached a level capable of constraining population growth.

We relied on the pattern of distinct year classes evident in Figure 2 to compare adult lengths. In addition to the visually intuitive evidence of cohorts, we quantified the number of age-0 fish captured in the years following those with large numbers of age-0 fish. In no case did the number of age-0 fish captured in the two years following a large cohort exceed 6% of the total numbers caught in the preceding year. In other words, we acknowledge some recruitment potentially occurred in every year, but the contributions these small cohorts made were negligible. Our analysis of the changes in the size distribution of age-3+ fish therefore does not rely on a single measure of central tendency but rather percentile values, which are more descriptive of the distribution of sizes. All of the percentiles listed in Table 4 (the 50th, 75th, 90th, and 95th) show reductions over successive year classes, strongly indicating a reduction in adult size distributions over time.

The apparent lack of meaningful recruitment from 2009 to 2013 provided an opportunity to examine how adult silver carp size distributions may have declined. A large number of age-0 fish (93,500) were captured in 2007 and 2008; in contrast, from 2009-2013, the number of age-0 fish caught (847) was two orders of magnitude lower. Because the effort was essentially constant among those years (Table 1), and the difference in catch was so dramatic (two orders of magnitude), differences in catches due to effort are trivial. Therefore, the most likely scenario is that fish over 300 mm TL captured in 2014 were nearly entirely composed of fish spawned in 2008 or earlier, which would have been age-6 or older. Although these putative age-

6+ fish in 2014 were larger than the same cohort in 2011, indicating they had continued to grow over the intervening three years, the sizes of each percentile group were smaller than the age-3+ fish in 2003 and 2008. The reduction in adult size persisted even as the silver carp had several additional years to grow.

We observed strong decreases in the size distributions of bigheaded carps, and the decrease in size distributions probably reflects lower growth rates. A plausible explanation for the changes in bigheaded carps size distributions comes from trends in prey availability. More rapid growth and larger maximum size of a cohort are more likely to occur when the fish are at low densities and have abundant food. Thus, it is not surprising that bigheaded carps achieved large sizes upon arrival in an area as productive as the Illinois River, where zooplankton densities are among the highest recorded (Wahl et al. 2008). As predation on zooplankton increased as a function of increasing bigheaded carps density, the composition of zooplankton shifted. After the establishment of bigheaded carps, cladoceran densities in the La Grange reach fell by 90% and copepod densities fell by 97%, while rotifers increased by 56 % (Sass et al. 2014). The large reductions in the most energetically favorable prey, which occurred as overall zooplankton densities fell by 27% (Sass et al. 2014), accompanied sharply rising densities of bigheaded carps. It is therefore plausible that increased competition for reduced zooplankton caused the observed changes in the size distribution of bigheaded carps. Further, two native planktivores, gizzard shad and bigmouth buffalo, showed reduced population sizes and body condition accompanying the rise of bigheaded carps; although size distributions were not explicitly considered (Irons et al. 2007; Pendleton et al. 2017), this evidence is also consistent with the hypothesis of prey limitation causing reduced growth rates.

Reduced size during the first growing season does not appear to be compensated by increased growth in later

years, as indicated by the downward shift in adult length distributions over time. Unlike other fishes, which routinely undergo ontogenetic diet shifts away from plankton, bigheaded carps remain planktivorous throughout their life. Reductions in the abundance or quality of plankton would therefore have similar effects on the growth of both age-0 and adult bigheaded carps.

Interpreting length-frequency data to infer age-classes must be done carefully under biologically appropriate circumstances. Overlapping sizes of different age-classes can produce substantial uncertainty about age estimates (e.g., Macdonald and Pitcher 1979). However, the unusually clear pattern of size distributions and the vast differences in recruitment success among years makes the length-frequency method suitable for our analysis (e.g., Irons et al. 2011). We were able to track cohorts shortly after their emergence, at sizes of 30 mm TL or smaller, through the summer growing season (e.g., Figure 3). Estimating hatch dates from these small fish reduces the error involved in their estimates, as variations in growth rates or imprecision in estimates of growth rates would be magnified in larger fish relative to smaller fish. The pattern of age-0 growth within a summer and the striking gap in size between age-0 fish and older age classes provided strong evidence to assess reductions sizes of age-0 fish. Similarly, we restricted our assessments of age-3+ fish to only three instances, and this was supported by large differences in recruitment among years (Table 2).

Migration of bigheaded carps into the La Grange Reach of the Illinois River probably occurred. Otolith chemistry suggests that 61 – 89% of silver carp and 97% of bighead carp captured in the Illinois River originate within the Illinois River, indicating some immigration from nearby waters (Norman and Whitledge 2015). However, these levels of immigration into the La Grange Reach would be unlikely to have a substantial effect on our analysis. The areas most likely to provide immigrants to the La Grange Reach of the Illinois River are those closest to it, where

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trends in bigheaded carps density and congeneric competition are probably similar to the La Grange Reach.

The observed reduction in sizes of adult silver carp are unlikely to have substantial effects on their vulnerability to fish predators, but age-0 fish are much more vulnerable. At 200 mm, the modal length of silver carp at the end of summer in 2000, fish enter their first winter at a size that is beyond the gape limit of most predatory fish in the river. The same is not true for fish at 60 mm, the modal length of age-0 fish in 2014. The combination of increased densities and smaller sizes of bigheaded carps may benefit native piscivores, particularly because bigheaded carps are vulnerable for a longer period of time. An increase in shortnose gar (*Lepisosteus platostomus*) populations in the La Grange Reach was coincident with rising bigheaded carps densities (Solomon et al. 2016). This increase in shortnose gar, a species whose physiology allows them to do well in the warm, shallow habitats favored by age-0 bigheaded carps (Becker 1983), could be at least partly attributable to increased prey availability. Observations of shortnose gar among dense clusters of small bigheaded carps support the idea that they are taking advantage of this new prey resource (L. Solomon, personal observation) A similar effect was observed for native predators in Lake Erie and Lake Ontario following the invasion of round goby (*Neogobius melanostomus*) (Crane et al. 2015). However, there is evidence that largemouth bass avoid consuming silver carp in favor of native prey species (Wolf and Phelps 2017), so the trophic effects of reduced bigheaded carps sizes may only extend to certain piscivores.

The reduction in zooplankton, a key food resource, will probably be the predominant effect of increasing densities of bigheaded carps. As nearly all fish rely on zooplankton, particularly as juveniles, condition and abundance is likely to decrease for most native species as it has for bigheaded carps. The sharp increase in catch rates of bigheaded carps in the La Grange Reach may even be strong enough to reverse

a decades-long trend of increasing richness and abundance of native species (McClelland et al. 2012).

In addition to shedding light on the individual growth patterns that drive population size structure, this research also highlights the importance of long-term monitoring for understanding ecosystems (e.g., Kratz et al. 2003). It was also fortuitous to have additional studies on zooplankton in the same area (Sass et al. 2014) to provide an empirical foundation for understanding changes in the food web. Without an existing, standardized program to monitor the Illinois River, it would not be possible to document the changes in the size distribution of an important invasive species.

LITERATURE CITED

Becker GC. 1983. Fishes of Wisconsin. The University of Wisconsin Press, Madison, Wisconsin.

Bøhn T, Amundsen P-A, Sparrow A. 2008. Competitive exclusion after invasion? Biological Invasions 10: 359-368.

Busacker GP, Adelman IR, Goolish EM. 1990. Growth. Pages 363-387 in Methods for fish biology. Schreck CB, Moyle PB, editors. American Fisheries Society, Bethesda, Maryland.

Chick JH, Pegg MA. 2001. Invasive carp in the Mississippi River Basin. Science 292: 2250-2251.

Chick JH, Soeken-Gittinger LA, Ratcliff EN, Gittinger EJ, Lubinski BJ, Maher R. 2013. A decade of monitoring on Pool 26 of the Upper Mississippi River System: water quality and fish data from the Upper Mississippi River Restoration Environmental Management Program. Illinois Natural History Survey Bulletin 39: article 6.

Cooling M, Hartley S, Sim DA, Lester PJ. 2012. The widespread collapse of an invasive species: Argentine ants (Linepithema humile). Biology Letters 8: 430-433.

Coulter DP, MacNamara R, Glover DC, Garvey JE. 2018. Possible unintended effects

of management at an invasion front: reduced prevalence corresponds with high condition of invasive bigheaded carps. Biological Conservation 221: 118-126.

Crane DP, Farrell JM, Einhouse DW, Lantry JR, Markham JL. 2015. Trends in body condition of native piscivores following invasion of Lakes Erie and Ontario by the round goby. Freshwater Biology 60: 111-124

DeBoer JA, Anderson AM, Casper AF. 2018. Multi-trophic response to invasive silver carp (*Hypophthalmichthys molitrix*) in a large floodplain river. Freshwater Biology 63: 597-611.

Elton CS. 1958. The Ecology of Invasions by Animals and Plants. Methuen, London, England, 181 pp.

Fritts MW, DeBoer JA, Gibson-Reinemer DK, Lubinski BJ, McClelland MA, Casper AF. 2017. Over 50 years of fish community monitoring in Illinois' large rivers: the evolution of methods used by the Illinois Natural History Survey's Long-Term Survey and Assessment of Large-River fishes in Illinois. Illinois Natural History Survey Bulletin 41: article 1.

García-Berthou E. 2007. The characteristics of invasive fishes: what has been learned so far? Journal of Fish Biology 71: 33-55.

Gibson-Reinemer DK, Solomon LE, Pendleton RM, Chick JH, Casper AF. 2017. Hydrology controls recruitment of two invasive cyprinids: bigheaded carp reproduction in a navigable large river. PeerJ 5: e3641.

Gutreuter S, Burkhardt R, Lubinski K. 1995. Long Term Resource Monitoring Program Procedures: Fish Monitoring. National Biological Service, Environmental Management Technical Center, Onalaska, Wisconsin. LTRMP 95-P002-1, 42 pp + Appendixes A-J.

Ickes BS, Sauer JS, Rogala JT. 2014. Monitoring rationale, strategy, issues, and methods: UMRR-EMP LTRMP fish component. U.S. Geological Survey Program Report 2014-P001a, 40 pp.

Irons KS, Sass GG, McClelland MA, Stafford MA. 2007. Reduced condition factor of two native fish species coincident with invasion of non-native Asian carps in the Illinois River, U.S.A. Journal of Fish Biology 71: 258-273.

Irons KS, Sass GG, McClelland MA, O'Hara TM. 2011. Bigheaded carp invasion of the La Grange Reach of the Illinois River: insights from the Long Term Resource Monitoring Program. Pp. 31-50 in Chapman DC, Hoff MH, editors. Invasive Asian carps in North America. American Fisheries Society, Symposium 74, Bethesda, Maryland.

Isely JJ, Grabowski TB. 2007. Age and growth. Pp. 187-228 in Guy, CS, Brown, ML, editors. Analysis and interpretation of freshwater fisheries data. American Fisheries Society, Bethesda, Maryland.

Jennings DP. 1988. Bighead carp (*Hypophthalmichthys nobilis*): a biological synopsis. U.S. Fish and Wildlife, Biology Report 88(29), 57 pp.

Kolar CS, Chapman DC, Courtenay Jr. WR, Housel CM, Williams JD, Jennings DP. 2005. Asian carps of the genus *Hypophthalmichthys* (Pisces, Cyprinidae) – A biological synopsis and environmental risk assessment. Report to U.S. Fish and Wildlife Service per Interagency agreement 94400-3-0128; 175.

Kratz TK, Deegan LA, Harmon ME, Lauenroth WK. 2003. Ecological variability in space and time: insights gained from the US LTER program. BioScience 53: 57-67.

Lamer JT, Ruebush BC, Arbieva ZH, McClelland M, Epifanio JM, Sass GG. 2015. Diagnostic SNPs reveal widespread introgressive hybridization between introduced bighead and silver carp in the Mississippi River Basin. Molecular Ecology 54: 3931-3943.

Lu M, Xie P, Tang HJ, Shao ZJ, Xie LQ. 2002. Experimental study of trophic cascade effect of silver carp (*Hypophthalmichthys molitrix*) in a subtropical lake, Lake Donghu: on plankton community and underlying mechanisms of changes of crustacean community. Hydrobiologia 487: 19-31.

LTRM (Long Term Resource Monitoring Element). 2016. Graphical Fish Database Browser. http://www.umesc.usgs.gov/data_library/fisheries/graphical/fish_front.html. (Accessed 28 Jun 2016)

Macdonald PDM, Pitcher TJ. 1979. Agegroups from size-frequency data: a versatile and efficient method of analyzing distribution mixtures. Journal of the Fisheries Board of Canada 36: 987-1001.

MacNamara R, Glover D, Garvey JE, Bouska W, Irons KS. 2016. Bigheaded carps (*Hypophthalmichthys* spp.) at the edge of their invaded range: using hydroacoustics to assess population parameters and the efficacy of harvest as a control strategy in a large North American river. Biological Invasions 18: 3293-3307.

Martino EJ, Houde ED. 2012. Density-dependent regulation of year-class strength in age-0 juvenile striped bass (*Morone saxatilis*). Canadian Journal of Fisheries and Aquatic Sciences 69: 430-446.

McClelland MA, Sass GG, Cook TR, Irons KS, Michaels NN, Smith TM, O'Hara CS. 2012. The long-term Illinois River fish population monitoring program. Fisheries 37: 340-350.

Michaeletz, PH. 1998. Population characteristics of gizzard shad in Missouri reservoirs and their relation to reservoir productivity, mean depth, and sport fish growth. North American Journal of Fisheries Management 18: 114-123.

Mills EL, Sherman R, Robson DS. 1989. The effect of zooplankton abundance and body size on growth of age-0 yellow perch (*Perca flavescens*) in Oneida Lake, New York, 1975-1986. Canadian Journal of Fisheries and Aquatic Sciences 46: 880-886.

Neuhemer AB, Taggart CT. 2007. The growing degree-day and fish size-at-age: the overlooked metric. Canadian Journal of Fisheries and Aquatic Sciences 64: 375-385.

Norman JD, Whitledge GW. 2015. Recruitment sources of invasive Bighead carp (*Hypophthalmichthys nobilis*) and Silver carp (*H. molitrix*) inhabiting the Illinois River. Biological Invasions 17: 2999-3014.

Pendleton RM, Schwinghammer C, Solomon LE, Casper AF. 2017. Competition among river planktivores: are native planktivores still fewer and skinner in response to the Silver Carp invasion? Environmental Biological of Fishes 100: 1213-1222.

Pyron M, Becker JC, Broadway KJ, Etchison L, Minder M, DeColibus D, Chezem M, Wyatt KH, Murry BA. 2017. Are long-term fish assemblage changes in a large US river related to the Asian Carp invasion? Test of the hostile take-over and opportunistic dispersal hypothesis. Aquatic Sciences 79: 631-642.

Ratcliff ER, Gittinger EJ, O'Hara TM, Ickes BS. 2014. Long Term Resource Monitoring Program Procedures: Fish Monitoring. U.S. Army Corps of Engineers, Upper Mississippi River Restoration-Environmental Monitoring Program, Report LTRMP-2014-P001, 98 pp.

Sampson SJ, Chick JH, Pegg MA. 2009. Diet overlap among two Asian carp and three native fishes in backwater lakes on the Illinois and Mississippi rivers. Biological Invasions 11: 483-496.

Sass GG, Cook TR, Irons KS, McClelland MA, Michaels NN, O'Hara TM, Stroub MR. 2010. A mark-recapture population estimate for invasive silver carp (*Hypophthalmichthys molitrix*) in the La Grange Reach, Illinois River. Biological Invasions 12: 433-436.

Sass GG, Hinz C, Erickson AC, McClelland NN, McClelland MA, Epifanio JM. 2014. Invasive bighead and silver carp effects on zooplankton communities in the Illinois River, Illinois, USA. Journal of Great Lakes Research 40: 911-921.

Shoup DE, Michaletz PH. 2017. Growth estimation: Summarization. Pages 233-264 in Quist MC, Isermann DA, editors. Age and growth of fishes: principles and techniques. American Fisheries Society, Bethesda, Maryland.

Simberloff D, Gibbons L. 2004. Now you see them, now you don't! – population crashes of established introduced species. Biological Invasions 6: 161-172.

Solomon LE, Pendleton RM, Chick JH, Casper AF. 2016. Long-term changes in fish community structure in relation to the establishment of Asian carps in a large floodplain river. Biological Invasions 18: 2883-2895. DOI 10.1007/s10530-016-1180-8.

Stuck JG, Porreca AP, Wahl DH, Columbo RE. 2015. Contrasting population demographics of invasive silver carp between an impounded and free-flowing river. North American Journal of Fisheries Management 35: 114-122.

Trexler JC, Loftus WF, Jordan F, Lorenz JJ, Chick JH, Konza RM. 2000. Empirical assessment of fish introductions in a subtropical wetland: an evaluation of contrasting views. Biological Invasions 2: 265-277.

Wahl DH, Goodrich J, Nannini MA, Dettmers JM, Soluk DA. 2008. Exploring riverine zooplankton in three habitats of the Illinois River ecosystem: where do they come from? Limnology and Oceanography 53: 2583-2593.

Wolf MC, Phelps QE. 2017. Prey selectivity of common predators on Silver carp (*Hypophthalmichthys molitrix*): controlled laboratory experiments support field observations. Environmental Biology of Fishes 100: 1139-1143.