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[Note]

Growth, Fecundity, and Diets of Newly Established Silver Carp in the Middle Mississippi River

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Abstract.—The silver carp *Hypophthalmichthys molitrix* has spread throughout the Mississippi River drainage. During 2003, we determined its population status and potential impact in the middle Mississippi River (MMR), the conduit between the lower Mississippi River and the upper Mississippi, Missouri, and Illinois rivers. We quantified growth, age structure, fecundity, and diets of silver carp sampled with trammel nets and AC electrofishing in main-channel areas. Mean length at age in the MMR exceeded that of populations in Asia by as much as 26%. Individuals were typically more than 1 year old and 230 mm total length, suggesting that small, young fish were absent. Individuals in this population matured earlier (age 2) than in the species' native range. Regardless of phytoplankton variation (using chlorophyll *a* as a surrogate) and zooplankton concentration at MMR sites, phytoplankton was consistently most abundant in diets. Silver carp are finding suitable resources within the MMR, allowing individuals to grow rapidly during early life, persist as adults, and successfully disperse upstream.

Successful introductions of nonnative fishes in North America are increasing exponentially (Fuller et al. 1999). One notorious, well-established group is Asian carp (e.g., common carp *Cyprinus carpio*, bighead carp *Hypophthalmichthys nobilis*, and grass carp *Ctenopharyngodon idella*), which are now widely distributed across the United States (Rahel 2000). In the Mississippi and Missouri rivers, common carp contributed more tonnage to the commercial catch than any other fish species for 37 of 47 years of records (Pflieger 1997). While the impacts of other Asian carp remain to be seen, the likelihood of benefits to the native species is remote (Laird and Page 1996).

A member of this group, silver carp *H. molitrix*, is large bodied and omnivorous (Spataru 1977; Bitterlich 1985a, 1985b). Its native range includes several major Pacific drainages of eastern Russia south to northern Vietnam (Fuller et al. 1999). However, it has been widely introduced across the world for food. In 1973, it was introduced in Arkansas ponds (Henderson 1976) and then propagated and distributed across the state by several state and private fish hatcheries. By 1980, silver carp occurred in the public waters of Arkansas, Louisiana, and Kentucky, apparently all escapees from fish hatcheries (Freeze and Henderson 1982). This species was discovered in the Missouri River in central Missouri in 1982 (Pflieger 1997) and in the Mississippi River drainage in southern Illinois in 1983 (Burr et al. 1996). By 1999, this species occurred in at least eight states within the Mississippi River drainage (Fuller et al. 1999).

With spawning requirements similar to those of the previously established bighead carp and grass carp, it was unlikely that natural reproduction could be avoided (Burr et al. 1996). Age-0 silver carp occurred in a ditch in the Cache River, Illinois, drainage (Burr et al. 1996), providing the first evidence of successful spawning in the United States. Larval silver carp have also been captured in backwaters of Pool 25 of the upper Mississippi River (Garvey et al. 2003; Adams 2004).

How silver carp may affect native fish species in the United States is a concern (Etnier and Starnes 1993; Laird and Page 1996; Pflieger 1997; Fuller et al. 1999). Its ability to consume detritus, phytoplankton, and zooplankton, combined with its high-consumptive capacity, may negatively affect other aquatic organisms in the Mississippi River drainage. Early life stages of many fishes rely heavily on zooplankton, rendering them susceptible to competition. Further, gizzard shad *Dorosoma cepedianum*, an important forage species for waterbirds and predaceous fishes (DeVries and Stein 1990), has similar omnivorous behavior as silver carp and may be particularly vulnerable (Pflieger 1997). To determine the potential impact of silver carp, basic information about its life history and foraging is needed.

Our main objective was to quantify basic population and ecological characteristics of silver carp in the middle Mississippi River (MMR), the conduit from the lower Mississippi River, where the species was probably introduced, to the upper Mis-

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sissippi, Missouri, and Illinois rivers, where populations are building. Age and growth data provide a useful metric that integrates all conditions affecting a fish species (DeVries and Frie 1996). Fecundity, age at sexual maturity, and spawning periodicity provide insight into reproductive potential. Diets relative to food availability provide insight into energy intake and potential impact on sympatric species. We compare this information with silver carp in its native range, giving us a sense of its relative success in the MMR and potential for dispersal into upstream reaches.

Methods

Study site.—The MMR is the reach between Lock and Dam 26 at Alton, Illinois (river kilometer [rkm] 321.9), and Cairo, Illinois (rkm 0.0). It is free–flowing but channelized and stabilized for navigation. Wing dikes, which divert flow to the navigation channel and deepen it through scour (Sheehan and Rasmussen 1999), are the most common structures on this reach, and silver carp are often observed behind them. These structures limit lateral migration of the channel, fixing the river within its bed and reducing habitat diversity (Sheehan and Rasmussen 1999).

Fish sampling.—For age and growth data, two sizes of trammel nets (35.56-cm-bar outer mesh, 7.62-cm-bar inner mesh; 35.56-cm-bar outer mesh, 5.08-cm-bar inner mesh) were used during June–July 2003 to collect adult silver carp in low-velocity, scoured dike pools (the area immediately downstream of a wing dike) and tributary mouths of the MMR. During July–November 2003, we used single-phase, boat-mounted AC electrofishing. For diet data, additional directed AC electrofishing was conducted monthly from July through December 2003 in 10 randomly selected wing dike pools within each of two 16-km river reaches of the MMR (Chester, Illinois: rkm 177–193; Grand Tower, Illinois: rkm 113–129).

All fish captured were weighed (g) and measured (mm; total length [TL]). The first pectoral fin ray was removed for age analysis (Beamish and Chilton 1977). Gonads were identified and ovaries were preserved in 10% buffered formalin. For fish specifically sampled for diets, the entire intestine was removed and either placed on wet ice for phytoplankton analysis ($N = 7$ fish per month for each site sampled) or preserved in 10% buffered formalin for zooplankton analysis ($N = 3$ per month for each site sampled).

Age and growth.—To determine whether the distributions of lengths sampled differed between gear types, a Kolmogorov–Smirnov (KS) cumulative distribution test was used. Using length as the covariate, analysis of covariance (ANCOVA) tested $\log_{10}$ transformed differences in weights of males and females.

To determine age, pectoral fin rays were dried and then sectioned with a low-speed Isomet saw (Isomet Corporation, Springfield, Virginia; Beamish and Chilton 1977). The sections were placed under a dissecting microscope and annuli were counted (see Nuevo et al. 2004 for age validation with the closely related bighead carp). Two independent readers aged each ray; if readers disagreed, a common age was decided when possible. A coefficient of variation was calculated to determine aging precision (Campana 2001). The direct proportion method was used to back-calculate length at age because the intercept of the regression of length versus fin ray margin was not different than zero (DeVries and Frie 1996).

Growth was modeled from back-calculated individual lengths at age with a von Bertalanffy equation ($l_t = L_\infty \cdot [1 - e^{-K(t-t_0)}]$), where l_t is length at time t, K is a growth parameter, L_∞ is the maximum possible length, and t_0 is the time at which l_t is 0 (von Bertalanffy 1938; Slipke and Maceina 2001). The model was fit with the nonlinear-regression (NLIN) procedure in SAS (SAS Institute 1990). Differences between male and female growth models were tested by reparameterizing the von Bertalanffy model with a new parameter, $\omega = K \cdot L_\infty$ (Gallucci and Quinn 1979), again with the NLIN procedure. The new parameters for each sex were then compared with a Student's t-test. For comparison with other populations, von Bertalanffy models were used to back-calculate mean lengths at age from systems where the silver carp is native (Amur River, Russia; Nikolskii 1961) and introduced (Gobindsagar Reservoir, India; Tandon et al. 1993).

Fecundity.—Oocytes within five 1-g samples of each mature ovary were counted, and the mean was multiplied by the weight of both ovaries for an estimate of fecundity (Crim and Glebe 1990). Spawning periodicity was analyzed with the gonadosomatic index (GSI; [GSI = 100 × wet gonad weight (g)/wet body weight (g)]; Crim and Glebe 1990). Linear least-squares regression was used to determine associations between total length and GSI and weight and GSI. An analysis of variance (ANOVA) with Tukey–Kramer honestly significant difference (HSD) was used to test differences of mean GSI between months.

Potential food.—Little is known about the tax-

onomic composition and abundance of zooplankton and phytoplankton in the MMR. Plankton was sampled monthly at the same 10 randomly chosen wing dike pools at which fish were sampled for diet analysis, regardless of fish collection at that site. Zooplankton was collected at one tow per site with a zooplankton net (20-cm diameter, 64-μm mesh) lowered 2 m vertically and then preserved in 4% buffered formalin. Phytoplankton was sampled with a 1-m integrated tube sampler. Samples were placed in dark bottles and taken directly to the laboratory for chlorophyll *a* extraction.

In the laboratory, zooplankton samples were viewed on a gridded petri dish under a dissecting microscope. Individuals were identified as rotifers, cladocerans, copepods, and other taxa and counted to generate number/L. A subsample was digitized to determine length for zooplankton dry-weight conversions (Dumont et al. 1975; Bottrell et al. 1976; Bowen 1996). For comparison with chlorophyll *a* concentrations, zooplankton dry weight was converted to wet weight by multiplying dry weight by 10 (Bottrell et al. 1976). To determine chlorophyll *a* concentrations, water samples were filtered through a glass fiber filter, extracted in 95% ethanol overnight, and analyzed with a spectrophotometer (APHA 1998). An ANOVA with Tukey–Kramer HSD was used to determine differences in chlorophyll *a* concentration and zooplankton biomass among months.

Gut content analysis.—Diets of silver carp are suspended in thick mucus contained in an undifferentiated gut tube. Thus, we quantified the concentration of the common items within three 1-mL subsamples of the mucus suspension from either the frozen or formalin-preserved foreguts. Frozen intestines were thawed for chlorophyll *a* extraction. Three 1-mL subsamples were removed from the foregut and chlorophyll *a* was extracted from the subsamples (see above) and expressed as average μg/L wet weight within the mucus. Guts for zooplankton analysis were removed from the formalin and three 1-mL subsamples were taken from the foregut; zooplankton from each of the subsamples was identified, counted, and average wet biomass concentration (μg/L) of the mucus biomass was estimated (see above). The average concentration of chlorophyll *a* and zooplankton in diets and the field were compared for each site and date with linear least-squares regression.

Results

We captured 145 silver carp for age and growth analyses (Figure 1). Both gears typically captured

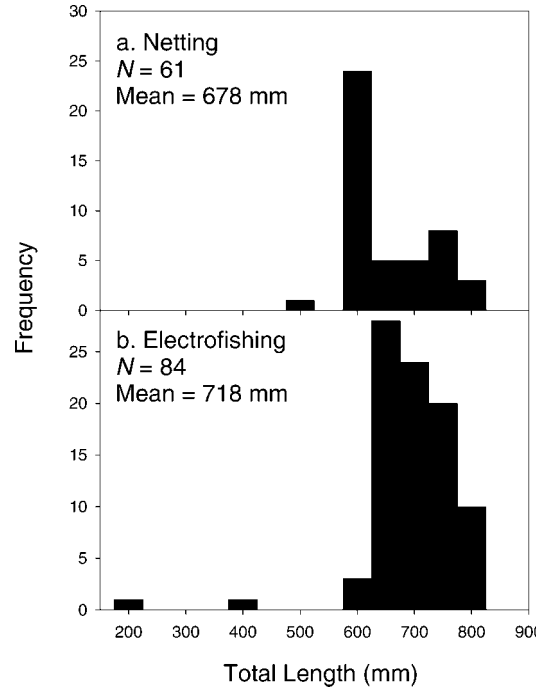

FIGURE 1.—Length-frequency distributions (mm TL) of silver carp from the middle Mississippi River during 2003, as determined by sampling with (**a**) trammel nets and (**b**) AC electrofishing.

fish 600–800 mm TL, although more small fish were netted than electrofished (KS = 0.049, $P < 0.001$; Figure 1). Total lengths ranged from 231 to 830 mm and weights ranged from 0.10 to 6.53 kg. Across all gears and months, 69 fish were males, 59 were females, and 17 were unidentified (sex ratio = 1.17:1). Average weights differed between males ($\log_{10}$[weight] = 3.11·$\log_{10}$ [length] −5.29) and females ($\log_{10}$[weight] = 3.10·$\log_{10}$[length] −5.25) and females were heavier than males (ANCOVA: $F = 5.73$; df = 1; $P = 0.02$).

Ages ranged from 0 to 5 years, age 2 being the most abundant (Table 1). Only 2 and 1 silver carp were age 0 and age 1, respectively. The coefficient of variation between the two readers was 13%. Agreement between readers was 60% exact and 100% within 1 year. The von Bertalanffy growth models (ω) of males and females did not differ ($t = 0.85$; $P > 0.05$; $N = 144$). The von Bertalanffy growth model for the entire population was $L_t = 778[1-e^{-0.629(t\ -\ 0.161)}]$ ($r^2 = 0.81$; $N = 384$ back-calculated lengths; Figure 2). Growth increments confirmed that older fish grew slower than younger fish (Table 1). The von Bertalanffy growth models (ω) of males and females did not differ ($t = 0.85$;

TABLE 1.—Back-calculated length at age (mm TL) of silver carp from the middle Mississippi River during 2003. Means are weighted by the number of individuals in each age-class.

Age-class and statistic	Year-class	*N*	Age 1	2	3	4	5
2	2001	74	312.3	560.9			
3	2000	46	331.8	522.1	671.8		
4	1999	22	312.2	464.8	618.9	710.1	
5	1998	2	257.5	349.6	484.0	637.9	723.3
Weighted mean			317.7	530.9	649.8	704.1	723.3
Growth increment (mm/year)			317.7	213.2	118.9	54.2	19.2

$P > 0.05$; $N = 144$). The von Bertalanffy models for mean lengths at age for the Amur River population was $L_t = 702[1-e^{-0.234(t-0.156)}]$ ($r^2 = 0.99$) and for the Gobindsagar Reservoir population was $L_t = 1{,}127[1-e^{-0.179(t-0.271)}]$ ($r^2 = 0.99$; Figure 2). The theoretical maximum lengths L_∞ from the MMR (778 mm TL) were intermediate between the Amur (702 mm TL) and Gobindsagar (1,127 mm TL) populations (Figure 2). The growth coefficient K and mean length at ages 1 through 4 for the MMR were greater than for the other two populations (Figure 2).

During July through November, the GSI of females ranged from 0.55% to 13.30% (mean = 3.71%). Mean female GSI did not differ among months ($F = 1.70$; df = 35; $P = 0.2000$). Female GSI was positively correlated with total length (GSI = 0.0275 mm TL −16.26; $r^2 = 0.51$; $P = 0.002$; $N = 36$) and weight (GSI = 0.001 g −2.138; $r^2 = 0.51$; $P = 0.0020$; $N = 36$). Six age-2 females with mature eggs were captured and the highest GSI was 11.99. Fecundity ranged widely among the 6 individuals from 57,283 to 328,538 eggs and averaged 156,312 eggs/female (95% confidence interval = ±74,042). Mean number of eggs/g of ovary was 672 (95% confidence interval = ±60).

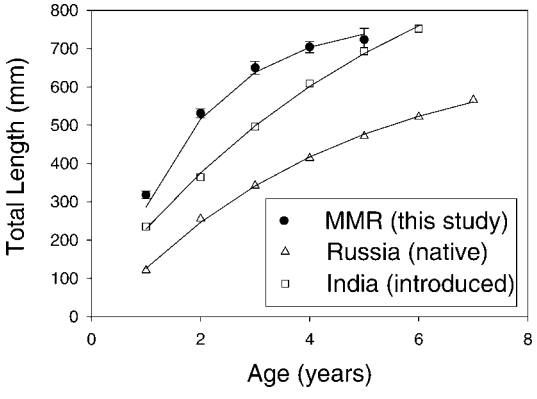

FIGURE 2.—Mean back-calculated length at age (±95% confidence limits) of silver carp from the middle Mississippi River (MMR) during 2003 (age 1, $N = 145$; age 2, $N = 144$; age 3, $N = 70$; age 4, $N = 24$; age 5, $N = 2$) together with mean lengths at age from a native (Amur River, Russia; Nikolskii 1961) and an introduced population (Gobindsagar Reservoir, India; Tandon et al. 1993). Lines are best least-squares fits of the von Bertalanffy model for each population.

We sampled the diets of 72 silver carp (548–845 mm TL and 1.68–7.46 kg) from July through November 2003. Total concentration (μg/L) of food in the subsampled gut mucus ($N = 56$ fish for chlorophyll *a*; $N = 16$ fish for zooplankton) peaked in August and September and declined during October through November at both sites (Figure 3). At Grand Tower, chlorophyll *a* concentrations in the gut mucus were highest in July and September and diminished by October and November (ANOVA: $F = 48.2$, df = 25, $P = 0.0001$; Tukey–Kramer HSD: $P < 0.05$; Figure 3a). Chlorophyll *a* concentrations in the gut mucus peaked in August and September and were lowest in November at Chester (ANOVA: $F = 25.9$, df = 22, $P = 0.0001$; Tukey–Kramer HSD: $P < 0.0500$; Figure 3b). Zooplankton concentration in the gut mucus did not differ among months at either site (Chester: $F = 3.1$, df = 7, $P = 0.1$; Grand Tower: $F = 0.64$, df = 7, $P = 0.6$; Figure 3e and 3f). Zooplankton taxa (wet weight across all individuals and dates) in silver carp diets were composed of 27% cladocerans and 69% rotifers at Grand Tower and 62% cladocerans and 37% rotifers at Chester. During July through October, 100% of the fish sampled had ingested food; however, by November 66% of fish sampled had empty intestines ($N = 9$). Detritus was uncommon in the gut samples.

Chlorophyll *a* concentrations behind wing dikes varied from 7.75 to 39.26 μg/L at Grand Tower and from 9.78 to 20.59 μg/L at Chester (Figure 3c, 3d). Concentrations at Grand Tower were highest in October (ANOVA: $F = 37.5$, df = 42, $P =$

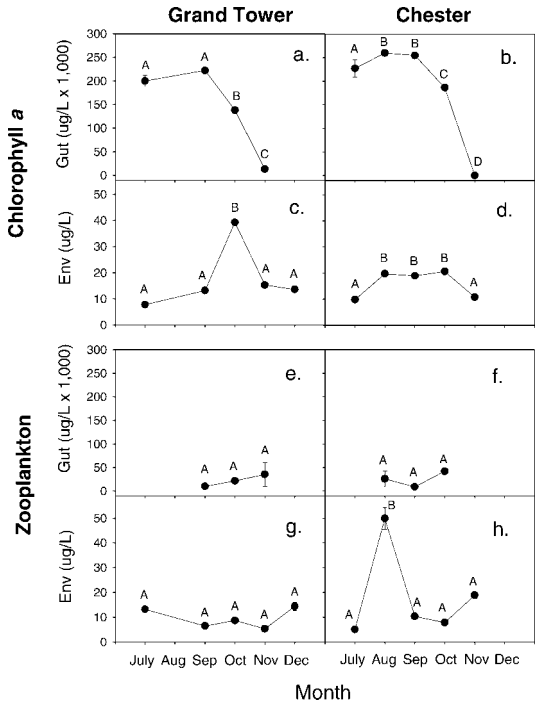

FIGURE 3.—Mean (±1 SE) concentrations of phytoplankton (wet biomass of chlorophyll *a*) and zooplankton (total wet biomass) in the middle Mississippi River (Env) and associated silver carp diets (Gut) during 2003. Differing letters denote means differing at $P < 0.0500$ (Tukey–Kramer honestly significant difference test).

0.0001; Tukey–Kramer HSD: $P < 0.05$) and the remaining months did not differ (Figure 3c). Concentrations at Chester were highest during August, September, and October (ANOVA: $F = 10.9$, df = 35, $P = 0.0001$; Figure 3d). Little variation occurred among sampling sites within months (SE range = 0.09–0.99; Figure 3). Zooplankton concentrations (wet weight) ranged from 5.4 to 14.4 μg/L at Grand Tower and from 5.1 to 49.9 μg/L at Chester (Figure 3g and 3h). Total zooplankton biomass did not differ among months at Grand Tower (ANOVA: $F = 2.1$, df = 35, $P = 0.1$; Figure 3g). At Chester, however, total zooplankton biomass peaked in August (ANOVA: $F = 8.2$, df = 38, $P = 0.0001$; Figure 3h). Copepods were the most common zooplankters at Grand Tower (mean across all dates and individuals = 67% by wet weight) and Chester (59% by wet weight). Rotifers (16%) and cladocerans (14%) at Grand Tower and cladocerans (30%) at Chester were also present. Concentrations in the environment and guts were unrelated for chlorophyll *a* ($r^2 = 0$; $P = 0.92$; $N = 9$ dates and sites) and zooplankton ($r^2 = 0$; $P = 0.95$; $N = 6$).

Discussion

The presence of multiple year-classes and mature individuals within the MMR represents an established population with successful recruitment. Fast-growing, young (age 2), and early-maturing silver carp were common in the MMR. The MMR and its associated wing dike and tributary macrohabitats appear to provide a suitable waypoint between the lower Mississippi River and upper reaches.

Small fish younger than age 2 were probably absent because we only sampled habitats directly adjacent to the main channel. While the gears used did not target young individuals, we expected to collect age-1 (>300 mm back-calculated TL) fish if they were present. Sampling with small-mesh trawls in the same locations also showed no evidence of small silver carp within these habitats (R. Brooks and J. Garvey, Southern Illinois University, unpublished data). In their native range, silver carp juveniles and adults occupy the floodplain and main river channel areas, respectively (Abdusamadov 1987). Thus, either young silver carp made use of the relatively rare extrachannel areas of the MMR or older individuals moved in from upstream or downstream river reaches where reproduction occurred.

Although silver carp in its native range matures by age 3 and lives for as many as 8 years (Kamilov 1985; Costa-Pierce 1992), individuals in the MMR appeared to be reproducing 1 year earlier and only reaching 5 years of age. The age of maturity of silver carp is determined by its growth rate during the first year of life (Kamilov 1987). Thus, high growth during early life in the MMR may be allowing females to mature earlier. The high proportion of young fish in the population could also cue early maturation (Diana 1983). Some females with high GSIs (up to 13%) were present during the entire summer. Because elevated GSI typically precedes gonadal maturation, this population may have a protracted spawning season.

While we did not quantify gear effectiveness, stationary trammel net sets did not appear to effectively sample silver carp because catch rates were extremely low (1.18 fish/net-night) in areas of high observed silver carp concentrations. On numerous occasions, silver carp jumped over nets, evading entanglement or entrapment. High incidental catch of other species also occurred with netting. Electrofishing selectively captured about

10 silver carp/h and, thus, was more effective (Williamson 2004). Because trammel-netting is commonly used in standardized fish community sampling by state agencies on the Mississippi River (Sheehan and Rasmussen 1999), a better evaluation of gear effectiveness is needed for this evasive species.

Young silver carp appear to be accessing adequate resources within the MMR or other source reaches. Conversely, growth of adults slows and lifespan appears to be limited. High early-growth rates and early maturation are common in newly established species, where density-dependent factors have yet to control population growth (Stauffer 1984). For adult silver carp aggregated and apparently foraging behind wing dike scour holes in the main river, plankton concentrations were quite similar among sites within dates, suggesting that these macrohabitats provide relatively predictable feeding areas.

In contrast to other systems in which the diet composition of silver carp reflected the relative abundance of prey in the environment (Spataru and Gophen 1985), the preponderance of phytoplankton (as estimated by chlorophyll *a*) in diets from MMR adults suggests that herbivory is common. Zooplankton may have been rare in diets because the ambient zooplankton behind wing dikes in the MMR is dominated by copepods (Williamson 2004; this study), which are known to evade filter-feeding planktivores (Drenner and McComas 1980; Drenner et al. 1987). Accordingly, copepods were rare among the few zooplankters in diets. The low digestibility of phytoplankton in silver carp (Bitterlich 1985a, 1985b) may help explain the rapid deceleration of adult growth, although, anecdotally, adults did not appear to be in poor condition.

Silver carp is established in the MMR, making extirpation unlikely. The population will probably expand, increasing the need for measures to prevent its introduction into other systems. Although this population appears to be self-sustaining, individual fish travel widely in the Mississippi River drainage (Garvey et al. 2004). The patterns of growth we quantified may, to some unknown extent, reflect conditions occurring beyond the MMR since migrants were probably included in our sampling. Information about the movement of this species is needed to provide better insight into population boundaries among river reaches.

Currently, silver carp inhabit most of the Mississippi River drainage and are moving closer to the Great Lakes system via the Illinois River (Chick and Pegg 2001). Determining how silver carp affect food webs will lend insight into future impacts and effects on native species. Because early growth is quite high, interactions between early life stages of native species in off-channel habitats should be a concern (see Schrank et al. 2003). Direct overlap between adults and other fishes for phytoplankton behind MMR structures is unknown but probably low, given that few other native river species appear to have similar filter-feeding, herbivorous behavior. Low-velocity structures in the main stem may facilitate the upstream dispersal of adult silver carp by enhancing phytoplankton production, thereby creating opportunities for foraging that might otherwise be absent.

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