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Linking Adult Reproduction and Larval Density of Invasive Carp in a Large River

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Abstract.—Identifying how temporal variation in the environment affects reproductive success of invasive alien species will aid in predicting future establishment and tracking dynamics of established populations. Asian carp *Hypophthalmichthys* spp. have become a nuisance in recent years in the Mississippi River basin. Their populations are apparently expanding, indicating favorable conditions for reproduction. During 2004 and 2005, we quantified mean density of Asian carp larvae, mean monthly gonadosomatic index (GSI) of adult males and females, and number of eggs within mature females in the lower Illinois River, a major tributary of the Mississippi River. A flood (water velocity $\geq$ 0.7 m/s) and drought ($<$0.2 m/s) occurred during apparent spawning in 2004 and 2005, respectively. During 2004, Asian carp larvae were found during 32% of sampling weeks; mean GSI and fecundity were relatively low for adults, probably reflecting partially spawned individuals and perhaps low reproductive investment. During the drought of 2005, larval stages were present during only one (5%) of the sampling weeks, whereas mean GSI and fecundity of adults were high through summer. Females resorbed their eggs instead of spawning during this year. Spawning conditions during low water periods appear to be unsuitable for Asian carps, inhibiting adult spawning and yielding few larvae. Spawning conditions during 2004 were better but still yielded low densities of larvae relative to native fishes. Reproduction in the lower Illinois River appears to be linked to river flow and its impact on adult spawning decisions, but conditions for strong year-class production (i.e., high larval densities) may be rarer than previously expected.

Many alien species successfully invade because they possess life history traits of r-selected species: rapid growth rates, short generation times, exceptional dispersal capabilities, high reproductive output early in life, high abundance in their original range, and broad environmental tolerance (Ehrlich 1984; Lodge 1993). These opportunistic characteristics allow them to reach massive population numbers soon after establishing (Lodge 1993; Williamson 1996; McMahon 2002). Two nonnative river-dwelling cyprinids with many of these characteristics are the bighead carp *Hypophthalmichthys nobilis* and silver carp *H. molitrix*. They became established in the Mississippi River drainage in the early 1980s (Freeze and Henderson 1982; Costa-Pierce 1992) and appear to be able invaders (Kolar et al. 2005).

Bighead carp and silver carp are present in at least 23 and 16 U.S. states, respectively (Fuller et al. 1999; Kolar et al. 2005). Commercial harvest of these fishes in the Illinois River increased by 124% during 2002 (Conover et al. 2006). Recent high population growth may lead to exploitative competition with native species (Koel et al. 2000; Schrank et al. 2003). For proper and effective management of these invasive species, temporal patterns of reproduction and spawning must be determined. If reproductive success varies annually with the environment or adult condition, then this information may be useful to forecast population growth and to potentially design control measures.

No data currently link reproductive status of adult Asian carp *Hypophthalmichthys* spp. to larval production in U.S. waters; the successful production of early life stages by adults is probably attributable to physiological and environmental factors affecting both life stages. Reproductive needs of adult bighead carp and silver carp are similar and have been documented as requiring water temperatures of at least 17°C, an optimum range of 21–26°C (Verigin et al. 1978; Krykhtin and Gorbach 1981; Abdusamadov 1987; Jennings 1988; Schrank et al. 2001), and a 0.7-m/s or higher water velocity (Krykhtin and Gorbach 1981; Abdusamadov 1987). Length of river required for successful spawning by silver carp may be 100 km or more (Gorbach and Krykhtin 1980). Conventional wisdom holds that uninterrupted river and swift current prevent the semibuoyant bathypelagic eggs from sinking and being covered with silt (Soin and Sukhanova 1972; Rothbard 1981). Adults are highly fecund in their native waters (Jennings 1988; Singh 1989; Kamilov 1987; Verigin et al. 1999) and in the invaded waters of the Mississippi River basin (Schrank and Guy 2002; Kolar et al. 2005; Williamson and Garvey 2005). Thus, ideal spawning and rearing conditions should generate large cohorts. Adults forage in the river and backwaters (see DeGrandchamp 2006), feeding on zooplankton, phytoplankton, and detritus. Presumably, energy reserves and reproductive invest-

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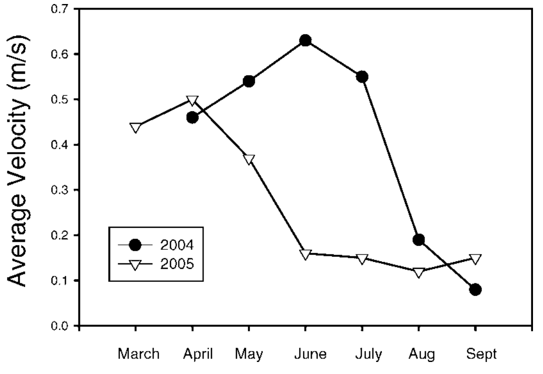

FIGURE 1.—Mean (±SE) monthly flow velocity (m/s) at ichthyoplankton sampling sites (4 sites/week, averaged across weeks) in the Illinois River, Illinois, where Asian carp larval density was examined during 2004 and 2005. Flow rates were averaged across sites and then among sampling dates.

ment of these species will be coupled with food availability, probably enhanced by inputs from the floodplain.

In many species, rapid early development of embryos and larvae improves survival and eventually recruitment to the adult population (Miller et al. 1988). Asian carp offspring follow this pattern by rapidly developing into free-swimming larvae at 1 d posthatch and exogenously feeding after 72 h posthatch (Soin and Sukhanova 1972; Murty et al. 1986). River regulation and flooding patterns also should influence larval success. High recruitment is likely in riverine environments when rising temperatures and river stage are coupled (Junk et al. 1989). However, the impact of a flood pulse on recruitment also may be a function of flood pulse predictability and the duration and area of inundation, where rapidly developing species with general spawning requirements are most successful (King et al. 2004). Asian carp larvae seem well adapted for recruiting in river floodplain habitats.

We quantified a field pattern comparing Asian carp adult reproductive status to larval fish production during a high-water year (2004) and a low-water year (2005) in the lower Illinois River, a large tributary of the Mississippi River, where populations of both species expanded explosively in the early 2000s (Chick and Pegg 2001). Although purely correlative and limited temporally, these patterns provide insight into the relative roles of (1) flow rates (i.e., is a velocity of 0.7 m/s required for spawning?) and (2) adult reproductive status on the production of larval densities of these congeners in North American rivers, thereby generating hypotheses that can be tested in the future with experiments, long-term data, and other novel approaches.

Study Site

The lower Illinois River extends between the La Grange Lock and Dam (river kilometer [rkm] 130 above the river mouth) at Beardstown, Illinois, to the confluence of the Mississippi River (rkm 0) at Grafton, Illinois. During spring and summer of 2004 and 2005, we sampled Asian carp between rkm 0 and rkm 19 and within Swan Lake, a large, adjacent, continuously connected backwater (1,100 ha) at rkm 8. Adults occasionally move into Swan Lake (DeGrandchamp 2006), and larvae from the river become entrained within it (Csoboth 2006). The lower Illinois River is undammed but has been channelized for navigation and is influenced by the Mel Price Lock and Dam in the Mississippi River downstream of the confluence. Despite a century of alterations, including dredging, water diversion from Lake Michigan, channelization, and levee construction, the river still retains an annual flood pulse (Karr et al. 1985; Sparks 1995). The Illinois River flooded its banks during late spring through summer of 2004; in contrast, water levels declined during the same period in 2005 (Csoboth 2006; DeGrandchamp 2006; Figure 1).

Methods

Adult fish sampling.—We collected Asian carp adults during April–October 2004 and March–August 2005, typically using experimental trammel nets (5.08, 7.62, 10.16, and 8.89-cm bar-mesh panels; 3.66, 3.96, 4.27, and 3.96-m outer walls; 91.44 m in length). Hoop nets (3.81-cm bar mesh; 0.91-m diameter, fiberglass hoops), trap nets, and fish jumping into the boat also were sources. For each adult, the species and sex were identified and the total length (TL, mm) and wet weight (g) were quantified. Gonads were removed from the fish to determine gender and were weighed (wet mass, g). Ovaries were preserved in 10% buffered formalin. Oocytes within three 1-mL samples of each ovary sample were counted, and the mean was multiplied by the total volume of the ovary sample to estimate number of eggs per female (hereafter, egg quantity; Crim and Glebe 1990).

For each species, sex-dependent adult TLs were compared between years by two-way analysis of variance (ANOVA; general linear model [GLM] procedure in the Statistical Analysis System; SAS Institute 1990). Spawning periodicity was quantified by tracking the average weekly gonadosomatic index (GSI = 100 × [wet gonad weight/wet body weight], where both weights are in grams; Crim and Glebe 1990) through time. A *t*-test was used to test differences in GSI between years for males and females of both species. Pearson's product-moment correlation was used to test the relationship between female bighead carp and silver carp GSIs for 2004 and 2005. Linear regression was used to determine the relationship between TL or weight and egg quantity of each species for 2005. Body size versus egg quantity data for 2004 were excluded from this analysis because many fish appeared to have already completely or partially spawned, thus rendering size-dependent relationships inaccurate. We used ANOVA with Tukey's honestly significant difference test (GLM procedure) to evaluate differences in egg quantity between years for bighead carp and silver carp.

Larval fish sampling.—During late March–September 2004 (21 weeks) and 2005 (22 weeks), surface ichthyoplankton tows were conducted weekly on the lower Illinois River and Swan Lake to quantify spawning of Asian carp. Weekly tows were conducted along four randomly chosen transects in the Illinois River (rkm 8.0 and 1.6) and along four transects in Swan Lake with a pair of bow-mounted ichthyoplankton nets (0.5-m diameter; 2-m length; 500-μm mesh). A calibrated mechanical flowmeter (General Oceanics, Inc.; Model 2030R) was mounted in the mouth of one net to estimate volume sampled (about 100 m^3 of water was sampled per transect). In the river, tows were conducted perpendicular to flow by beginning at the main channel border and sampling across the main channel. In Swan Lake, two tows were conducted near the shore and two near the center of the lake. Flow rate was quantified in the river channel during each sampling event using either a Marsh-McBirney electronic flowmeter or the General Oceanics mechanical flowmeter near the surface. Velocities (m/s) were averaged across sampling weeks within each month.

Net contents were preserved in 95% ethanol in individually labeled jars. Samples were subsampled with a Folsom plankton splitter (Aquatic Research Instruments, Hope, Idaho) so that approximately 200 fish/sample were processed and counted. Asian carp larvae were identified by using voucher specimens (D. Snyder, Colorado State University, Larval Fish Laboratory, Fort Collins). Larvae were difficult to key to species, and hybrids do occur (K. Irons, Illinois Natural History Survey, Havana, personal communication), so we restricted analyses to genus. Data were standardized by volume of water sampled. Densities from each pair of nets per transect were averaged. On each date, a single average was then calculated across all river and Swan Lake transects (i.e., 8 sites/date). Finally, monthly means were calculated across those daily averages. A one-way repeated-measures ANOVA (GLM procedure) was used to test for differences in mean monthly density between years on $\log_{10}(x + 1)$ transformed data. To quantify patterns among weeks, the presence or absence of Asian carp larvae in tows were compared by using a two-tailed, binomial test in which the expected distribution across weeks was generated from 2004 and compared with the observed distribution during 2005.

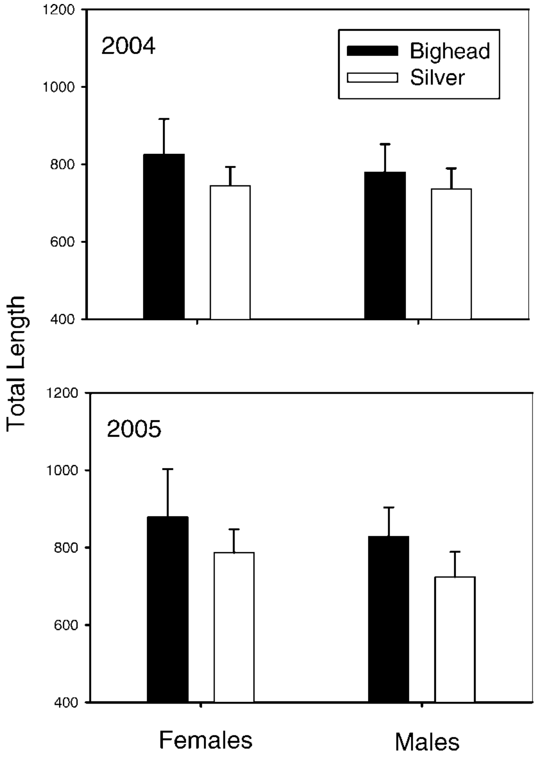

FIGURE 2.—Mean (+SD) TL of adult bighead carp and silver carp collected in trammel nets in the lower Illinois River, Illinois, during spring and summer of 2004 and 2005.

Results

Female bighead carp were larger than males during both years, as determined by two-way ANOVA (sex: $F = 23.6$, df = 1, 349, $P < 0.0001$; sex × year: $P > 0.05$; Figure 2). Bighead carp were longer in 2005 than in 2004 (year: $F = 23.6$, df = 1, 349, $P < 0.0001$; Figure 2). Female silver carp were longer than males during 2005 (sex: $F = 12.6$, df = 1, 134, $P = 0.0005$), but a sex × year interaction (sex: $F = 7.5$, df = 1, 134, $P = 0.007$) indicated that average TLs were similar between sexes in 2004 (Figure 2). Mean TLs of silver carp did not differ between years (year: $P > 0.05$; Figure 2).

Mean GSI showed no seasonal pattern; some individuals had high values as late as September (Figure 3). Bighead carp and silver carp GSI (averaged across all individuals caught during the sampling

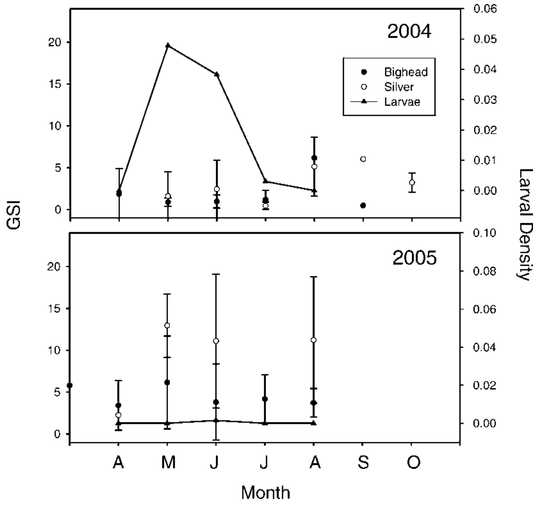

FIGURE 3.—Seasonal patterns of mean (±SE) monthly gonadosomatic index (GSI; [gonad weight/body weight] × 100) values for adult female bighead carp and silver carp (primary *y*-axis) and mean larval density (fish/m^3; secondary *y*-axis; both species combined) during 2004 and 2005 in the lower Illinois River, Illinois. The GSI values for males (not shown) also varied among months and exhibited no discernable peak.

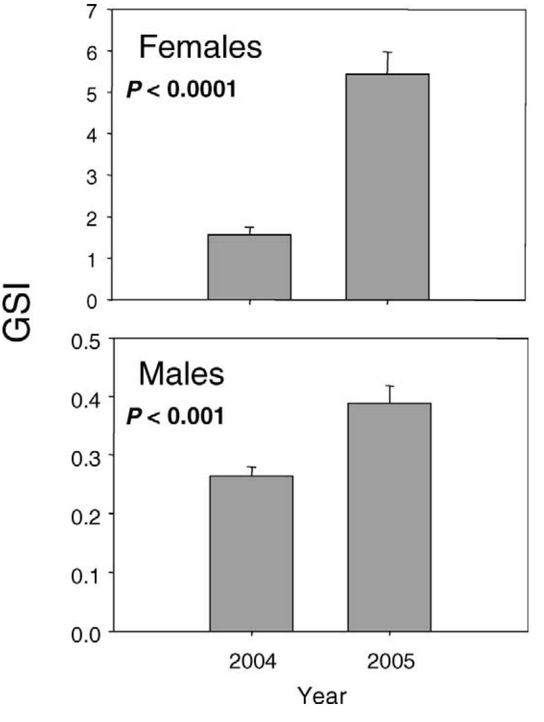

FIGURE 4.—Mean (+SE) gonadosomatic index (GSI; [gonad weight/body weight] × 100) of female (top) and male (bottom) bighead carp and silver carp from the lower Illinois River and Swan Lake, Illinois, during 2004 (137 females; 153 males) and 2005 (99 females; 102 males). Species are combined because data showed similar patterns between years.

season) differed between 2004 and 2005 for females ($F = 58.36$, df = 1, 235, $P < 0.0001$; Figure 4) and males ($F = 15.57$, df = 1, 254, $P = 0.0001$; Figure 4). Monthly mean GSIs were positively correlated between female bighead carp and female silver carp ($r = 0.87$, $P = 0.02$) but were not correlated between males of the two species. Bighead carp and silver carp egg quantities differed between years (bighead carp: $F = 35.16$, df = 1, 89, $P < 0.0001$; silver carp: $F = 22.84$, df = 1, 28, $P < 0.0001$). Mean (±SE) egg quantity in 2004 was 1.8×10^5 eggs/female ($\pm 0.3 \times 10^5$) for bighead carp and 2.8×10^5 eggs/female ($\pm 0.5 \times 10^5$) for silver carp; egg quantities in 2005 were 7.5×10^5 ($\pm 0.6 \times 10^5$) and 16×10^5 ($\pm 2.0 \times 10^5$) eggs/female, respectively. In 2005, bighead carp egg quantity increased with TL (egg quantity = [2,226.67 × TL] − 1,261,512; $r^2 = 0.28$, $P < 0.0001$) and weight (egg quantity = [128.47 × Wt] − 315,083; $r^2 = 0.38$, $P < 0.0001$). Silver carp egg quantity in 2005 also was positively related to weight (egg quantity = [325.14 × Wt] − 581,908; $r^2 = 0.24$, $P = 0.04$) but not to TL ($r^2 = 0.07$, $P = 0.30$). Of 137 bighead carp and silver carp females sampled in 2004, 19% had ovaries with mature oocytes and 5% appeared to have completely spawned. During 2005, 51% of 99 females sampled contained mature oocytes, but by fall there was no evidence that females had spawned. About 27% of the females examined in 2005 had resorbed their oocytes.

Larval and early juvenile Asian carp were present in ichthyoplankton nets in both the river (mean ± SD across dates when larvae were present: 0.03 ± 0.03 fish/m^3) and Swan Lake (0.13 ± 0.25 fish/m^3) during May–July 2004, peaking at an average near 0.06 fish/m^3 across river and lake sites combined in May (Figure 3). Conversely, during 2005 larvae appeared during only 1 week of sampling and only in Swan Lake (Figure 3). On average, Asian carp larval densities were typically low during both 2004 (May–July mean ± SE = 0.03 ± 0.02 fish/m^3) and 2005 (0.0006 ± 0.0006 fish/m^3); Asian carp larvae appeared in larval tows on 32% of sampling weeks during 2004 and on only 5% of weeks during 2005 (binomial test: $P = 0.008$; Figure 3).

Discussion

During the two very different years, river flow appeared to influence spawning of the adult invaders. These results are consistent with reports from native waters in Asia, where an increase in activity and movement was associated with river stage (Krykhtin and Gorbach 1981; Abdusamadov 1987). Yi et al.

(1988; also see translations in Chapman 2006) discovered Asian carp eggs during the rise in river stage of the Yangtze River, China. In the Illinois River, river stage was the primary cue for movement of adults during the spawning season (DeGrandchamp 2006). Adult reproductive condition (i.e., GSI and egg quantity) also differed between years. Below, we discuss how river stage and adult reproduction were apparently related and thereby influenced the production of larvae in the Illinois River.

Adult Response to Flow

Adult reproductive condition differed dramatically between years for both species and probably affected larval output. Adults may use specific environmental conditions (e.g., river stage or temperature) to cue maturation and then initiate spawning. A lack of certain criteria would in turn adversely affect reproductive output of the adults, resulting in a lack of input to the system for that year. Spawning criteria documented to be associated with flow (velocity $\geq$ 0.7 m/s; Krykhtin and Gorbach 1981; Abdusamadov 1987) for both species were met only in 2004. Reproductive characteristics in 2004 included relatively low GSI values for males and females, overall relatively low fecundity, and evidence of spawned-out fish. Previous spawning activity probably contributed to the lower fecundity and GSIs observed in that year, although poor condition of nonspawning adults also may have been a factor. No spawned-out fish were observed in 2005, but many fish of both species had apparently initiated resorption of eggs and had relatively higher fecundity and GSI values. The declining flow in 2005 may have curbed spawning in the river, yielding higher observed fecundity and GSI values. Retention of eggs often results in follicular atresia, a common phenomenon in teleosts that can be induced by stress, fasting, or environmental conditions, such as those not conducive to spawning (Nagahama 1983; Linares-Casenave et al. 2002). During 2005, shovelnose sturgeon *Scaphirhynchus platorynchus* in the Mississippi River also contained eggs that were apparently being resorbed rather than spawned (S.J. Tripp and J.E. Garvey, Southern Illinois University, unpublished data). Thus, it is plausible that spawning and larval production were curbed in 2005 relative to 2004 across many species that require adequate flow to spawn.

Larval Response to Flow

After spawning, it is possible that an annual flood pulse is necessary to keep eggs suspended in the water column, therefore increasing the chance of larval survival. The Illinois River flooded during the apparent spawning season every year since the late 1990s (except 2005; Figure 5), perhaps facilitating the recent increase of Asian carp populations in this system. In addition to keeping eggs and larvae suspended, the regular inundation of the floodplain environment with each seasonal flood probably created suitable habitat for larval and juvenile fish, enhancing survival and recruitment (see Csoboth 2006).

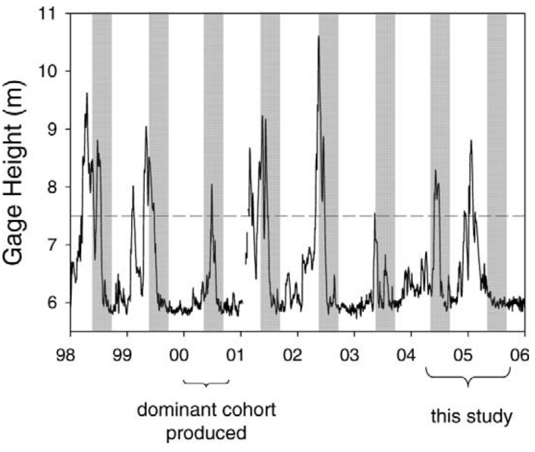

FIGURE 5.—Maximum daily gauge height (m) at the U.S. Geological Survey gaging station on the Illinois River at Hardin, Illinois, during January 1998–January 2006 (dashed line = gauge height at flood stage). Shaded bars indicate the possible Asian carp spawning months (May–October).

Although we found nearly no larval production in the Illinois River during the low water year, there is still some speculation about adequate flow (i.e., 0.7 m/s) being the driving force behind successful reproduction. Kolar et al. (2005) cited an instance in which bighead carp eggs were inadvertently sampled in a sediment study, and the eggs, although covered in mud, hatched and survived for 4 d. Our group also found recently hatched Asian carp larvae in an isolated, unconnected backwater of the Illinois River (Garvey et al. 2005). Furthermore, the lower Illinois River, characteristic of a low-gradient stream, rarely meets 0.7 m/s throughout the spring and summer; only during times of high flooding does it exceed this velocity. Even during the relatively high water of 2004 (compared with 2005), water velocities approached 0.7 m/s only during 1 week in June, although larvae were present during several months (May–August). Thus, high river stage may augment egg and larval survival but may not be critical for reproductive success.

Adult Condition

Although the interaction among adult physiology, environmental conditions, and adult behavioral decisions probably drove spawning, the maternal condition of the adults also may affect reproductive output (Madenjian et al. 1996). A threshold maternal condition is presumably met when the enrichment of the floodplain environment supplies more food for adults, leaving them in high overwintering condition. This condition also would be reflected during the subsequent year by enhancing fecundity and reproductive potential. We saw this result in both species: fecundity was positively related to weight in 2005 after the 2004 flood year. If environmental conditions had been favorable for adult spawning in 2005, then we might have quantified high production of larvae that year, given the high reproductive potential in the adults. However, poor larval production through time and apparent resorption of eggs suggest that good maternal condition is necessary but not sufficient for successful reproduction.

Implications

During this effort, the bighead carp and silver carp populations in the Illinois River were dominated by cohorts produced during 2000 (Garvey et al. 2007). Year-class strength in these species varies tremendously and probably depends on congruence among environmental conditions and adult spawning. In reality, neither 2004 nor 2005 was a year of strong reproduction and recruitment. Peak densities of all larval fish taxa combined in the Illinois River exceeded $10/m^3$ during spring of both years (Csoboth 2006); Asian carp larval abundance was about 100 times lower than total larval abundance at its peak in 2004. Water levels in the Illinois River during spring through summer of 2000 were intermediate between those in 2004 and 2005 (Figure 5), suggesting that flow was not exclusively responsible for the marked population expansions during that year. Conditions for successful adult spawning and larval production might be rarer than expected in the Illinois River—requiring congruence among adult maternal condition, a stable spring rise in streamflow, and perhaps sufficient flow for larval development.

Population growth of Asian carp species in the Illinois River is probably driven by high reproductive potential and relatively long life span (see Williamson and Garvey 2005), both of which are necessary for persistence in variable environments (i.e., the storage effect; Warner and Chesson 1985). The regular spring flood pulse in the Illinois River probably serves to provide a predictable cue for spawning during most years. Even if spawning is not successful in the Illinois River, this system is near unimpounded reaches of the lower Mississippi and Missouri rivers. Recent telemetry work in these systems has demonstrated that both species move widely during spring, spanning river reaches and crossing locks and dams (DeGrandchamp 2006). Thus, even if populations are poorly sustained in the Illinois River, individuals from other reaches will presumably continue to invade, potentially stabilizing population dynamics.

In our view, Asian carp populations within the Illinois River have high reproductive potential, but realization of this potential varies widely with climate and connectivity to other populations. At the regional scale and possibly the rangewide scale, this suggests that variable local responses to reproductive conditions are ameliorated by environmental heterogeneity among reaches. The key to predicting population dynamics and controlling these species is a refined understanding of the relative roles of connectivity, movement, and reach-specific reproduction in the Mississippi River basin.

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