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Life History Attributes of Asian Carps in the Upper Mississippi River System

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INTRODUCTION: The Upper Mississippi River (UMR) system starts at the confluence of the Ohio River at Cairo, Illinois, and serves as a conduit for many aquatic invasive species to enter the waterways of the central and northern interior of the United States, including the Great Lakes. One well-established group found in this waterway is the Asian carps including the common carp *Cyprinus carpio*, grass carp *Ctenopharyngodon idella*, and two recent invaders, the bighead carp (*Hypophthalmichthys nobilis*) and silver carp (*H. molitrix*). Their impact is not minor. In the UMR and Missouri River drainages, common carp typically contributes more tonnage to the commercial fishery than any other fish species (Pflieger 1997). Although the impact of the newly established Asian carp species is currently unknown, benefits to native fishes are unlikely (Laird and Page 1996). The risk is not restricted to the inland rivers of the United States. If these species breach the electric barrier constructed by the U.S. Army Corps of Engineers in the Chicago Sanitary and Ship Canal, then they will threaten the Great Lakes as well (Pegg and Chick 2002, Kolar et al. 2005).

Although these species have been widely introduced throughout the world for food, the native range of silver and bighead carp is eastern Asia (Fuller et al. 1999). In the early 1970s, these fishes were introduced into the southern United States for private aquaculture. By the 1980s, these species occurred in public waters, probably escapees from hatcheries (Freeze and Henderson 1982). Successful reproduction of both species is occurring in the UMR and Missouri drainages (Burr et al. 1996, Koel et al. 2000, Schrank et al. 2003). Population densities of silver carp increased dramatically in the early 2000s (Chick and Pegg 2001), greatly increasing the visibility of this species, which is notorious for breaching the surface of the water in large aggregations. In the spring of 2006, a sizeable die-off of Asian carp occurred in the Upper Illinois River in the vicinity of Peoria and Havana, Illinois, further increasing their nuisance status. Decaying carcasses foul the air and are unsightly, likely deterring recreational boating and public use of riverside areas. A similar problem occurred during the massive mortality events of invasive alewife (*Alosa pseudoharengus*) in Lake Michigan in the 1950s and 1960s. This nuisance problem was not alleviated until predatory Pacific salmon were stocked into this system.

Asian carp collected at one location. From top to bottom: Grass carp, common carp, and silver carp

How barriers, habitat enhancement programs (e.g., reconnecting backwaters), and navigation improvement projects (e.g., upgrading locks) affect the dispersal and establishment of Asian carps is unknown. Further, the feasibility of eradication efforts such as selective harvest in conjunction with other mitigation efforts has not been evaluated. To understand how Corps activities directly and indirectly affect these species, the growth and mortality rates, age structure, reproductive potential, and feeding behavior of these species need to be quantified. Growth, mortality, and age structure provide insight into potential increases in population density. Indices of reproduction generate information about the timing and intensity of offspring produced. Feeding behavior reflects competitive potential and the relative value of surrounding habitat to population success. Incorporating these data into basic fisheries stock assessment models will aid Corps planners in assessing how navigation and flood control activities affect population trends as well as dispersal of Asian carps and other non-native fish species into novel waters. The Corps can also use these tools to monitor success of Asian carp control programs by tracking population responses through time.

SITES OF ESTABLISHMENT: The Middle Mississippi River (MMR) is the unimpounded reach of the UMR extending about 200 miles from Cairo, Illinois to above the confluence of the Missouri River. It is the conduit by which Asian carps disperse from established reaches in the southern United States into northern reaches and perhaps eventually the Great Lakes. Asian carp populations in the MMR were compared to those in the pooled confluence area of the Illinois River and UMR Pool 26 (CONFL). Although the Illinois River portion of the CONFL is impounded under non-flood conditions and regulated for flood control and navigation, it still retains its annual flood pulse (Karr et al. 1985, Sparks 1995). The research described herein compares populations of Asian carps between the MMR and CONFL reaches. From this, how reach-specific characteristics such as flow and habitat affect populations may be assessed.

Silver carp were sampled in the MMR using trammel nets from June through July 2003 in low-velocity, scoured dike pools (the areas immediately downstream of wing dikes) and tributary mouths (Figure 1). From July through November 2003, single-phase, boat-mounted AC electrofishing was used. Bighead carp were not collected during this effort.

Silver and bighead carp were sampled in the CONFL reach from spring 2004 through spring 2005 using experimental trammel nets, hoop nets, trap nets, commercial fishers, and electrofishing; fish jumping into the boat were also kept. Size, weight, age, sex, maturation stage, GSI (gonadosomatic index=gonad weight/fish weight), and fecundity (number of eggs per female) of each silver and bighead carp were quantified. Diets of silver carp from the MMR also were quantified (Williamson and Garvey 2005).

Figure 1. Removing bighead and silver carp from trammel nets in the Illinois River — Pool 26 confluence of the Upper Mississippi River system

GROWTH, AGE STRUCTURE, AND MORTALITY: Growth through life is quantified by aging individual fish and then using models to assess annual rates and maximum size. To determine age, pectoral fin rays were dried and then sectioned (Beamish and Chilton 1977). The sections were placed under a dissecting scope and annuli were counted (see Neuvo et al. (2004) for age validation). Each ray was aged by two independent readers. 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). The von Bertalanffy model was used to characterize length-age relationships for all populations

$$L_t = L_\infty \left(1 - e^{-k(t-t_0)}\right)$$

where L is length in mm, k is a growth coefficient, L_∞ is the theoretical maximum length, t is the age in years, and t_0 is the age when L=0, which is usually non-zero.

Silver carp from the MMR grew more rapidly, reaching a smaller maximum length than counterparts in the CONFL area (Table 1). Bighead carp grew more slowly but reached greater ages and lengths than silver carp (Table 1). The CONFL populations of both silver and bighead carp were dominated by age 4 fish, which were produced during 2000 (Figure 2). This confirms the results of others (Chick and Pegg 2001; K. Irons unpublished data; USFWS Carterville Fisheries Resource Office, unpublished data) that in 2000 these populations may have either (1) experienced positive but currently unknown environmental conditions conducive to reproductive success, or (2) simultaneously reached critical threshold densities that allowed for high reproductive output. The former is more likely than the latter. Bighead carp already were well established in the CONFL area by 2000, while silver carp had only recently arrived. Thus, it is unlikely that both species were sufficiently similar demographically to simultaneously produce large cohorts based solely on their population status. Focusing on (1) then, identifying the suite of environmental conditions that create strong year classes needs to be a research priority. Spring discharge during 2000 was average (see next section); in concurrence with other important but unidentified conditions, flow may have been optimal for offspring production, rearing, and recruitment to adulthood (see below).

Table 1
Population Statistics for Asian Carps from Two Reaches in the Upper Mississippi River System[1]

Reach	Species	Maximum Age (t, years)	Maximum Length (L_∞, mm TL)	Growth Rate (k)
MMR[2]	Silver carp	5	778	0.63
CONFL	Silver carp	5	867	0.41
	Bighead carp	10	1242	0.24

[1] Parameters derive from age-length relationships incorporated into von Bertalanffy models. All models fit empirical data well (R^2 > 0.9)
[2] Williamson and Garvey (2005)

REPRODUCTIVE POTENTIAL: Patterns of reproductive potential generated from both the MMR and the CONFL reaches were similar. The GSIs for adult female silver carp in the MMR did not differ from July through November, with gonads ranging from 1 to 13 percent of body weight. Females with mature ovaries (Figure 3) were present as early as age 2 years. Females produced on average 156,312 eggs in the MMR (also see Williamson and Garvey (2005)). In the CONFL reach, female GSIs for both species and years varied but were similar to those of silver carp in the MMR (GSI range was 2-15 percent). The range of fecundity for bighead carp in 2004 (N=27) was 4,792 to 473,200 eggs with a mean of 118,485 eggs. Silver carp egg production in 2004 (N=11) ranged from 26,650 to 598,767 eggs with a mean of 269,388 eggs. In 2005, egg densities per female were higher. In 2005, bighead carp egg number (N=57) ranged from 88,133 to 1,938,333 eggs with a mean of 777,154 eggs. Silver carp egg production in 2005 (N=15) ranged from 274,917 to 3,683,150 eggs with a mean of 1,478,331 eggs. Fecundity was positively correlated with weight in both species (bighead $p<0.001$, $r=0.5149$; silver $p=0.0038$, $r=0.5473$). When recently spawned fish occurred, ovaries were red and spongy, and were accompanied by a torn cloaca. Forty-nine fish (10 percent of sampled fish) were found to have either a spent ovary or were starting to reabsorb eggs. Only spent females occurred in 2004, and only fish reabsorbing eggs occurred in 2005. Silver carp and bighead carp matured at ages 3 and 4, respectively, in the CONFL area. Given their high fecundity and potential for prolonged spawning, the reproductive potential of both Asian carps appears to be very high relative to native river-specialist species in the UMR system (e.g., maxima for channel catfish, *Ictalurus punctatus*: 70,000 eggs; paddlefish, *Polyodon spathula*: 142,000 eggs; gizzard shad, *Dorosoma cepedianum*: 350,000 eggs; Carlander 1969).

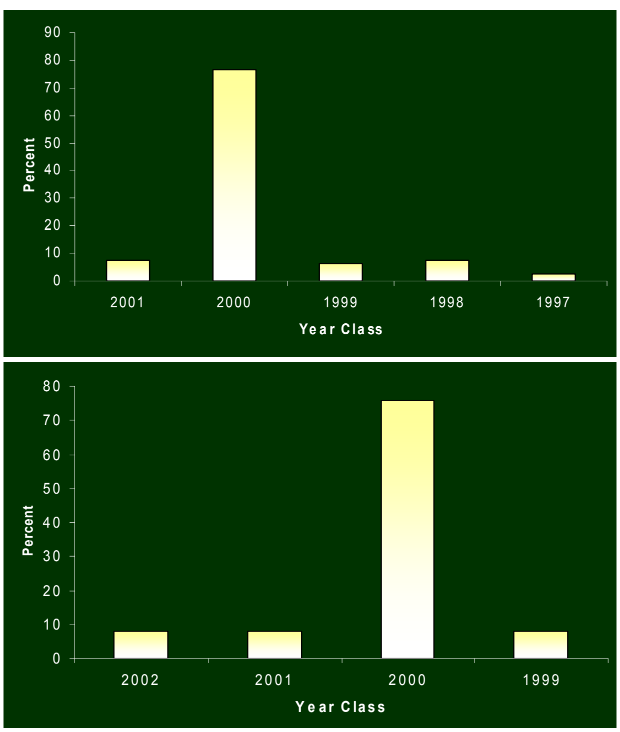

Figure 2. Relative frequency of annual cohorts present in the CONFL reach of the Upper Mississippi River system during 2004

Figure 3. Mature ovary of a female silver carp. Each small white spherical structure is a mature egg

Silver carp in the MMR appeared to reproduce at an earlier age but to invest similar energy into reproduction as conspecifics in the CONFL. Given that indices of reproductive investment showed no monthly pattern during the growing season among all populations, it is likely that reproduction was protracted and probably started at about 18° C as the literature suggests (Kolar et al. 2005), with no seasonal pulse. The differences in reproductive investment between years in the CONFL reach for both species (Figure 4) were likely related to patterns of discharge. A flood occurred during spring 2004 while a drought occurred during the following spring (2005). Spawning occurred during the high water of 2004 leading to the presence of spawned-out females. Although adults were in high spawning condition during 2005, a lack of flowing water, long believed to be important for spawning of Asian carps, may have inhibited spawning. Adults may have invested high energy into gonads in anticipation of proper spawning conditions that never materialized in 2005. Only one year of data is currently available for the MMR and a similar comparison cannot be conducted.

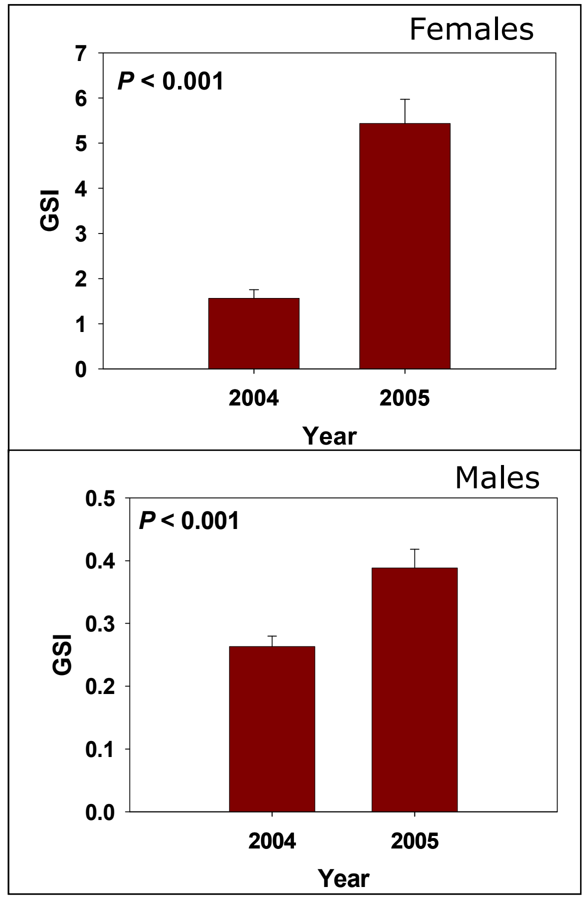

Figure 4. Average GSI (gonad weight index) combined between species in the CONFL reach

FEEDING BEHAVIOR: Bighead carp and silver carp can consume detritus, phytoplankton, and zooplankton and have a high consumptive capacity (Etnier and Starnes 1993, Laird and Page 1996, Pflieger 1997, Fuller et al. 1999). These characteristics may allow them to negatively affect other aquatic organisms in the UMR drainage. Early life stages of many fishes rely heavily on zooplankton, rendering them susceptible to competition. Further, gizzard shad, an important forage species for waterbirds and predaceous fishes (DeVries and Stein 1990), has omnivorous behavior similar to silver carp and may be particularly vulnerable (Pflieger 1997). Diets of adult silver carp at two sites in the MMR were quantified from July through November 2003 to gauge their potential impact behind the wing dike areas in which they aggregate.

Chlorophyll *a* was extracted from three diet subsamples per fish, and expressed as average µg/L wet weight within the mucus (see Williamson and Garvey (2005)). Zooplankters from each of the subsamples were identified, counted, and average wet biomass concentration (µg/L) of the mucus was estimated. Diets of 72 silver carp (548-845 mm and 1.68-7.46 kg) revealed that total concentration (µg/L) of food in the subsampled gut mucus (N= 56 fish for chl a; N=16 for zooplankton) peaked in August and September and declined from October through November (Figure 5). At Grand Tower, chlorophyll *a* concentrations in the gut mucus were highest in July and September and diminished by October and November (Figure 5). Chlorophyll *a* concentrations in the guts peaked in August and September and were lowest in November at Chester (Figure 5).

Zooplankton concentration in the gut mucus did not differ among months at either site (Figure 5). Zooplankton taxa (wet weight across all individuals and dates) in diets were comprised of 27 percent cladocerans and 69 percent rotifers at Grand Tower and 62 percent cladocerans and 37 percent rotifers at Chester. During July through October, 100 percent of the fish sampled had ingested food. However, by November, 66 percent of fish sampled had empty intestines (N = 9). Detritus was uncommon in guts.

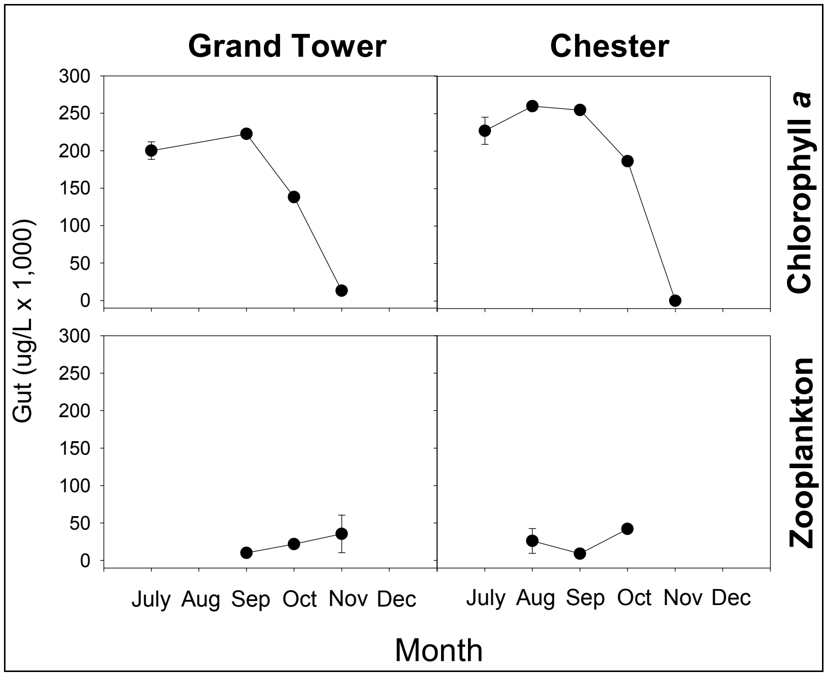

Figure 5. Concentration of phytoplankton (as estimated by chl a concentration) and zooplankton in diets of silver carp from the MMR reach at two sites (Grand Tower RM 80 and Chester RM 110)

These and related feeding studies suggest that regardless of food availability, silver carp congregating behind wing dikes in the MMR preferentially foraged on phytoplankton (Williamson 2004). This is in contrast to other systems in which diet composition of silver carp reflect the relative abundance of prey in the environment (Spataru and Gophen 1985). The masses of phytoplankton produced behind wing dikes of the MMR likely provide suitable waypoints for adult silver carp dispersing between the lower Mississippi River and the UMR. Obligate planktivorous herbivores are rare in the MMR, so direct overlap between adult silver carp and other fishes for phytoplankton behind MMR structures may be low (Williamson and Garvey 2005). However, indirect effects on zooplankton via modifications to the density and composition of algal resources may negatively affect zooplanktivores such as paddlefish, gizzard shad, and most larval fishes.

POPULATION TRAJECTORY: Successfully reducing populations through selective removal or barriers requires knowledge about which life stages affect population growth. Typically population dynamics are either sensitive to fluctuations in the recruitment of early life stages to adulthood or to survival of adults and their ability to reproduce (Cole 1954). Given that year class strength varies widely annually for both species (Figure 2), evidence is mounting that the populations are sensitive to environmental conditions such as precipitation and spring/summer flow (Figure 4). Modeling of population production can provide insight into the sensitivity of populations to age and size-dependent mortality of adult stages.

The Beverton-Holt equilibrium yield model (Ricker 1975) in the yield-per-recruit function in Fishery Analysis and Simulation Tools (FAST) software (Slipke and Maceina 2000) was used to model adult dynamics. This model modifies the original Beverton-Holt model (Ricker 1975, Slipke et al. 2002), but it is similar to the yield model of other programs (Quist et al. 2002). The Beverton-Holt yield per recruit model estimates yield using the following formula (Slipke and Maceina 2000):

$$Y = \frac{F * N_t * e^{Zr} * W_\infty}{K} * \left[\beta\left(X, P, Q\right)\right] - \left[\beta\left(X_1, P, Q\right)\right]$$

where F = instantaneous fishing mortality; N_t = the number of recruits entering the fishery at some time t; Z = instantaneous mortality rate; r = time to recruitment ($t_r - t_0$); W_∞ = maximum theoretic length estimated from L_∞ and the length weight regression; K = the Brody growth constant from the von Bertalanffy model; β = the incomplete beta function; $X = e^{-Kr}$; $X_1 = e^{-K(\text{Max Age} - t0)}$, Max Age is the maximum age from the sample; P = Z/K; Q = slope of the weight-length regression. Several parameters are needed to run the simulation models using FAST. Information regarding the growth, longevity, and weight-length regression was calculated from the data collected during this study (Table 2).

The effect of harvest on the reproductive potential of the population was estimated by simulating the spawning potential ratio (SPR). The SPR has been used extensively in marine systems (Goodyear 1993) and has recently been used to determine the point of recruitment overfishing in freshwater systems (Quist et al. 2002, Slipke et al. 2002). The SPR estimates the number of eggs produced in a harvested fishery compared to an unexploited one by estimating the lifetime fecundity potential of recruits (Goodyear 1993).

Simulations were designed to determine how management strategies such as exclusion of adults from spawning areas or direct removal of individuals through eradication (e.g., with rotenone in shallow backwaters) might affect the production and reproductive potential of populations. Harvesting gears are age- and size-selective and different life stages have different movement patterns and habitat preferences. As such, management strategies are likely to differ in their size and age-dependent impact on populations. The model evaluated how management that excludes or removes individuals at different minimum lengths and ages affects population dynamics (Table 2).

For a hypothetical silver carp population of 1,000 individuals, highest catch or removal of individuals would be for gear or barriers that target individuals larger than or equal to 100 mm total length at high rates (50 percent; Figure 6). This would be the lower right-hand quadrant of the resulting isocline graph (Figure 6), where about 54 percent of the population would be removed by the gear or prevented from moving to spawning areas by barriers. If possible, removing individuals smaller than 100 mm total length would incur a greater positive effect on catch rates/removal, although densities of young, small individuals are typically very high in populations making efficient removal difficult and costly.

Table 2
Selected Population Demographics and Parameters Used to Simulate the Effect of Size-Selective Removal or Barriers on Silver Carp Populations in the Upper Mississippi River System

Parameter	Value
L_∞	778 mm total length
K	0.6
t_0	-0.16
Conditional natural mortality[1]	0.6
Conditional induced mortality	0.0 – 0.5
Log (weight) : Log(length) coefficients	a = -5.7; b = 3.27
Age at sexual maturity[2]	2
Linear fecundity : length relationship[b]	a = 5700; b = 204
Percent of 2- to 3-year-old females spawning	50 percent
Percent of 4- to 5-year-old females spawning	100 percent
Maximum age	5
Vulnerable lengths for removal or exclusion	100-700 mm total length

[1] From analysis of catch curves in Williamson (2004).
[2] Williamson (2004)

The model produces an estimate of production (i.e. yield) per unit recruit. In most populations, production of biomass is maximized at intermediate harvest or removal as surviving individuals are released from intraspecific competition (Ricker 1975). Beyond this level of exploitation, removal of productive adults will begin to reduce population-level production. Removal of individuals greater than 300 mm total length, causing the equivalent of about 50 percent annual mortality, will result in compensatory responses of the population and actually increase population production of biomass (Figure 7). Reducing the vulnerable minimum total length below 300 mm will begin to reduce productive capacity of the population because small individuals will be removed before meeting their maximum growth capacity (Figure 7). The SPR of silver carp probably needs to decline below 30 percent for reproductive output to be substantively reduced (Goodyear 1993). Reduction of individuals greater than 300 mm total length and at rates exceeding 20 percent annual mortality are likely necessary to achieve this goal (Figure 8).

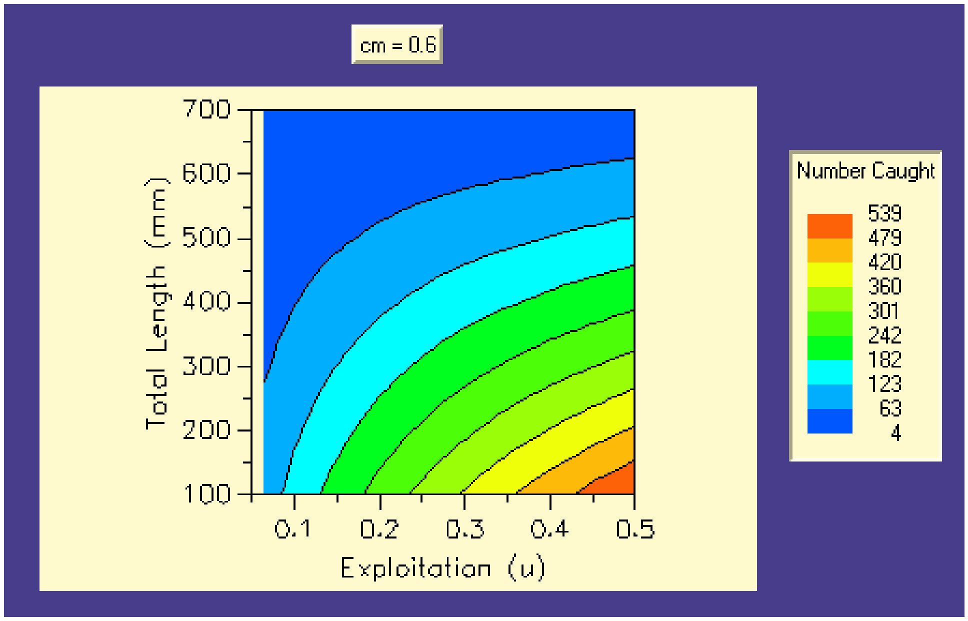

Figure 6. Potential impact of selective removal of ≥ minimum lengths (y-axis) of silver carp in a population of 1,000 fish with 60 percent natural annual mortality. As annual exploitation or exclusion of individuals increases from 0-50 percent (x-axis), the number caught or removed increases

These modeling results for the silver carp population suggest that, even with the high natural mortality rates experienced by this species (Williamson 2004), considerable additional loss of fish either through selective removal or exclusion from spawning areas would be necessary to significantly affect population dynamics. Current gears used to collect this species are quite selective for large-bodied individuals (Williamson and Garvey 2005). Because strong impacts on populations will not occur unless small individuals also are affected, programs to selectively remove this species will require greater efficiency at harvesting small fish, perhaps in areas such as backwaters where older, larger fish are not present.

Bighead carp appear to have slower population-level somatic growth rates, lower fecundity, higher survival, later maturity, and longer lives relative to silver carp. These life history characteristics should make this congener relatively more vulnerable to removal efforts targeted at young individuals that have not yet reached their reproductive potential.

The modeling assumes constant recruitment among years. This is not the case with either Asian carp species (Figure 2). Both species have variable reproductive output so succession of poor recruitment years (e.g., a prolonged drought and low river discharge) combined with concerted removal or exclusion efforts may have a greater impact on population persistence than modeling suggests.

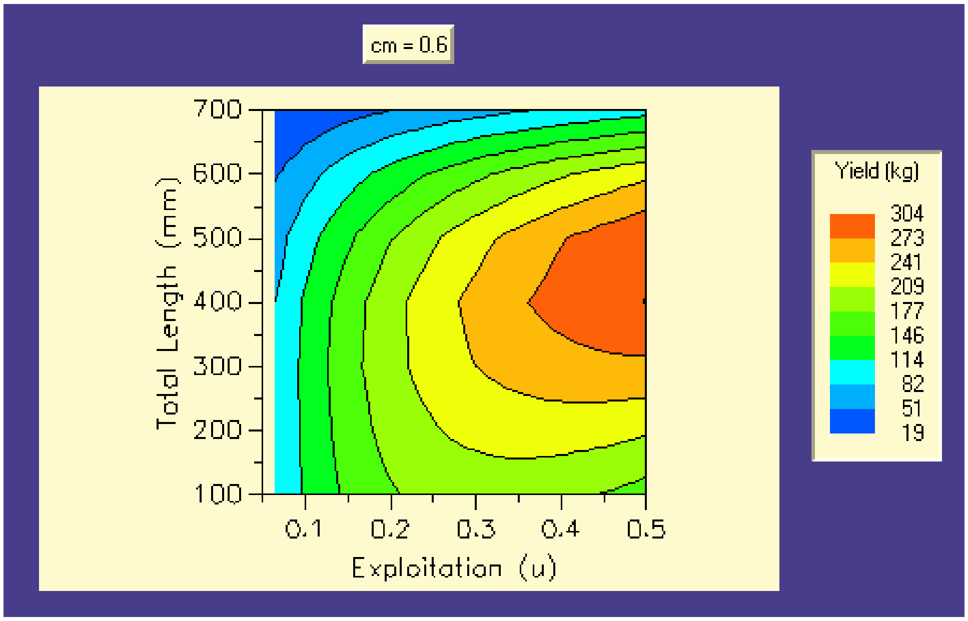

Figure 7. Production of biomass per each new recruit in a hypothetical population of silver carp with 60 percent natural annual mortality and varying vulnerable minimum total lengths (y-axis) and rates of removal or exclusion (x-axis)

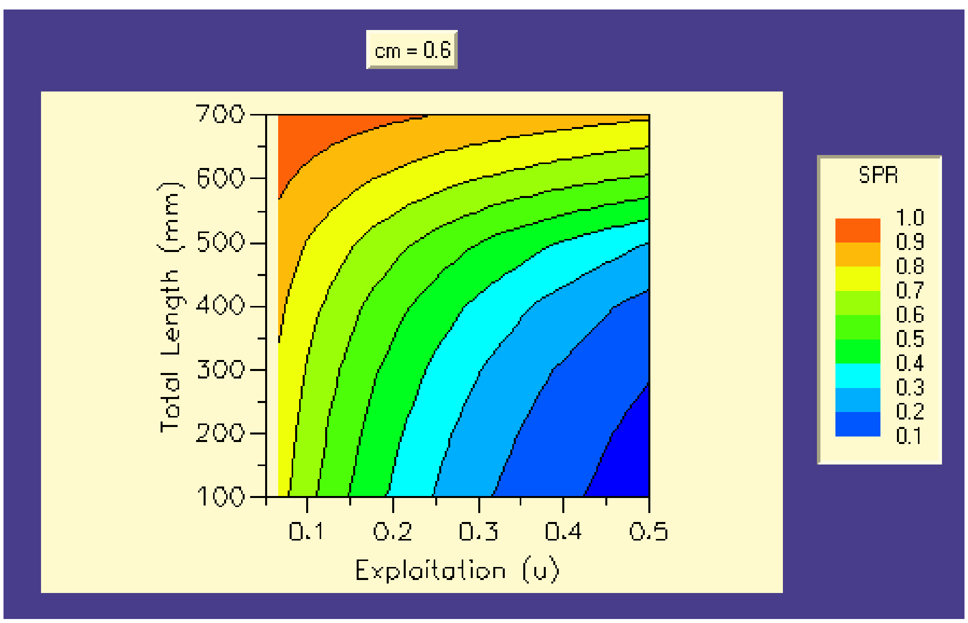

Figure 8. Spawning potential ratio (SPR) of a recruit in a hypothetical silver carp population as a function of minimum vulnerable length (y-axis) and rate of removal or exclusion (x-axis)

SUMMARY: Both species are well established in the United States, with bighead carp being present in 19 states, and silver carp occurring in at least 12 states (Fuller et al. 1999, Kolar et al. 2005). The populations in the unimpounded and impounded UMR system are particularly robust (Chick and

Pegg 2001), with the 2000 year class currently predominating. The unimpounded MMR reach is clearly providing adequate habitat for silver carp by providing algal resources behind wing dikes and perhaps other structures. Production of adults and offspring of both species is high in the CONFL area, although growth rates of silver carp were slightly lower in this reach. Given that density data for populations are lacking, it is impossible to determine whether differences in growth are due to density-dependent, intraspecific competition for food resources (i.e., carrying capacity is being approached in the CONFL reach) or other factors. To illustrate, growth of fishes depends on seasonal temperature. Temperature differences between reaches may have affected growth patterns. Similarly, food quantity and quality may have differed between the MMR and CONFL areas affecting growth patterns. The high inter-annual variability in production of cohorts suggests that reproductive success of both species varies with annual climatic conditions (e.g., precipitation) and that wide fluctuations in population density will be likely. The high reproductive capacity of both species, in particular silver carp, ensures that attempts to exclude or remove individuals will require a massive undertaking that targets young, small-bodied fish as well as adults. If barriers such as species-selective acoustic bubble curtains or strobes are emplaced (Pegg and Chick 2002), attempts at reducing extant populations entrained behind barriers should occur following a series of successive year-class failures. Given the apparent dependency of reproduction and offspring production on flow rates, summer impoundment and interruption of flow during drought years may inhibit reproduction in these areas. Thus, the pooled portions of the UMR and Illinois River may be the best candidates for implementing a series of barriers combined with population reduction. The cause and extent of the fish kill of Asian carp currently occurring (spring 2006) in the Illinois River is unknown. However, the pre-mortality data herein will provide a baseline by which population responses can be compared, ultimately providing a natural test of the efficacy of human-induced removal or exclusion.

POINT OF CONTACT: For additional information, contact Dr. Jack Killgore (601-634-3397), the author, Dr. James E. Garvey (618-536-7761, *jgarvey@siu.edu*), or the manager of the Aquatic Nuisance Species Research Program, Mr. Glenn Rhett (601-634-3171). This technical note should be cited as follows:

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