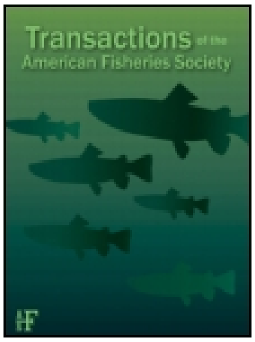

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Competitive Interactions between Age-0 Bighead Carp and Paddlefish

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Abstract.—The effects of bighead carp *Hypophthalmichthys nobilis* on native planktivores in the USA is unknown. The objectives of this study were to experimentally test for competitive interactions between age-0 bighead carp and age-0 paddlefish *Polyodon spathula*. Differences among water chemistry variables, invertebrate densities, and relative growth of fish were assessed in mesocosms. Water chemistry variables were similar among treatments throughout the experiment and only exhibited a temporal effect. Zooplankton density declined in mesocosms after fish were introduced. In general, zooplankton densities did not differ among treatments but did differ from the control. The relative growth of paddlefish was negative in the paddlefish and paddlefish–bighead carp treatments. The relative growth of bighead carp was negative in the bighead carp treatment but positive in the paddlefish–bighead carp treatment. Age-0 paddlefish exhibited the greatest decrease in relative growth in mesocosms with bighead carp. Bighead carp exhibited the greatest increase in relative growth in mesocosms with paddlefish. These data suggest that bighead carp have the potential to negatively affect the growth of paddlefish when food resources are limited.

The effects of introduced exotic fish on native fish populations and aquatic communities have been documented in the USA (Taylor et al. 1984). Many fish introductions have occurred from accidental escapement of fishes from aquaculture facilities (e.g., bighead carp *Hypophthalmichthys nobilis*, silver carp *H. molitrix*, blue tilapia *Tilapia aurea*; Courtenay and Williams 1992; Davidson et al. 1992). Aquatic communities that are depauperate of species and disturbed aquatic ecosystems are most often affected by introduced species (Herbold and Moyle 1986; Ross 1991). The Missouri River has undergone many alterations since the turn of the century, and in 1997 it was rated the most endangered river in North America (Pflieger and Grace 1987; American Rivers 1997). Bighead carp numbers have increased in the Missouri River since they were introduced into the USA in the 1970s, but the effects of bighead carp on the altered aquatic communities of the Missouri River are unknown (Freeze and Henderson 1982; Tucker et al. 1996; Pflieger 1997; Robinson 1998; Fuller et al. 1999).

Paddlefish populations have been declining in major river systems since 1900 because of overexploitation, habitat alterations, and habitat destruction (Russell 1986; Graham 1997). The introduction of bighead carp may further affect paddlefish through competition for food resources (Pflieger 1997) because both species are planktivores that consume similar food items (copepods, cladocerans, insect larvae, and amphipods) of the same size; that is, gill raker spacing is similar for bighead carp (85 μm) and paddlefish (60–90 μm; Cremer and Smitherman 1980; Rosen and Hales 1981; Hageman et al. 1988; Hoxmeier and DeVries 1997). However, bighead carp are able to produce a mucous in their gill rakers to trap smaller food items (nauplii, rotifer, and phytoplankton) during periods when zooplankton densities are low (Cremer and Smitherman 1980; Jennings 1988; Opuszynski et al. 1991; Dong and Li 1994; Takamura et al. 1993; Gu et al. 1996).

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Identifying competition between two species and within a species is difficult, but some indicators are useful in demonstrating competition (Crowder 1990). Three conditions must exist for competition to occur: (1) organisms must share a common resource, (2) resources must be limited, and (3) there must be a negative effect on growth or some other measure of fitness (Crowder 1990). The objective of this study was to assess interspecific competition between bighead carp and paddlefish through a manipulative experiment. Interspecific competition for this study was defined as the selection by paddlefish and bighead carp for food resources from the environment that are in excess of immediate supply, as identified by the differential growth response (Larkin 1956).

Methods

Experimental ponds at the Columbia Environmental Research Center in Columbia, Missouri, were used from 3 August to 14 September 1999. A randomized complete block design was used to assess the competitive interactions between age-0 bighead carp and age-0 paddlefish. Four ponds were the blocking factor, and the experimental units were four mesocosms in each pond. Circular mesocosms were constructed of reinforced polyethylene (impermeable) and had a sealed bottom to prevent contact with the benthos. Each mesocosm had a diameter of 3.1 m and height of 2.0 m (volume = 14.6 m^3). The four mesocosms per pond included three treatments and one control: six bighead carp, six paddlefish, three bighead carp and three paddlefish (mix), and no fish (control). Treatments were randomly assigned within each pond, and mesocosms were placed in ponds on 3 August 1999. There were four replications of each treatment and control. Three bighead carp were missing from a mix treatment at the end of the study; therefore, this mesocosm was removed from all analyses. Therefore, the mix treatment only had three replicates for all analyses.

Water chemistry variables in each mesocosm were assessed before addition of fish and weekly during the experiment. Dissolved oxygen (mg/L) and water temperature (°C) were measured with a YSI Model 85 probe at the surface and at 1.5 m deep. Conductivity (μS), turbidity (nephelometric turbidity units [NTU]), and pH were measured at the surface with a YSI model 85 probe, a Hach 2100P Turbidimeter, and a Hach EC10 pH meter, respectively. To evaluate phytoplankton abundance, we measured suspended chlorophyll *a* (mg/L) in surface water samples (150 mL) taken from each mesocosm each week (APHA et al. 1998; Schrank 2000). We also measured attached chlorophyll *a* (mg/cm^2) to index periphyton abundance by suspending six 10-cm^2 strips of plastic within each mesocosm. One strip was removed weekly and analyzed for attached chlorophyll *a*.

Before introducing fish into the mesocosms and weekly during the experiment, invertebrate samples were taken with a 80-μm-mesh Wisconsin plankton net (diameter, 127 mm). One vertical tow (2 m) was taken in each mesocosm and contents were placed in 200 mL of 10% formalin for identification and enumeration in the laboratory. Invertebrates were identified to the lowest possible taxa using keys by Needham and Needham (1962) and Merritt and Cummins (1996). From these subsamples a mean was calculated and extrapolated to estimate the number of invertebrate taxa per liter. Zooplankton in three, 5-mL subsamples from each sample were identified and counted (Schrank 2000) using a zooplankton wheel (Wetzel and Likens 1991).

We were concerned that the fish would consume all available prey in the mesocosms before the completion of the experiment. Thus, invertebrates were added to each mesocosm weekly (including control) after water chemistry variables and invertebrate samples had been taken. Invertebrates were acquired from water surrounding the mesocosms. A diaphragm pump was used to pump 1,000 L of water from ponds and then water was filtered through an 80-μm-mesh bucket. For replacement in each mesocosm, filtered water was mixed continuously while subsamples were taken. Weekly, three to seven replacement subsamples were preserved in 10% formalin and enumerated in the laboratory following the same procedure as the invertebrate samples.

Age-0 bighead carp (204–212 mm total length) and paddlefish (273–295 mm body length) were stocked into mesocosms on 10 August 1999. Only bighead carp and paddlefish with fully developed gill rakers were used, which simulated adult feeding (Cremer and Smitherman 1980; Rosen and Hales 1981; Michaletz et al. 1982). Length (mm) and weight (g) of each fish were recorded before placement into mesocosms and at completion of the experiment. On 14 September 1999, ponds were drained and all fish were removed from mesocosms. Relative growth (i.e., [final weight − initial weight]/initial weight) was calculated for each mesocosm, and mean relative growth was calculated for each treatment (Busacker et al. 1990). Gill raker spacing was measured on the anterior

TABLE 1.—Pooled mean, minimum, maximum, and standard error (SE) values for water chemistry and zooplankton (number/L) data in mesocosms in experimental ponds, 15 August to 14 September 1999, where competitive interactions between bighead carp and paddlefish were investigated.

Variable	Mean	Minimum	Maximum	SE
Chlorophyll *a*, suspended (mg/L)	0.1	0.0	0.1	0.0
Chlorophyll *a*, attached (mg/cm)	0.6	0.4	1.0	0.1
Conductivity (μS)	638	617	667	3.4
Dissolved oxygen, surface (mg/L)	10.4	9.8	11.2	0.1
Dissolved oxygen, 1.5-m depth (mg/L)	11.4	10.6	12.5	0.1
pH	8.3	8.1	8.5	0.0
Temperature, surface (°C)	24.8	23.9	25.3	0.1
Temperature, 1.5-m depth (°C)	23.7	23.1	24.1	0.1
Turbidity (nephelometric turbidity units)	4.3	3.3	5.7	0.2
Total zooplankton density	62.7	14.3	193.2	11.8
Bosmina spp.	0.8	0.0	3.9	0.3
Calanoidae	0.4	0.0	2.5	0.2
Cyclopoidae	9.7	2.1	21.8	1.6
Daphnia pulex	18.5	0.7	87.0	6.0
Nauplii	23.7	2.8	71.7	5.1
Rotifer	9.6	3.9	16.4	1.0

side of the first gill arch (left side) for 10 bighead carp and 6 paddlefish (Rosen and Hales 1981). The distance between gill rakers was measured (0.01 mm) within 1 mm of the base of the gill rakers with an optical image analysis system.

Mixed-model analysis of variance (ANOVA) was used to determine whether water chemistry variables and zooplankton densities differed among treatments before the experiment. Two-way ANOVA with repeated measures was used to compare the change in water chemistry variables by date and among treatments (Littell et al. 1996). We used an autoregressive order-1 covariance matrix with ponds as blocks. Temperature, suspended chlorophyll *a*, and attached chlorophyll *a* did not fit this covariance matrix structure, so instead we used the compound symmetric covariance matrix without a blocking factor. We used least-squares means to compare significant treatment main effects. When significant interactions occurred, least-square means were used to examine differences between treatments on individual sampling dates (Milliken and Johnson 1992). Mixed model ANOVA with ponds as blocks was used to test for the change in relative growth of bighead carp and paddlefish between treatments. Sample size was four for paddlefish and bighead carp treatments and three for the mixed treatment. All statistical analyses were performed using SAS (SAS Institute 1996). Statistical significance was set a posteriori at $\alpha = 0.20$ because we were concerned about the probability of committing a type II error at $\alpha = 0.05$ (type I error).

Results

Chlorophyll *a* (suspended and attached), conductivity, dissolved oxygen, pH, turbidity, and water temperature were consistent throughout the study (Table 1) and did not differ significantly ($F = 0.03-1.83$, $P = 0.34-0.99$) among mesocosms before fish introductions, except for suspended chlorophyll *a* ($F = 1.83$, $P = 0.20$). After fish were introduced into the mesocosms, surface and 1.5-m temperature, turbidity, conductivity, pH, suspended chlorophyll *a*, and attached chlorophyll *a* differed significantly by date ($F = 3.69-374.7$, $P = 0.02$ to <0.0001) but not among treatments ($F = 0.25-1.51$, $P = 0.26-0.98$). However, dissolved oxygen at the surface and at 1.5 m differed significantly among treatments ($F = 4.16-4.99$, $P = 0.01-0.02$) and dates ($F = 29.5-36.9$, $P < 0.0001$). In general, dissolved oxygen was higher in the control than the mixed treatment.

Ten invertebrate taxa were identified in the mesocosms. Chironomidae, Conchostraca, Ephemeroptera, and Odonata had densities of less than 3 individuals/L and were present in less than 50% of the mesocosms. Therefore, further analyses were not performed on these taxa. Predominant zooplankton included copepods (cyclopoid, calanoid, and nauplii), cladocerans (*Daphnia pulex* and *Bosmina* spp.), and rotifers (Table 1). The density (number/L) of predominant zooplankton varied throughout the study (Table 1) but did not differ significantly among mesocosms before introduction of fish ($F = 0.19-1.62$, $P = 0.25-0.90$). After fish were placed in the mesocosms, mean

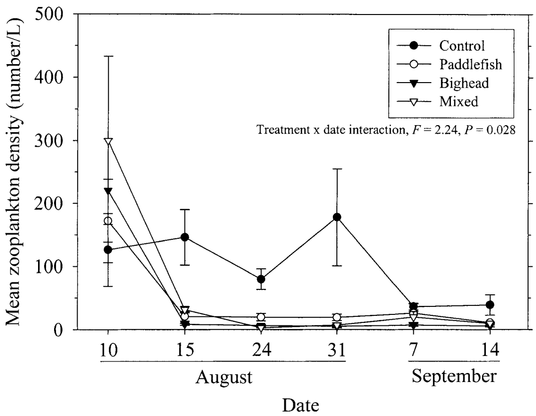

FIGURE 1.—Mean zooplankton density for samples collected from 10 August (before fish introduction) to 14 September 1999 for four treatments (bighead carp, paddlefish, paddlefish and bighead carp [mixed], and control) in experimental ponds. Error bars represent one standard error. Two-way analysis of variance with repeated measures was used to statistically compare changes by date and treatment. Statistics presented represent the treatment × date interaction.

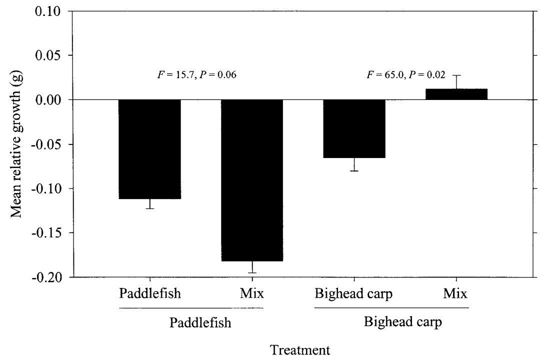

FIGURE 2.—Relative growth (i.e., [final weight − initial weight]/initial weight) of paddlefish and bighead carp by treatment (paddlefish, paddlefish and bighead carp [mix], and bighead carp) held in mesocoms in experimental ponds, 10 August to 14 September 1999. Statistics presented are from a mixed-model analysis of variance comparing relative growth within a species by treatment. Error bars represent one standard error.

zooplankton density declined in all treatments (Figure 1) and subsequently zooplankton density never exceeded 30/L in the paddlefish treatment, 10/L in the bighead carp treatment, and 35/L in the mixed treatment. There was a significant treatment × date interaction for mean zooplankton density ($F = 2.24$, $P = 0.028$). Mean zooplankton density did not differ significantly among treatments on 15, 24, and 31 August and 14 September ($t = -1.03$ to 1.21, $P = 0.25-0.97$). On 7 September mean zooplankton density in the paddlefish treatment was significantly higher than the bighead carp treatment ($t = -1.53$, $P = 0.16$). Mean zooplankton density was significantly different among treatments and control on all dates except 7 September ($t = -5.73$ to 5.55, $P = 0.0001-0.05$). On 7 September, mean zooplankton density did not differ significantly between the paddlefish treatment and the control ($t = 0.82$, $P = 0.43$) nor between the mixed treatment and control ($t = 1.23$, $P = 0.24$).

Bighead carp initial mean total length was 208 mm (SE = 1.3) and initial mean weight was 87.9 g (1.2). Paddlefish initial mean body length was 282 mm (4.2) and initial mean weight was 77.1 g (3.1). Relative growth varied from 0.05 to −0.09 for bighead carp and from −0.10 to −0.20 for paddlefish. Relative growth of paddlefish decreased in all treatments and differed significantly between the paddlefish-only and mix treatments ($F = 15.7$, $P = 0.058$; Figure 2). Relative growth of bighead carp differed significantly between treatments ($F = 65.04$, $P = 0.02$; Figure 2). Bighead carp in the bighead carp treatment decreased in relative growth, whereas bighead carp in the mix treatment increased in relative growth.

Discussion

Any variation observed in chlorophyll *a*, conductivity, pH, turbidity, and water temperature was a function of temporal effects, not treatment effects. Conversely, variation in zooplankton density was a function of treatment effects. After fish were introduced, zooplankton density in the mesocosms was reduced. The reduction in zooplankton relative to the control indicates that paddlefish and bighead carp were feeding on zooplankton in the mesocosms. The decline in zooplankton observed in this study was similar to results for other studies on paddlefish (Burke and Bayne 1986) and bighead carp (Burke et al. 1986; Lieberman 1996) in culture ponds. Unfortunately, we are unaware of any studies documenting the effects of paddlefish and bighead carp on zooplankton communities in natural systems. The low density of zooplankton in the treatments with fish suggests that food was limited. Zooplankton density in the mesocosms was lower than those reported for the Missouri River near main-stem reservoirs (Repsys and Rogers 1982). However, zooplankton densities tend to be higher near reservoir effluents and decline downstream (Repsys and Rogers 1982). We were unable to find any comparable zooplankton density data for areas where bighead carp and paddlefish occur sympatrically. Zooplankton assemblage in the mesocosms was similar to the assemblage in the Missouri River, which is a function of zooplankton taxa in the Missouri River being common throughout the USA (Repsys and Rogers 1982).

The predominant zooplankton taxa in the mesocosms were similar to food items known to be eaten by paddlefish and bighead carp. Paddlefish in rivers and experimental ponds feed on *Bosmina* spp., *Daphnia pulex*, *Dipahnosoma* spp., cyclopoid and calanoid copepods, amphipods, and insect larvae (Rosen and Hales 1981; Burke and Bayne 1986; Hageman et al. 1988; Hoxmeier and DeVries 1997). Stomach content analysis of paddlefish indicates that they do not feed on invertebrates less than 0.025 mm (Rosen and Hales 1981; Burke and Bayne 1986; Hoxmeier and DeVries 1997). Studies on bighead carp found that cladocerans, copepods, and rotifers are important food items, and bighead carp can switch to phytoplankton when zooplankton concentrations are low (Lazareva et al. 1978; Cremer and Smitherman 1980; Opuszynski 1981; Spataru et al. 1983; Burke et al. 1986; Opuszynski et al. 1991; Takamura et al. 1993; Dong and Li 1994; Gu et al. 1996; Lieberman 1996).

The relative growth of paddlefish decreased in all treatments, indicating that food resources were limiting. However, there was a larger decrease in relative growth of paddlefish in the mix treatment than in the paddlefish treatment. Paddlefish relative growth was negatively affected by interspecific competition. Relative growth of paddlefish and bighead carp appeared to be negatively affected by intraspecific competition. However, to adequately evaluate intraspecific competition, we would have needed treatments that increased or decreased the density relative to the paddlefish or bighead carp only treatments (Schoener 1983). We were unfortunate to not have the space and time for such an analysis; therefore, this is an area for further investigation. Interestingly, paddlefish had the lowest relative growth in the treatment that probably provided an intraspecific competitive release.

Bighead carp performed better in the mix treatment than in the bighead carp treatment, and paddlefish performed worse in the mix treatment than in the paddlefish treatment. These results indicate that asymmetric competition was occurring in the mix treatment and that bighead carp were probably the dominant competitor (Keddy 1989). The difference in performance between bighead carp and paddlefish in the mix treatment may be caused by exploitative competition, morphological differences, or interference competition (Keddy 1989; Hiram and Moyle 1993). Probably, exploitative competition was occurring; that is, in the mix treatment, bighead carp may have fed more quickly or efficiently than paddlefish and thus depleted the food resources for paddlefish. In experimental and population studies on other zooplanktivores, exploitative competition caused a decrease in the growth rates of one species (Hanson and Leggett 1985; Prout et al. 1990; DeVries and Stein 1992; Teuscher and Luecke 1996). This explanation is partially supported by the higher mean density of zooplankton in the paddlefish treatment than the bighead carp treatment.

There are also morphological differences between the bighead carp and paddlefish. Bighead carp and paddlefish consume similar-sized zooplankton; for example, in this study bighead carp gill raker spacing varied from 0.07 to 0.08 mm and paddlefish from 0.05 to 0.06 mm. However, bighead carp can switch to smaller food items when large zooplankton are limited (Dong and Li 1994). The ability of bighead carp to switch food items (i.e., from zooplankton to phytoplankton) may be an ecological advantage over paddlefish. Many fish have the ability to switch diets to avoid competition (Larkin 1956). We were unable to detect a change in the small invertebrates among treatments because the mesh size of the invertebrate net was 80 μm. Finally, bighead carp may have prevented paddlefish from consuming invertebrates through aggressive behavior or interference competition.

Paddlefish and bighead carp probably use similar habitats within large river ecosystems; thus, they potentially compete for food resources. However, for competition to occur, food resources need to be limiting (Larkin 1956). Assessments of zooplankton and phytoplankton in large river ecosystems are difficult to quantify and probably vary temporally and spatially (Basu and Pick 1995). This study supports the hypothesis that bighead carp can negatively affect paddlefish through competition for zooplankton and establishes the possibility that competition can occur in the Mississippi River or Missouri River, given a scenario similar to this study. This study probably represents the worst-case scenario for competitive interactions between bighead carp and paddlefish.

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References

American Rivers. 1997. North America's most endangered and threatened rivers of 1997. American Rivers, Washington D.C.

APHA (American Public Health Association), American Water Works Association, and Water Environment Federation. 1998. Standard methods for the examination of water and wastewater, 20th edition. APHA, Washington, D.C.

Basu, B. K., and F. R. Pick. 1995. Longitudinal and seasonal development of planktonic chlorophyll *a* in the Rideau River, Ontario. Canadian Journal of Fisheries and Aquatic Sciences 52:804–815.

Burke, J. S., and D. R. Bayne. 1986. Impact of paddlefish on plankton and water quality in catfish ponds. Progressive Fish-Culturist 48:177–183.

Burke, J. S., D. R. Bayne, and H. Rea. 1986. Impact of silver and bighead carp on the plankton communities of channel catfish ponds. Aquaculture 55:59–68.

Busacker, G. P., I. R. Adelman, and E. M. Goolish. 1990. Growth. Pages 363–387 *in* C. B. Schreck and P. B. Moyle, editors. Methods for fish biology. American Fisheries Society, Bethesda, Maryland.

Courtenay, W. R., Jr., and J. D. Williams. 1992. Dispersal of exotic species from aquaculture sources, with emphasis on freshwater fishes. Pages 49–81 *in* A. Rosenfield and R. Mann, editors. Dispersal of living organisms into aquatic ecosystems. University of Maryland, Sea Grant Publication, College Park.

Cremer, M. C., and R. O. Smitherman. 1980. Food habits and growth of silver and bighead carp in cages and ponds. Aquaculture 20:57–64.

Crowder, L. B. 1990. Community ecology. Pages 609–632 *in* C. B. Schreck and P. B. Moyle, editors. Methods for fish biology. American Fisheries Society, Bethesda, Maryland.

Davidson, J. R., J. A. Brock, and L. G. L. Young. 1992. Introduction of exotic species for aquaculture purposes. Pages 83–101 *in* A. Rosenfield and R. Mann, editors. Dispersal of living organisms into aquatic ecosystems. University of Maryland, Sea Grant Publication, College Park.

DeVries, D. R., and R. A. Stein. 1992. Complex interactions between fish and zooplankton: quantifying the role of an open-water planktivore. Canadian Journal of Fisheries and Aquatic Sciences 49:1216–1227.

Dong, S., and D. Li. 1994. Comparative studies on the feeding selectivity of silver carp *Hypophthalmichthys molitrix* and bighead carp *Aristichthys nobilis*. Journal of Fish Biology 44:621–626.

Freeze, M., and S. Henderson. 1982. Distribution and status of the bighead carp and silver carp in Arkansas. North American Journal of Fisheries Management 2:197–200.

Fuller, P. L., L. G. Nico, and J. D. Williams. 1999. Nonindigenous fishes introduced into inland waters of the United States. American Fisheries Society, Special Publication 27, Bethesda, Maryland.

Graham, K. 1997. Contemporary status of the North American paddlefish, *Polyodon spathula*. Environmental Biology 48:279–289.

Gu, B., D. M. Schell, X. Huang, and F. Yie. 1996. Stable isotope evidence for dietary overlap between two planktivorous fishes in aquaculture ponds. Canadian Journal of Fisheries and Aquatic Sciences 53:2814–2818.

Hageman, J. R., D. C. Timpe, and R. D. Hoyt. 1988. The biology of the paddlefish in Lake Cumberland, Kentucky. Proceedings of the Annual Conference Southeastern Association of Fish and Wildlife agencies 40(1986):237–248.

Hanson, J. M., and W. C. Leggett. 1985. Experimental and field evidence for inter- and intraspecific competition in two freshwater fishes. Canadian Journal of Fisheries and Aquatic Sciences 42:280–286.

Herbold, B., and P. B. Moyle. 1986. Introduced species and vacant niches. American Naturalist 128:751–760.

Hiram, W. L., and P. B. Moyle. 1993. Management of introduced fishes. Pages 287–308 *in* C. C. Kohler and W. A. Hubert, editors. Inland fisheries management in North America. American Fisheries Society, Bethesda, Maryland.

Hoxmeier, R. J., and D. R. DeVries. 1997. Habitat use, diet, and population structure of adult and juvenile paddlefish in the lower Alabama River. Transactions of the American Fisheries Society 126:288–301.

Jennings, D. P. 1988. Bighead carp (*Hypophthalmichthys nobilis*): a biological synopsis. U.S. Fish and Wildlife Service Biological Report 88.

Keddy, P. A. 1989. Competition. Chapman and Hall, New York.

Larkin, P. A. 1956. Interspecific competition and population control in freshwater fish. Journal of the Fisheries Research Board of Canada 13:327–342.

Lazareva, L. P., M. O. Omarov, and A. N. Lezina. 1978. Feeding and growth of the bighead, *Aristichthys nobilis*, in waters of Dagestan. Journal of Ichthyology 17:65–75.

Lieberman, D. M. 1996. Use of silver carp (*Hypophthalmichthys molotrix*) and bighead carp (*Aris-*

tichthys nobilis) for algae control in a small pond: changes in water quality. Journal of Freshwater Ecology 11:391–397.

Littell, R. C., G. A. Milliken, W. W. Stroup, and R. D. Wolfinger. 1996. SAS system for mixed models. SAS Institute, Cary, North Carolina.

Merritt, R. W., and K. W. Cummins. 1996. The introduction to the aquatic insects of North America, 3rd edition. Kendall/Hunt, Boston.

Michaletz, P. H., C. F. Rabeni, W. W. Taylor, and T. R. Russell. 1982. Feeding ecology and growth of young-of-the-year paddlefish in hatchery ponds. Transactions of the American Fisheries Society 111: 700–709.

Milliken, G. A., and D. E. Johnson. 1992. Analysis of messy data, volume 1: designed experiments. Chapman and Hall, New York.

Needham, J. G., and P. R. Needham. 1962. A guide to the study of fresh-water biology, 5th edition. McGraw-Hill, New York.

Opuszynski, K. 1981. Comparison of the usefulness of the silver carp and the bighead carp as additional fish in carp ponds. Aquaculture 25:223–233.

Opuszynski, K., J. V. Shireman, and C. E. Cichra. 1991. Food assimilation and filtering rate of bighead carp kept in cages. Hydrobiologia 220:49–56.

Pflieger, W. L. 1997. The fishes of Missouri, 2nd edition. Missouri Department of Conservation, Jefferson City.

Pflieger, W. L., and T. B. Grace. 1987. Changes in the fish fauna of the lower Missouri River, 1940–1983. Pages 166–177 *in* W. J. Mathews and D. C. Heins, editors. Community and evolutionary ecology of North American stream fishes. University of Oklahoma Press, Norman.

Prout, M. W., E. L. Mills, and J. L. Forney. 1990. Diet, growth, and potential competitive interactions between age-0 white perch and yellow perch in Oneida Lake, New York. Transactions of the American Fisheries Society 119:966–975.

Repsys, A. J., and G. D. Rogers. 1982. Zooplankton studies in the channelized Missouri River. Pages 125–145 *in* L. W. Hesse, G. L. Hergenrader, H. S. Lewis, S. D. Reetz, and A. B. Schlesinger, editors. The middle Missouri River. Missouri River Study Group, Norfolk, Nebraska.

Robinson, J. W. 1998. Missouri commercial fish harvest 1994–1996. Missouri Department of Conservation, Final Report, Columbia.

Rosen, R. A., and D. C. Hales. 1981. Feeding of paddlefish, *Polyodon spathula*. Copeia 1981:441–455.

Ross, S. T. 1991. Mechanisms structuring stream fish assemblages: are there lessons from introduced species. Environmental Biology of Fishes 30:359–368.

Russell, T. R. 1986. Biology and life history of the paddlefish—a review. Pages 2–21 *in* J. G. Dillard, L. K. Graham, and T. R. Russell, editors. The paddlefish: status, management and propagation. American Fisheries Society, North Central Division, Special Publication 7, Bethesda, Maryland.

SAS Institute. 1996. SAS/STAT user's guide, version 6.11. SAS Institute, Cary, North Carolina.

Schoener, T. W. 1983. Field experiments on interspecific competition. American Naturalist 122:240–285.

Schrank, S. J. 2000. Population characteristics of bighead carp *Hypophthalmichthys nobilis* larvae and adults in the Missouri River and interspecific dynamics with paddlefish *Polyodon spathula*. Master's thesis. Kansas State University, Manhattan.

Spataru, P., G. W. Wohlfarth, and G. Hulata. 1983. Studies on the natural food of different fish species in intensively manured polyculture ponds. Aquaculture 35:283–298.

Takamura, N., J. L. Li, H. Q. Yang, X. B. Zhu, and T. Miura. 1993. A novel approach to evaluate feeding by mixed cyprinids species in a Chinese integrated fish culture pond using measurements of chlorophyll derivatives and photosynthesis in gut contents. Canadian Journal of Fisheries and Aquatic Sciences 50:946–952.

Taylor, J. N., W. R. Courtenay, Jr., and J. A. McCann. 1984. Known impacts of exotic fishes in the continental United States. Pages 322–373 *in* W. R. Courtenay, Jr. and J. R. Stauffer, Jr., editors. Distribution, biology and management of exotic fishes. Johns Hopkins University Press, Baltimore, Maryland.

Teuscher, D., and C. Luecke. 1996. Competition between Kokanees and Utah chub in Flaming Gorge Reservoir, Utah–Wyoming. Transactions of the American Fisheries Society 125:505–511.

Tucker, J. K., F. A. Cronin, R. A. Hrabik, M. D. Peterson, and D. P. Herzog. 1996. The bighead carp (*Hypophthalmichthys nobilis*) in the Mississippi River. Journal of Freshwater Ecology 11:241–243.

Wetzel, R. G., and G. E. Likens. 1991. Limnological analyses, 2nd edition. Springer-Verlag, New York.