

## Research Article

## Mesohabitat associations in the Mississippi River Basin: a long-term study on the catch rates and physical habitat associations of juvenile silver carp and two native planktivores

Kevin J. Haupt<sup>1,2\*</sup> and Quinton E. Phelps<sup>1</sup>

<sup>1</sup>Big Rivers and Wetlands Field Station, Missouri Department of Conservation, 3815 East Jackson Boulevard, Jackson, Missouri, 63755 USA

<sup>2</sup>Southeast Missouri State University, Biology Department, 1 University Plaza, Cape Girardeau, Missouri, 63701 USA

\*Corresponding author

E-mail: [khaupt@dnr.in.gov](mailto:khaupt@dnr.in.gov)

Received: 5 November 2014 / Accepted: 19 October 2015 / Published online: 21 December 2015

Handling editor: Vadim Panov

### Abstract

Fish community structure is a complex and integrated part of an aquatic ecosystem; a balanced system is often rich in species diversity and abundance. Invasive species can alter this balance, and the expansion of invasive silver carp may have similar deleterious effects. Recently, catches of silver carp in the Midwestern United States have increased and there is evidence of successful spawning and recruitment. However, early life history attributes of silver carp have not been fully evaluated within the Mississippi River Basin. A thorough understanding of early-life history is imperative to facilitate control efforts for silver carp populations. Furthermore, age-0 silver carp survival and subsequent recruitment may be regulated by habitat availability during this critical life stage. Thus, the objective of this study was to evaluate age-0 silver carp mesohabitat (i.e., depth, velocity, and substrate) use in three reaches of the Mississippi River Basin and potential habitat overlap with two native planktivorous fish species, gizzard shad *Dorosoma cepedianum* and emerald shiner *Notropis atherinoides*. Using data collected from the three lower most reaches of the Long Term Resource Monitoring Program (Pool 26 at Alton, Illinois, USA; Open River at Cape Girardeau, Missouri, USA of the Mississippi River; and the LaGrange reach at Havana, Illinois, USA of the Illinois River), we investigated age-0 silver carp, age-0 gizzard shad and age-0 emerald shiner habitat associations from 2007 to 2012. Overall, 79,358 age-0 silver carp, 89,990 gizzard shad and 41,119 emerald shiner were captured with mini fyke nets during this long-term study. Generally, all three species were collected most frequently in shallow (< 1.5 meters), low velocity (<0.6 meters/second) habitat with greater variability in substrate use ranging from silt to rock. Given the scarcity of these habitat types in the channelized Mississippi River Basin, our results suggest that invasive silver carp exhibit habitat overlap with gizzard shad and emerald shiner. This overlap may result in reduced growth and body condition of these fishes. To this end, this extensive data set has provided new information about silver carp early life history mesohabitat use and overlap occurring between two age-0 native planktivores in the Mississippi River Basin and potential consequences of this association.

**Key words:** invasion, silver carp, gizzard shad, emerald shiner, early life history

### Introduction

Native fish communities have been affected by invasive fish introductions and these introductions can lead to the restructuring of fish communities (Ross 1991; Bronte et al. 2003). Historical accounts of changes in the aquatic community following the establishment of an invasive planktivore have occurred in systems as large as Lake Michigan (Wells 1970) and in smaller systems in northern Wisconsin (Hrabik et al. 1998) by alewife, *Alosa pseudoharengus* (Wilson, 1811) and rainbow smelt,

*Osmerus mordax* (Mitchill, 1814) respectively. These changes include the reduced abundance of large zooplankton populations (Wells 1970) as well as changes to the fish community by a reduction in numbers of native planktivores (Hrabik et al. 1998). The recent establishment of silver carp, *Hypophthalmichthys molitrix* (Valenciennes, 1844), a large, highly efficient planktivore, poses a similar threat to the zooplankton and fish communities in the Mississippi River Basin (Irons et al. 2007; Laird and Page 1996; Tucker et al. 1996). Furthermore, anthropogenic changes

(e.g. channelization and floodplain disconnectivity) to aquatic systems have likely contributed to the simplification of and less optimal habitat available to fishes. Also, invasive species, through competition, can further displace native fish from desired habitats (Byers 2002). Thus, a thorough understanding of habitat co-utilization is needed to understand the potential impact habitat overlap may have on the fish community structure (Werner and Hall 1979; Werner et al. 1983).

The objective of this study was to summarize data from the Long Term Resource Monitoring Program (LTRMP) to better understand the early life history attributes of age-0 silver carp, age-0 gizzard shad, *Dorosoma cepedianum* (Lesueur, 1818) and age-0 emerald shiner, *Notropis atherinoides* (Rafinesque, 1818). Potential associations between these planktivores were evaluated by comparing mesohabitat (i.e., depth, velocity, and substrate) use from three unique reaches of the Mississippi River Basin. Two advantages of this approach exist, the first being that the expansion of silver carp has been documented by the LTRMP which provides insight into early life history attributes of this species (Charlebois and TePas 2011). The second advantage is that this data set offers the ability to investigate potential habitat overlap that may occur between silver carp and two native planktivores over a large spatial and temporal scale (Chick et al. 2003). These species were chosen for the potential competition for food resources that may exist and the importance of gizzard shad and emerald shiner as a forage base for piscivorous fish. Furthermore, age-0 silver carp survival and subsequent recruitment may be regulated by habitat availability and utilization during this critical life stage. Evaluating potential habitat co-utilization among these species is essential in furthering our knowledge on potential impacts and alterations (i.e. shift in resource use by native fish, reduction in fitness and number of individuals after invasion) to this large river ecosystem.

## Methods

We used data collected from 2007–2012 in three reaches of the Upper Mississippi River Basin by the LTRMP to evaluate young-of-year mesohabitat use by gizzard shad, emerald shiner, and silver carp. This time frame was used as catches of silver carp in all three reaches allowed for relevant statistical analysis to be performed. Study areas consisted of the Alton reach (Alton, Illinois, RKM

325–389 of the Mississippi River), the LaGrange reach (LaGrange, Illinois, RKM 128–252 of the Illinois River ) and the Open River reach (Cape Girardeau, Missouri, RKM 47–129 of the Mississippi River). Mini-fyke nets (3mm mesh size, 4.5 meter lead, 0.6 meters high) were set annually from June 15 to October 30, 2007–2012, following the stratified random sampling design developed by Gutreuter et al. (1995). Each net was set for 24 hours with one net set at each site, with total effort summarized in Table 1. At each sampling location, mesohabitat data (i.e., depth, velocity, and substrate) was recorded following protocol developed by Gutreuter et al. (1995). Specifically, depth was recorded to the nearest 1 m intervals and water velocity was recorded to the nearest 0.1 m/s using a Marsh-McBirney flow meter. The sampling site consists of a 50 × 50 meter area, in which the net was placed; velocity and depth data were recorded simultaneously. Substrate was determined by visual and tactile observation of the predominant substrate within the 50 × 50 meter area, and categorized as silt, clay, sand, or gravel following Gutreuter et al. (1995).

To ensure only young-of-year fish were used in the analysis, fish with a total length greater than 270mm for silver carp (Irons et al. 2011), 100mm for gizzard shad (Ickes et al. 2005a) and 60 mm for emerald shiner (Fuchs 1966) were omitted from the analysis. Catch rates were then normalized using a z-score transformation (normalized catch per unit effort; NCPUE) due to high variation seen within and among study sites to allow for comparisons. A NCPUE score of zero is the overall average for that mesohabitat category in question. Any score above zero, a positive z-score, indicates catch rates were above the overall average for that mesohabitat category. Catches below the average, a negative z-score, indicates catch rates were below the overall average. The transformation does not change the shape of the original distribution or change the location of any individual score relative to others in the distribution. To determine levels of habitat co-utilization, we incorporated a homogeneity of slopes test using analysis of co-variance (ANCOVA) at each study reach and mesohabitat characteristic between silver carp and gizzard shad, and silver carp and emerald shiner (Colombo et al. 2008). Hereafter, references to shallow habitat refers to areas less than 1.5 meters in depth and reference to low velocities refers to measurements less than 0.6 meters per second, as defined in United States Fish and Wildlife (2000).

**Table 1.** The LaGrange, Alton, and Open River reach total catch data by year, effort, and species.

Reach	Year	# Net Sets	GZSD	CPUE	ERSN	CPUE	SVCP	CPUE
LaGrange	2007	79	18702	236.734	5679	71.886	7658	96.937
	2008	83	26224	315.952	11671	140.614	66804	804.867
	2009	84	109	1.298	1413	16.821	3	0.036
	2010	84	2100	25.000	12694	151.119	15	0.179
	2011	77	8286	107.610	631	8.195	27	0.351
	2012	79	18831	238.367	1646	20.835	729	9.228
Alton	2007	45	600	13.333	1347	29.933	207	4.600
	2008	43	13421	312.116	1744	40.558	2671	62.116
	2009	43	755	17.558	1045	24.302	367	8.535
	2010	42	116	2.762	146	3.476	581	13.833
	2011	45	130	2.889	212	4.711	5	0.111
	2012	43	7	0.163	2375	55.233	4	0.093
Open River	2007	55	46	0.836	1266	23.018	28	0.509
	2008	50	241	4.820	287	5.740	31	0.620
	2009	56	131	2.339	190	3.393	26	0.464
	2010	48	175	3.646	332	6.917	187	3.896
	2011	50	110	2.200	42	0.840	14	0.280
	2012	41	6	0.146	1399	34.122	1	0.024

## Results

Overall, 1,047 mini fyke net sets captured 89,990 young-of-year gizzard shad, 41,119 emerald shiner and 79,358 silver carp (Table 1). At each location and every year, age-0 gizzard shad, age-0 emerald shiner and age-0 silver carp were collected, evidence that successful spawning has occurred within each reach.

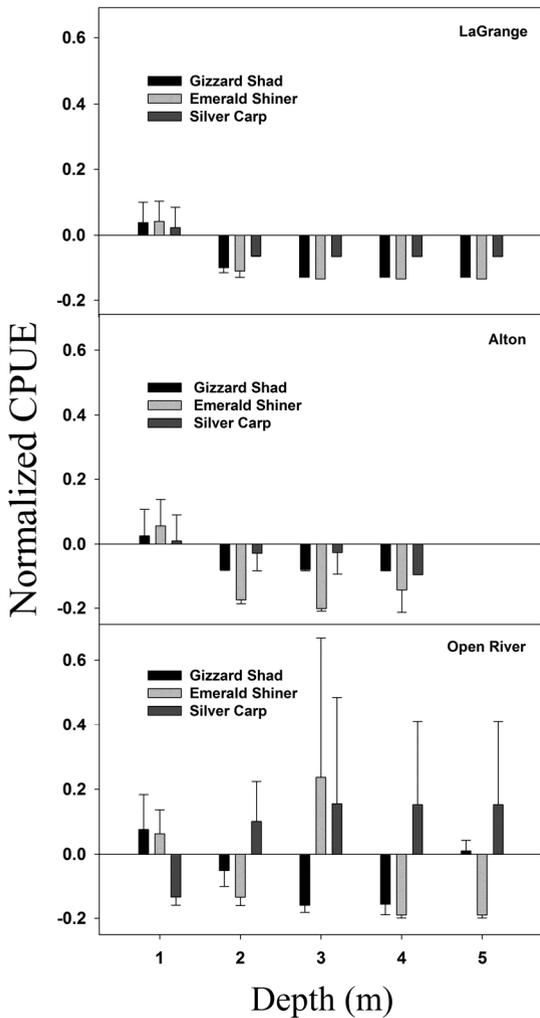
### Depth

Normalized catch-per-unit-effort (NCPUE) at depths in meters (m) at the Alton reach demonstrates all three species using shallow water habitat (Figure 1). Testing for homogeneity of slopes across depths at Alton revealed no difference in depth use between silver carp and gizzard shad ( $F_{519,522}=0.01$ ;  $P=0.7452$ ) or between silver carp and emerald shiner ( $F_{519,522}=0.11$ ;  $P=0.7542$ ). At depths in meters, NCPUE at the LaGrange reach depicted all three species using shallow water habitat (Figure 1). Testing for homogeneity of slopes across depths at LaGrange revealed no difference in depth use between silver carp and gizzard shad ( $F_{969,972}=0.03$ ;  $P=0.8651$ ) or between silver carp and emerald shiner ( $F_{969,972}=0.04$ ;  $P=0.8418$ ). At the Open River reach, NCPUE at depths (m) depicted high variability in habitat use (Figure 1). Testing for homogeneity of slopes across depths revealed no difference in depth use at the Open River reach

between silver carp and gizzard shad ( $F_{599,602}=1.62$ ;  $P=0.2036$ ) or between silver carp and emerald shiner ( $F_{599,602}=1.09$ ;  $P=0.2977$ ).

### Velocity

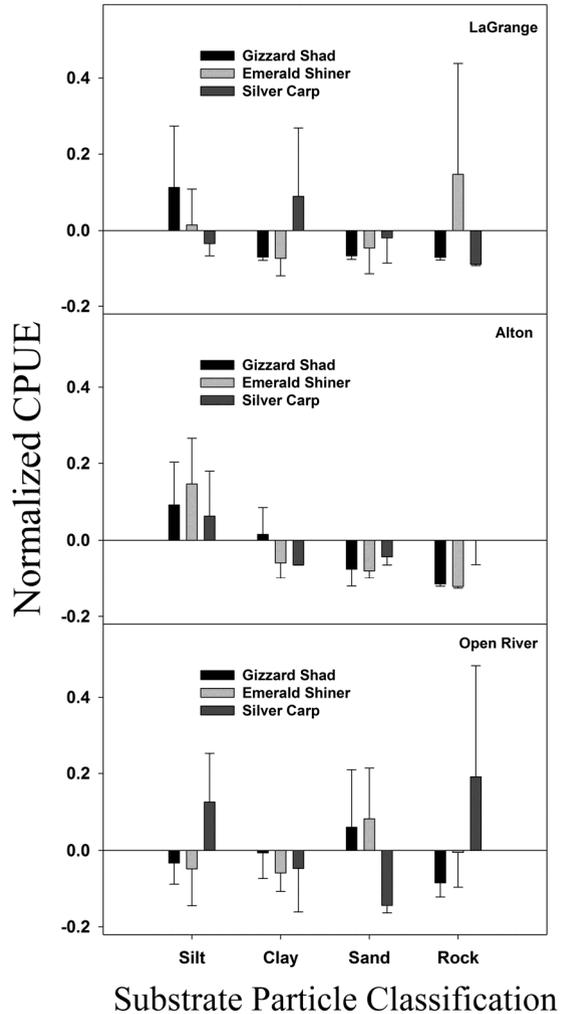
Results at the Alton reach for velocity (m/s) indicated use of low velocity habitat occurring for all three species, with NCPUE values all above the average at 0.1 m/s. (Figure 2). Testing for homogeneity of slopes across velocities revealed no difference in velocity use between silver carp and gizzard shad ( $F_{519,522}=0.01$ ;  $df=519, 522$ ;  $P=0.9064$ ) or between silver carp and emerald shiner ( $F_{519,522}=0.03$ ;  $P=0.8707$ ). The LaGrange reach followed a similar pattern as Alton, with normalized catch rates above the average at velocities of 0.1 m/s and 0.2 m/s. Testing for homogeneity of slopes across velocities revealed no difference in velocity use between silver carp and gizzard shad ( $F_{969,972}=0.01$ ;  $P=0.9731$ ) or between silver carp and emerald shiner ( $F_{969,972}=0.15$ ;  $P=0.7026$ ). At the Open River reach, catch rates were slightly more variable but continued to follow the general pattern of lower velocity habitat having the highest catch rates, with above average catches occurring in 0.1, 0.2 and 0.3 m/s. Testing for homogeneity of slopes across velocities at the Open River reach revealed no difference in velocity use between silver carp and gizzard shad ( $F_{599,602}=0.01$ ;  $P=0.9441$ ) or between silver carp and emerald shiner ( $F_{599,602}=0.06$ ;  $P=0.8101$ ).



**Figure 1.** Mean ( $\pm$ SE) normalized catch per unit effort (NCPUE) for age-0 gizzard shad, emerald shiner and silver carp in relation to depth given in meters (m) at LaGrange, Alton and Open River from June 15 to October 31, 2007–2012. A positive normalized value indicates catch rates above the average at that depth category for that species; a negative NCPUE indicates catch rates below the average at that depth category.

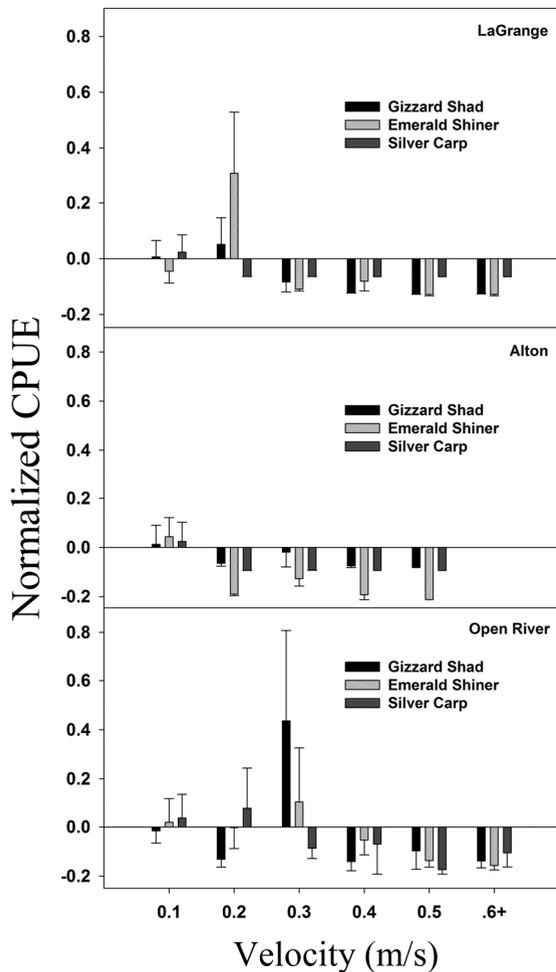
*Substrate*

Results at the Alton reach showed all three species using silt, with normalized catch rates all above the average for this mesohabitat. The homogeneity of slopes test revealed no difference in substrate use between silver carp and gizzard shad ( $F_{519,522}=0.07$ ;  $P=0.7862$ ) or between silver carp and emerald shiner ( $F_{519,522}=0.07$ ;  $P=0.7857$ ). High variability in catch rates was observed with substrate particle classification for the LaGrange reach and the Open River reach, with normalized



**Figure 2.** Mean ( $\pm$ SE) normalized catch per unit effort (NCPUE) for age-0 gizzard shad, emerald shiner and silver carp in relation to velocity given in meters per second (m/s) at LaGrange, Alton and Open River from June 15 to October 31, 2007–2012. A positive normalized value indicates catch rates above the average at that velocity category for that species; a negative NCPUE indicates catch rates below the average at that velocity category.

values between 0.191 and -0.146 (Figure 3). At the LaGrange reach, results from the homogeneity of slopes test between silver carp and gizzard shad ( $F_{969,972}=0.16$ ;  $P=0.6854$ ) and between silver carp and emerald shiner ( $F_{969,972}=0.31$ ;  $P=0.5803$ ) revealed no difference in substrate use. At the Open River reach, results from the homogeneity of slopes test between silver carp and gizzard shad ( $F_{599,602}=0.03$ ;  $P=0.852$ ) and between silver carp and emerald shiner ( $F_{599,602}=0.10$ ;  $P=0.7518$ ) also revealed no difference in substrate use.



**Figure 3.** Mean ( $\pm$ SE) normalized catch per unit effort (NCPUE) for age-0 gizzard shad, emerald shiner and silver carp in relation to substrate particle classification at LaGrange, Alton and Open River from June 15 to October 31, 2007–2012. A positive normalized value indicates catch rates above the average at that substrate particle category for that species; a negative NCPUE indicates catch rates below the average at that substrate particle category.

**Discussion**

We have demonstrated that age-0 silver carp, age-0 gizzard shad, and age-0 emerald shiner utilize similar depths and velocities across a large expanse of the Mississippi River Basin with higher variability in substrate use seen at the LaGrange reach and the Open River reach. Therefore, we can use this information to guide management of native planktivores and also determine areas to concentrate management and control efforts of age-0 silver carp. Specifically, NCPUE for velocity for gizzard shad, emerald shiner and silver carp followed the same trends for each reach, with all three species utilizing

low velocity habitat. Therefore, this mesohabitat characteristic likely plays an important role in the ability of each species to carry out its early life history. Depth use was also very similar at the LaGrange reach and the Alton reach, which may suggest this habitat type is important to early life history of all three species. Substrate utilization was most variable, potentially indicating this mesohabitat type is less vital to the early life history stage than velocity and depth. However, one must take into account many biotic and abiotic factors that we were unable to analyze when evaluating these results.

The high variability observed in the NCPUE in the Open River may be explained by the differences in velocities and depths that occurred during the course of sampling in this reach. This unimpounded stretch of the Mississippi River is maintained by wing dykes and rock structures to maintain flows and depths to sustain the navigational channel, creating an environment in which fluctuations in velocities and depths can occur quickly. In contrast, the Alton reach and the LaGrange reach are part of a system of impoundments, creating an environment in which variations in velocities and depths are less frequent and habitat availability is more constant over time (Ickes et al. 2005b). These differences in flow regime likely play a factor in the variability seen in catch rates in the Open River reach and may have contributed to the lack of differences observed in our statistical analysis.

The spatial overlap that exists between these three species on a mesohabitat level increases the potential for interactions (e.g., competition for resources) to occur. This is problematic for several reasons. Studies indicate changes to the plankton community occur in the presence of silver carp in terms of a reduction in zooplankton biomass (Burke et al. 1986; Lu et al. 2002) and a shift in the zooplankton community towards smaller sizes (Kolar et al. 2007). These changes to the zooplankton community may result in slower growth rates and subsequently lower survival of all native fish species, as fast growth during early life stages enhance survival (Miller et al. 1988; Anderson 1988; Beyer and Laurence 1980) and all native fish require zooplankton at some stage during their life history. Sampson et al. (2009) revealed diet overlap was present between silver carp and gizzard shad. Also, Irons et al. (2007) found a reduction in body condition of bigmouth buffalo, *Ictiobus cyprinellus* (Valenciennes, 1844) and gizzard shad in the LaGrange reach since the establishment of silver carp in 2000. Furthermore,

Phelps et al. (unpublished data) described newly inundated floodplain lakes with high silver carp abundance can reduce or eliminate native planktivores as well as many other native fishes (e.g., bluegill, *Lepomis macrochirus* (Rafinesque, 1819), green sunfish, *Lepomis cyanellus* (Rafinesque, 1819), white bass, *Morone chrysops* (Rafinesque, 1820) and sauger, *Stizostedion canadense* (Griffith and Smith, 1834)). Although evidence of mesohabitat overlap described in this study does not infer interspecific competition is taking place, our findings suggest the possibility of such interactions may be occurring or could occur in the future given the results of this and the aforementioned studies. Thus, a reduction in fitness and abundance of gizzard shad and emerald shiner in preferred habitats may be occurring or could occur in the future in these highly altered systems in the Mississippi River Basin. Efforts to minimize negative impacts on native planktivores and subsequently the fish community may be found in restoring natural flow regimes.

Research conducted by Phelps et al. (2014) suggests that restoring lateral connectivity (i.e., floodplain connectivity) can lead to greater growth rates of native fish species while providing no additional benefit to silver carp. Nearly 90% of floodplain habitat in the Mississippi River is behind levees (Ickes et al. 2005b) leaving this highly productive and beneficial resource unavailable to native fishes. The scarcity of this habitat, along with the known impact invasive planktivores can cause (e.g., habitat displacement, Byers 2002) may lead to decreased survival of gizzard shad and emerald shiner due to sub-optimal resource availability. Therefore, management actions targeted at restoring floodplain connectivity and function of large rivers may promote native fish conservation by allowing native fish to utilize these optimal habitats, leading to increased growth rates, body condition, and ultimately, greater survival.

## Acknowledgements

This study was funded by the U.S. Army Corps of Engineers' Upper Mississippi River Restoration - Environmental Management Program's Long Term Resource Monitoring component implemented by the USGS Upper Midwest Environment Sciences Center and performed by Missouri Department of Conservation. We would also like to thank Ivan Vining and Sam Finney for the extensive help in statistical analyses and for providing a critical review of an earlier version of this manuscript and the anonymous reviewers for all the hard work put forth towards this manuscript.

## References

- Anderson JT (1988) A review of size-dependent survival during pre-recruit stages of fishes in relation to recruitment. *Journal of Northwest Atlantic Fishery Science* 8: 55–66
- Beyer JE, Laurence GC (1980) A stochastic model of larval fish growth. *Ecology Model* 8: 109–132, [http://dx.doi.org/10.1016/0304-3800\(80\)90032-0](http://dx.doi.org/10.1016/0304-3800(80)90032-0)
- Bronte CR, Ebener MP, Schreiner DR, DeVault DS, Petzold MM, Jensen DA, Richards C, Lozano SJ (2003) Fish community change in Lake Superior, 1970-2000. *Canadian Journal of Fisheries and Aquatic Sciences* 60: 1552–1574, <http://dx.doi.org/10.1139/f03-136>
- Burke JS, Bayne DR, Rea H (1986) Impact of silver and bighead carps on plankton communities of channel catfish ponds. *Aquaculture* 55: 59–68, [http://dx.doi.org/10.1016/0044-8486\(86\)90056-6](http://dx.doi.org/10.1016/0044-8486(86)90056-6)
- Byers JE (2002) Impact of non-indigenous species on natives enhanced by anthropogenic alteration of select regimes. *Oikos* 97: 449–458, <http://dx.doi.org/10.1034/j.1600-0706.2002.970316.x>
- Charlebois PM, TePas KM (2011) Comprehensive plan for increasing effectiveness of bighead and silver carp outreach. *American Fisheries Society Symposium* 74: 191–197
- Chick JH, Ickes BS, Pegg MA, Barko VA, Hrabik RA, Herzog DP (2003) Spatial structure and temporal variation of fish communities in the Upper Mississippi River. U.S. Geological Survey Upper Midwest Environmental Sciences Center, LaCrosse, Wisconsin, LTRMP Technical Report 2005–T004
- Colombo RE, Phelps QE, Garvey JE, Heidinger RC, Stefanavage T (2008) Gear-specific population demographics of Channel Catfish in a large un-impounded Midwestern river. *North American Journal of Fisheries Management* 28: 241–246, <http://dx.doi.org/10.1577/M06-200.1>
- Fuchs EH (1966) Life history of emerald shiner in Lewis and Clark Lake, South Dakota. M.S. 2415
- Gutreuter S, Burkhardt R, Lubinski K (1995) Long Term Resource Monitoring Program Procedures; Fish Monitoring. National Biological Service, Environmental Management Technical Center, Onalaska, Wisconsin, July 1995. LTRMP 95-P002-1. 42 pp. + Appendixes A-J
- Hrabik TR, Magnuson JJ, McLain AS (1998) Predicting the effects of rainbow smelt on native fishes in small lakes: Evidence from long-term research on two lakes. *Canadian Journal of Fisheries and Aquatic Sciences* 55: 1364–1371, <http://dx.doi.org/10.1139/f98-032>
- Ickes BS, Bowler MC, Bartels AD, Kirby DJ, DeLain S, Chick JH, Barko VA, Irons KS, Pegg MA (2005a) Multiyear synthesis of the fish component from 1993 to 2002 for the Long Term Resource Monitoring Program. U.S. Geological Survey, Upper Midwest Environmental Sciences Center, La Crosse, Wisconsin, LTRMP 2005-T005, 60 pp
- Ickes BS, Vallazza J, Kalas J, Knights B (2005b) River floodplain connectivity and lateral fish passage: A literature review. U.S. Geological Survey, Upper Midwest Environmental Sciences Center, La Crosse, Wisconsin, June 2005, 25 pp
- Irons KS, Sass GG, McClelland MA, Stafford JD (2007) Reduced condition factor of two native fish species coincident with invasion of non-native Asian carps in the Illinois River, U.S.A. Is this evidence for competition and reduced fitness? *Journal of Fish Biology* 71: 258–273, <http://dx.doi.org/10.1111/j.1095-8649.2007.01670.x>
- Irons KS, Sass GG, McClelland MA, O'Hara TM (2011) Bigheaded carp Invasion of the La Grange Reach of the Illinois River: Insights from the Long Term Resource and Monitoring Program. *American Fisheries Society Symposium* 74: 31–50

- Kolar CS, Chapman DC, Courtenay Jr WR, Housel CM, Williams JD, Jennings DP (2007) Bigheaded carps: a biological synopsis and environmental risk assessment. American Fisheries Society, Special Publication 33
- Laird CA, Page LM (1996) Non-native fishes inhabiting the streams and lakes of Illinois. *Illinois Natural History Survey Bulletin* 35: 1–51, <http://dx.doi.org/10.5962/bhl.title.50306>
- Lu M, Xie P, Tang H, Shao Z, Xie L (2002) Experimental study of trophic cascade effect of silver carp (*Hypophthalmichthys molitrix*) in a subtropical lake, Lake Donghu: on plankton community and underlying mechanisms of changes of crustacean community. *Hydrobiologia* 487: 19–31, <http://dx.doi.org/10.1023/A:1022940716736>
- Miller TJ, Crowder LB, Rice JA, Marschall EA (1988) Larval size and recruitment mechanisms in fishes: Toward a conceptual framework. *Canada Journal of Fisheries and Aquatic Sciences* 45: 1657–1670, <http://dx.doi.org/10.1139/f88-197>
- Ross ST (1991) Mechanisms structuring stream fish assemblages: are there lessons from introduced species? *Environmental Biology of Fishes* 30: 359–368, <http://dx.doi.org/10.1007/BF02027979>
- Phelps QE, Tripp SJ, Herzog DP, Garvey JE (2014) Temporary connectivity: the relative benefits of large river floodplain inundation in the lower Mississippi River. *Restoration Ecology* 23: 53–56, <http://dx.doi.org/10.1111/rec.12119>
- Sampson SJ, Chick JH, Pegg MA (2009) Diet overlap among two Asian carp and three native fishes in backwater lakes on the Illinois and Mississippi rivers. *Biological Invasions* 11: 483–496, <http://dx.doi.org/10.1007/s10530-008-9265-7>
- Tucker JK, Cronin FA, Hrabik RA, Petersen MD, Herzog DP (1996) The bighead carp (*Hypophthalmichthys nobilis*) in the Mississippi River. *Journal of Freshwater Ecology* 11: 241–243, <http://dx.doi.org/10.1080/02705060.1996.9663484>
- United States Fish and Wildlife Service (2000) Biological Opinion on the Operation of the Missouri River Main Stem Reservoir System, Operation and Maintenance of the Missouri River Bank Stabilization and Navigation Project, and Operation of the Kansas River Reservoir System. U.S. Fish and Wildlife Service, Minneapolis, Minnesota
- Wells L (1970) Effects of alewife predation on zooplankton populations in Lake Michigan. U.S. Bureau of Commercial Fisheries, Great Lakes Fishery Laboratory No. 424, <http://dx.doi.org/10.4319/lo.1970.15.4.0556>
- Werner EE, Hall DJ (1979) Foraging efficiency and habitat switching in competing sunfishes. *Ecology* 60: 256–264, <http://dx.doi.org/10.2307/1937653>
- Werner EE, Mittelbach GG, Hall DJ, Gilliam JF (1983) Experimental tests of optimal habitat use in fish: the role of relative habitat profitability. *Ecology* 64: 1525–1539, <http://dx.doi.org/10.2307/1937507>