

Research Article

Effect of lipid levels and size in invasive carp overwinter survivalHae H. Kim^{1*}, Elaine A. Ewigman¹, Quinton E. Phelps¹, Timothy M. Judd² and Sara J. Tripp³¹Department of Biology, College of Natural and Applied Sciences, Missouri State University, Springfield, MO, USA²Department of Biology, Southeast Missouri State University, Cape Girardeau, MO, USA³Big Rivers and Wetland Field Station, Missouri Department of Conservation, Jackson, MO, USA

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OPEN ACCESS**Abstract**

Recruitment is one of the most important dynamic rate functions (i.e., recruitment, growth, and mortality). Often, recruitment can be heavily dependent on overwinter survival. Wintertime presents thermal and metabolic challenges to fish. Studies have suggested that overwinter survival and mortality is correlated to lipid content before entering winter. Inadequate lipid reserves are related to poor condition and may lead to overwinter mortality. Young fish need to accumulate adequate lipid reserves before entering winter. In the Mississippi River, where silver carp *Hypophthalmichthys molitrix* Valenciennes, 1844 are hyper abundant, silver carp are not experiencing recruitment issues. As such, we evaluated lipid levels and size as potential silver carp recruitment regulators. Silver carp were collected by the Long Term Resource Monitoring element in 2015 on the middle Mississippi River using mini fyke nets; total lengths ranged from 34–177 mm. Lipid levels of whole carp were determined using the phosphovanillin assay. No difference in lipid levels (mg/g) was observed between spring and fall fishes. Additionally, we observed no relation between total length and lipid levels. Size structure did not significantly differ between fall age-0 and spring age-1 silver carp. Our results suggest there may not be a size dependent overwinter mortality/survival in silver carp in the middle Mississippi River. Additionally, lipids may not be a driving factor in overwinter mortality/survival. Our research suggests silver carp in the Mississippi River basin do not follow most early life history paradigms and may explain the successful nature of the silver carp invasion.

Key words: recruitment, early life-history, invasive species, Mississippi River, population dynamics

Introduction

North America freshwater ecosystems support highly diverse fauna but have been highly manipulated (Vitousek et al. 1997; Abernethy and Turner 1987; Abell et al. 2000; Helfman 2007; Jelks et al. 2008). Throughout these systems, fish diversity is high, but many fish taxa are imperiled (e.g., threatened or endangered) due to anthropogenic impacts (e.g., channelization, invasive species, pollution; Jelks et al. 2008). Across freshwater ecosystems, introduction of non-native fauna has led to a reduction in native species diversity, condition and abundance (Abernethy and Turner 1987; Vitousek

et al. 1997; Abell et al. 2000; Turner and Rabalais 2003; Helfman 2007; Irons et al. 2007; Jelks et al. 2008; Phelps et al. 2017).

Four species of non-native invasive carp species (i.e., bighead carp *Hypophthalmichthys nobilis* Richardson, 1845, silver carp *H. moltrix* Valenciennes, 1844, grass carp *Ctenopharygodon idella* Valenciennes, 1844, black carp *Mylopharygodon piceus* Richardson, 1846) inhabit the Mississippi River basin (Phelps et al. 2017). Of these, silver and bighead carps possess the characteristics of an extremely successful invader (e.g., fast generation time, high fecundity, low mortality) and as such are hyper abundant in the lower portions of the Upper Mississippi River (Ehrlich 1984; Fuller et al. 1999; DeGrandchamp et al. 2008; Stueck et al. 2010). Silver and bighead carp have shown to have deleterious effects to native fauna (Kolar et al. 2005; Irons et al. 2007; Solomon et al. 2015; Phelps et al. 2017). Overall, silver and bighead carp management has focused on control and eradication efforts, in addition to preventing spread (Conover et al. 2007). However, more research is needed to develop novel control methods, especially for invasive fishes (Simberloff 2003). Specifically, we need to understand the biotic and abiotic factors that influence population dynamics (Ricker 1975; Simberloff 2003).

Fish populations are driven by the dynamic rate functions (i.e., recruitment, growth and mortality; Ricker 1975). In most temperate climates, overwinter survival regulates recruitment (Ricker 1975; Oliver et al. 1979). Wintertime presents thermal, metabolic, and physiological challenges to fish (e.g., hypothermia, physical damage) and may lead to mortality (Seelbach 1987; Cunjak 1988; Phelps et al. 2008). This results from physiological changes during the winter and often these changes lead to a decrease in condition (i.e., loss of energy reserves; Cunjak 1988). Many studies have demonstrated the importance of lipid levels in regulating overwinter survival (Oliver et al. 1979; Post and Evans 1989; Schultz and Conover 1999; Post and Parkinson 2001; Morgan et al. 2005; Pratt and Fox 2002; Biro et al. 2021). Moreover, size is often directly related to the accumulation of lipids (i.e., higher condition; Schultz and Conover 1999). Young fish need to accumulate adequate lipid reserves before entering winter (Oliver et al. 1979; Schultz and Conover 1999; Post and Parkinson 2001; Pratt and Fox 2002). Thus, hatch date should play an important role in regulating lipid levels and subsequently determining overwinter survival (Schultz and Conover 1999). Generally, earlier hatch dates provide prolonged growing season and potentially greater lipid accumulation (Oliver et al. 1979; Schultz and Conover 1999; Post and Parkinson 2001; Pratt and Fox 2002; Biro et al. 2021). As such, we sought to evaluate biotic factors (e.g., lipid level, size) that may be regulating overwinter survival. We examined the influence of size and its role in regulating lipid levels. Further, we evaluated the role of lipid concentrations in regulating silver carp overwinter survival.

Materials and methods

Fish collection

The Middle Mississippi River (MMR) extends from Cairo, Illinois (i.e., Ohio River confluence) to Alton, Illinois near Mel Price Lock and Dam. This section is free-flowing (i.e., unimpounded) and largely regulated by channel-training structures (e.g., wing dikes). Lateral connectivity (e.g., side-channels) is limited, especially during low river stage, and flow is generally diverted into the channel. Silver carp were collected by Missouri Department of Conservation (MDC) staff at the Big Rivers and Wetland Field Station through the Upper Mississippi River Restoration (UMRR) Program's Long Term Resources Monitoring (LTRM) element (Ratcliff et al. 2014). The LTRM utilizes stratified random sampling designed to target all available habitats (Ratcliff et al. 2014) In 2015 and 2016, a random sample of silver carp were collected in LTRM standard mini-fyke nets in the fall ($N = 53$; Sept–Nov) and spring ($N = 40$; Mar–Jun) and subsequently used for lipid analysis. Silver carp cohorts were followed based on total length from age-0 (fall) to age-1 (subsequent spring). All LTRM standard mini-fyke nets are fished overnight and set in appropriate river strata. Each mini-fyke consists of a 4.6 m \times 0.6 m lead (3 mm bar mesh) attached to two rectangular frames (0.6 m \times 1.2 m) and tapers into two 0.6 diameter rings.

Lipid analysis

Fish condition was assessed using lipid concentrations. Whole silver carp were homogenized in a 20 ml 1:1 methanol: chloroform. Each sample was vortexed and centrifuged for approximately two minutes (at 14,000 rpm). The chloroform was removed, and each sample received 200 μ l of concentrated sulfuric acid. The resulting solution was heated at 100 °C for 10 min. Lipid levels were determined by adding 3 ml of vanillin reagent and analyzed using the phosphovanillin assay (Barnes and Blackstock 1973; van Handel 1985; Marandel et al. 2016). Absorbance was measured at 525 nm in a spectrophotometer (Beckmann DU® 730, Beckman Coulter Inc, Brea, CA, USA).

Statistical analysis

A two-sample Kolmogorov-Smirnov test was used to determine differences in length frequencies of fall age-0 and spring age-1 silver carp. Lipid levels were expressed as lipid (mg) / fish mass (g). Lipid levels were regressed (i.e., simple linear regression) against total length (mm) to observe the effects of total length on lipid levels. Additionally, a two-sample t-test was used to test for differences in lipid levels between fall age-0 and spring age-1 silver carp. All analyses were conducted in SAS 9.4 software (SAS/STAT Software, SAS Institute Inc., Cary, NC, USA).

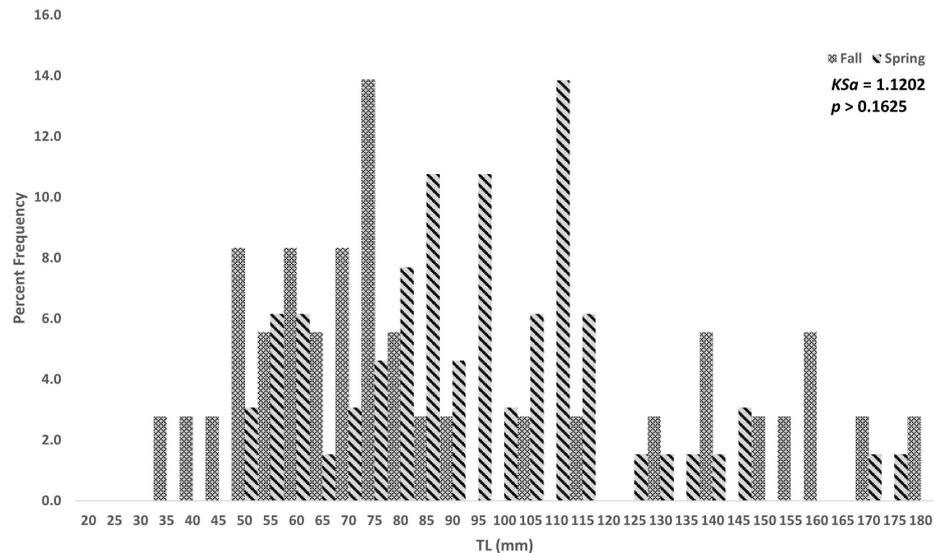


Figure 1. Size distributions of silver carp collected in the fall and the spring. Fish ranged from 34 mm–177 mm (Fall) and 50 mm–172 mm (Spring). There was no significant difference in length-frequency distributions between fall and spring silver carp (Two-sample Kolmogorov-Smirnov test, $KSa = 1.1202$; $p > 0.1625$).

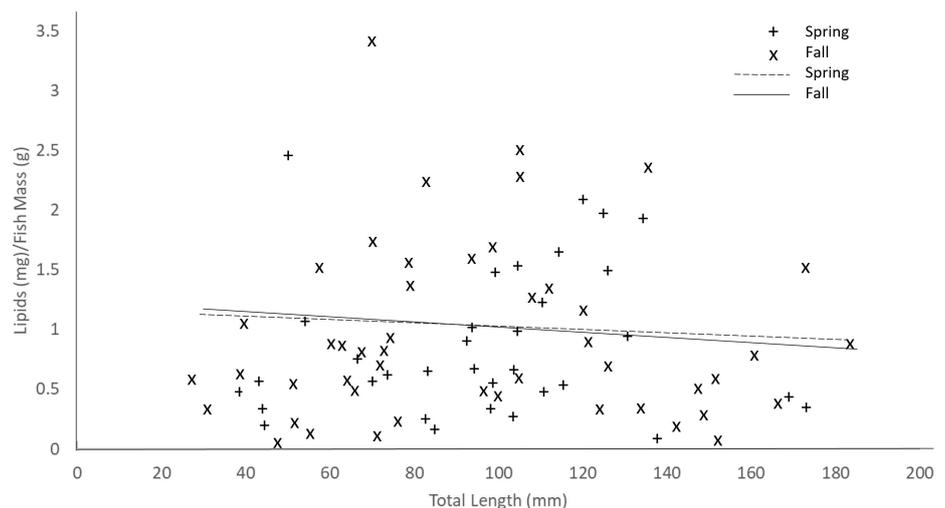


Figure 2. Silver carp total length plotted against lipid levels for both fall and spring collected fish. No relationship was observed for fall (2015; $r^2 = 0.0084$; $P = 0.51$) and spring (2016; $r^2 = 0.0054$; $P = 0.65$) collected silver carp.

Results

Fish ranged from 34 mm–177 mm TL and 50 mm–172 mm TL for fall and spring collected silver carp, respectively. Two-sample Kolmogorov-Smirnov test detected no difference in length-frequency distributions of fall and spring collected silver carp ($KSa = 1.1202$; $Pr > 0.1625$; Figure 1). We observed no relationships between silver carp length and lipid levels, in both fall (2015; $r^2 = 0.0084$; $P = 0.51$) and spring (2016; $r^2 = 0.0054$; $P = 0.65$; Figure 2). A two-sample t-test showed no statistical differences ($P = 0.2821$; $T = 0.57861$; $df = 92$) in average lipid levels between fall (0.95 ± 0.12) and spring (0.86 ± 0.08) collected silver carp (Figure 3).

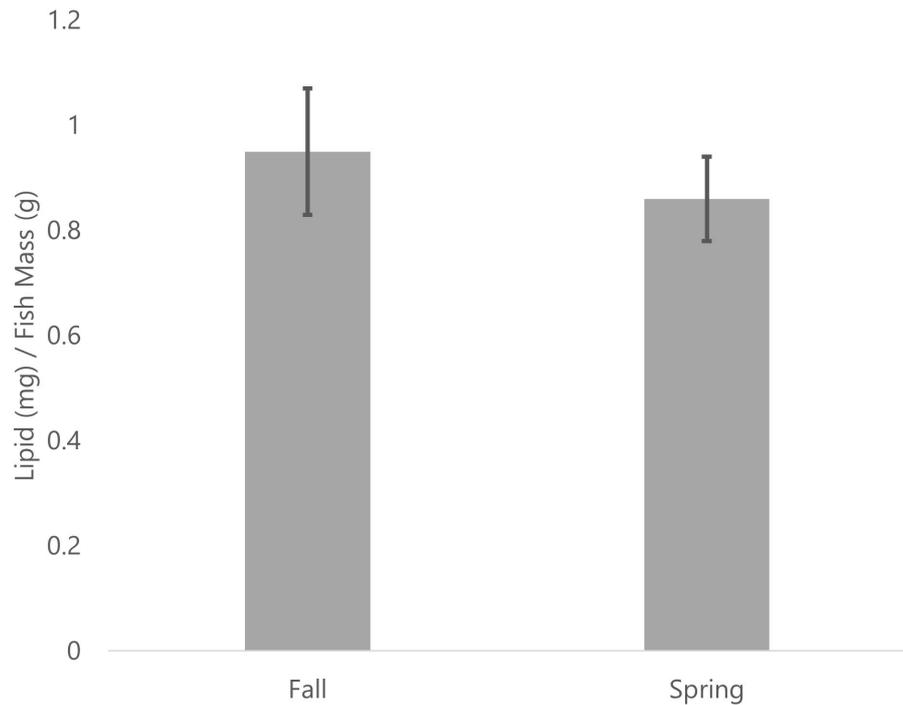


Figure 3. Mean (\pm SE) lipid levels for fall and spring silver carp. No significant differences were found between the fish collected during both seasons (Two-sample t-test; $T = 0.57861$; $df = 92$, $P = 0.2821$).

Discussion

Where silver carp are established, they are hyper-abundant, suggesting low mortality at juvenile stages and subsequent strong recruitment (Conover et al. 2007; Phelps et al. 2017). Recruitment is likely one of the most important factors regulating fish populations (i.e., Type III survivorship; Ricker 1975; Winemiller and Rose 1992; Pritt et al. 2014). No difference between fall age-0 and spring age-1 silver carp length-frequency distributions (Figure 1), suggests that size dependent overwinter mortality may not be an important factor in regulating silver carp overwinter survival in the Middle Mississippi River (e.g., Phelps et al. 2008). For most fish, properly timing their spawning is an important factor for juvenile survival (Phelps et al. 2008). Fish need to maximize the summer growing period to build adequate energy reserves in preparation of entering winter (Oliver et al. 1979; Cunjak 1988; Schultz and Conover 1999; Post and Parkinson 2001; Pratt and Fox 2002). Within the same species, larger members of the age-0 cohort are assumed to have hatched earlier than smaller fish (Phelps et al. 2008). As such, we assume larger fish have a longer growing period to build up lipid reserves before entering winter. However, our results indicated no statistically significant relationship between silver carp total length and lipid levels (Figure 2). Generally, most fish in temperate zones face difficult physiological and metabolic demands during winter (Seelbach 1987; Cunjak 1988). Which ultimately leads to a decline in condition and energy reserves (i.e., lipids) are depleted (Cunjak 1988). However, our results suggest

lipids may not be an important factor in regulating overwinter survival in silver carp. As such several other regulating mechanisms could be influencing (e.g., gauge height and velocity, thermograph and temperature cycling) overwinter survival (Houde 1994; Miranda and Hubbard 1994; Sammons et al. 2001; Smith et al. 2005; Phelps et al. 2008; Tripp et al. 2009).

Our results elucidate factors that may drive silver carp population dynamics. Vital rates (i.e., recruitment, growth, mortality) drive population dynamics and fish are managed by manipulating these metrics (Ricker 1975). The population structure is largely shaped by early life vital rates. Silver carp are a type III strategist and is characterized by high mortality in early life, followed by high survival past that stage. However, we do not fully understand the biotic and abiotic factors that influence early life vital rates. Our results suggest that silver carp may not follow early life history paradigms that native fishes exhibit (i.e., the importance of lipid levels on over winter survival). Further, our findings help explain the very successful nature of silver carp as non-native invaders.

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Authors' contribution

HHK – research conceptualization, investigation and data collection, data analysis and interpretation, writing – original draft, reviewing and editing; EAE – research conceptualization, investigation and data collection, data analysis and interpretation, writing – original draft, reviewing and editing; QEP – research conceptualization, investigation and data collection, data analysis and interpretation, writing – original draft, reviewing and editing; TMJ – research conceptualization, investigation and data collection, data analysis and interpretation, writing – original draft, reviewing and editing; SJT – research conceptualization, investigation and data collection, data analysis and interpretation, writing – original draft, reviewing and editing.

References

- Abell RA, Olsen DM, Dinersrein E, Hurley PT, Diggs JT, Eichbaum W, Walters S, Wettengel W, Allnutt T, Loucks CJ, Hedao P (2000) Freshwater ecoregions of North America: a conservation assessment. Island Press, Washington, D.C., 368 pp
- Abernethy Y, Turner RE (1987) US forested wetlands: 1940-1981. *BioScience* 37: 721–727, <https://doi.org/10.2307/1310469>
- Barnes H, Blackstock J (1973) Estimation of lipids in marine animals and tissues: detailed investigation of the sulphophosphovanilun method for “total” lipids. *Journal of Experimental Marine Biology and Ecology* 12: 103–118, [https://doi.org/10.1016/0022-0981\(73\)90040-3](https://doi.org/10.1016/0022-0981(73)90040-3)
- Biro PA, Post JR, Beckmann C (2021) Autumn lipid reserves, overwinter lipid depletion, and high winter mortality of rainbow trout in experimental lakes. *Canadian Journal of Fisheries and Aquatic Sciences* 78: 738–743, <https://doi.org/10.1139/cjfas-2020-0276>
- Conover G, Simmonds R, Whalen M (2007) Management and control plan for Bighead, Black, Grass, and Silver carps in the United States. Asian Carp Working Group, Aquatic Nuisance Species Task Force, Washington, D.C., 223 pp, www.asiancarp.org/Documents/CarpsManagementPlan.pdf
- Cunjak RA (1988) Physiological consequences of overwintering in streams: the cost of acclimatization? *Canadian Journal of Fisheries and Aquatic Sciences* 45: 443–452, <https://doi.org/10.1139/f88-053>

- DeGrandchamp KL, Garvey JE, Colombo RE (2008) Movement and habitat selection by invasive Asian carps in a large river. *Transactions of the American Fisheries Society* 137: 45–56, <https://doi.org/10.1577/T06-116.1>
- Ehrlich PR (1984) Which animal will invade? In: Mooney HA, Drake JA (eds), *Ecology of biological invasions of North America and Hawaii*. Springer-Verlag, New York., pp 79–95, https://doi.org/10.1007/978-1-4612-4988-7_5
- Fuller PL, Nico LG, Williams JD (1999) Nonindigenous fishes introduced into inland waters of the United States. American Fisheries Society, Special Publication 27, Bethesda, Maryland, 622 pp
- Helfman GS (2007) *Fish conservation: a guide to understanding and restoring global aquatic biodiversity and fishery resources*. Island Press, Washington, D.C., 608 pp
- Houde ED (1994) Differences between marine and freshwater fish larvae: implications for recruitment. *ICES Journal of Marine Science* 51: 91–97, <https://doi.org/10.1006/jmsc.1994.1008>
- 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, <https://doi.org/10.1111/j.1095-8649.2007.01670.x>
- Jelks HL, Walsh SJ, Burkhead NM, Contreras-Balderas S, Díaz E, Hendrickson DA, Lyons J, Mandrak NE, McCormick F, Nelson JS, Plantania SP, Porter BA, Renaud CB, Schmitter-Soto JJ, Taylor EB, Warren ML (2008) Conservation Status of Imperiled North American Freshwater and Diadromous Fishes. *Fisheries* 33: 372–407, <https://doi.org/10.1577/1548-8446-33.8.372>
- Kolar CS, Chapman DC, Courtenay Jr. WR, Housel CM, Williams JD, Jennings DP (2005) Asian carps of the genus *Hypophthalmichthys* (Pisces, Cyprinidae): a biological synopsis and environmental risk assessment. U.S. Fish and Wildlife Service, Washington, D.C., <https://digitalcommons.unl.edu/cgi/viewcontent.cgi?article=1004&context=natinvasive> (accessed 31 July 2021)
- Marandel L, Véron V, Surget A, Plagnes-Juan É, Panserat S (2016) Glucose metabolism ontogenesis in rainbow trout (*Oncorhynchus mykiss*) in the light of the recently sequenced genome: new tools for intermediary metabolism programming. *Journal of Experimental Biology* 219: 734–743, <https://doi.org/10.1242/jeb.134304>
- Miranda, LE, Hubbard WD (1994) Winter survival of age-0 largemouth bass relative to size, predators, and shelter. *North American Journal of Fisheries Management* 14: 790–796, [https://doi.org/10.1577/1548-8675\(1994\)014<0790:WSOALB>2.3.CO;2](https://doi.org/10.1577/1548-8675(1994)014<0790:WSOALB>2.3.CO;2)
- Morgan IJ, McCarthy ID, Metcalfe NB (2005) The influence of life-history strategy on lipid metabolism in overwintering juvenile Atlantic salmon. *Journal of Fish Biology* 60: 674–686, <https://doi.org/10.1006/jfbi.2002.1886>
- Oliver, JD, Holeyton GF, Chua KE (1979) Overwinter mortality of fingerling smallmouth bass in relation to size, relative energy stores, and environmental temperature. *Transactions of the American Fisheries Society* 108: 130–136, [https://doi.org/10.1577/1548-8659\(1979\)108<130:OMOFBS>2.0.CO;2](https://doi.org/10.1577/1548-8659(1979)108<130:OMOFBS>2.0.CO;2)
- Pritt JJ, DuFour MR, Mayer CM, Roseman EF, DeBruyne RL (2014) Sampling little fish in big rivers: Larval fish detection probabilities in two Lake Erie tributaries and implications for sampling effort and abundance indices. *Transactions of the American Fisheries Society* 143: 1011–1027, <https://doi.org/10.1080/00028487.2014.911204>
- Phelps QE, Graeb BDS, Willis DW (2008) First year growth and survival of common carp in two glacial lakes. *Fisheries Management and Ecology* 15: 85–91, <https://doi.org/10.1111/j.1365-2400.2007.00568.x>
- Phelps QE, Tripp SJ, Bales KR, James D, Hrabik RA, Herzog DP (2017) Incorporating basic and applied approaches to evaluate the effects of invasive Asian Carp on native fishes: A necessary first step for integrated pest management. *PLoS ONE* 12: e0184081, <https://doi.org/10.1371/journal.pone.0184081>
- Post JR, Evans DO (1989) Size-dependent overwinter mortality of young-of-the-year yellow perch (*Perca flavescens*): laboratory, in situ enclosure and field experiments. *Canadian Journal of Fisheries and Aquatic Sciences* 46: 1958–1968, <https://doi.org/10.1139/f89-246>
- Post JR, Parkinson EA (2001) Energy allocation strategy in young fish: allometry and survival. *Ecology* 82: 1040–1051, [https://doi.org/10.1890/0012-9658\(2001\)082\[1040:EASIYF\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2001)082[1040:EASIYF]2.0.CO;2)
- Pratt TC, Fox MG (2002) Influence of predation risk on the overwinter mortality and energetic relationships of young-of-year walleyes. *Transactions of the American Fisheries Society* 131: 885–898, [https://doi.org/10.1577/1548-8659\(2002\)131<0885:IOPROT>2.0.CO;2](https://doi.org/10.1577/1548-8659(2002)131<0885:IOPROT>2.0.CO;2)
- Ratcliff EN, Gittinger EJ, O'Hara TM, Ickes BS (2014) Long Term Resource Monitoring Program Procedures: Fish monitoring, 2nd edition. A program report submitted to the U.S. Army Corps of Engineers' Upper Mississippi River Restoration-Environmental Management Program, June 2014. Program Report LTRMP 2014-P001, 88 pp, including Appendixes A-G, <http://pubs.usgs.gov/mis/ltrmp2014-p001>
- Ricker WE (1975) Computation and interpretation of biological statistics of fish populations. *Fisheries Research Board of Canada Bulletin* 191, 401 pp, <https://waves-vagues.dfo-mpo.gc.ca/Library/1485.pdf>

- Sammons SM, Bettoli PW, Gear VA (2001) Early life history characteristics of age-0 white crappies in response to hydrology and zooplankton densities in Normandy Reservoir, Tennessee. *Transactions of the American Fisheries Society* 130: 442–449, [https://doi.org/10.1577/1548-8659\(2001\)130<0442:ELHCOA>2.0.CO;2](https://doi.org/10.1577/1548-8659(2001)130<0442:ELHCOA>2.0.CO;2)
- Schultz ET, Conover DO (1999) The allometry of energy reserve depletion: test of a mechanism for size-dependent winter mortality. *Oecologia* 119: 474–483, <https://doi.org/10.1007/s004420050810>
- Smith SM, Odenkirk JS, Reeser SJ (2005) Smallmouth Bass Recruitment Variability and Its Relation to Stream Discharge in Three Virginia Rivers. *North American Journal of Fisheries Management* 25: 1112–1121, <https://doi.org/10.1577/M04-047.1>
- Simberloff, D (2003) How much information on population biology is needed to manage introduced species? *Conservation Biology* 17: 83–92, <https://doi.org/10.1046/j.1523-1739.2003.02028.x>
- Seelbach PW (1987) Effect of winter severity on steelhead smolt yield in Michigan: an example of the importance of environmental factors in determining smolt yield. *American Fisheries Society Symposium* 1: 441–450
- Solomon LE, Pendleton RM, Chick JH, Casper AF (2015) Long-term changes in fish community structure in relation to the establishment of Asian carps in a large floodplain river. *Biological Invasions* 18: 2883–2895, <https://doi.org/10.1007/s10530-016-1180-8>
- Stueck MJ, Yess S, Pitlo J, Van Vooren A, Rasmussen J (2010) Distribution and relative abundance of Upper Mississippi River Fishes. Upper Mississippi River Conservation Committee, Onalaska, WI, 21 pp
- Tripp SJ, Phelps QE, Columbo RE, Garvey JE, Burr BM, Herzog DP, Hrabik RA (2009) Maturation and Reproduction of Shovelnose Sturgeon in the Middle Mississippi River. *North American Journal of Fisheries Management* 29: 730–738, <https://doi.org/10.1577/M08-056.1>
- Turner RE, Rabalais NN (2003) Linking landscape and water quality in the Mississippi River Basin for 200 years. *BioScience* 53: 563–572, [https://doi.org/10.1641/0006-3568\(2003\)053\[0563:LLAWQI\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2003)053[0563:LLAWQI]2.0.CO;2)
- van Handel E (1985) Rapid-determination of total lipids in mosquitos. *Journal of the American Mosquito Control Association* 1: 302–304, https://www.biodiversitylibrary.org/content/part/JAMCA/JAMCA_V01_N3_P302-304.pdf
- Vitousek PM, Mooney HA, Lubchenco J, Melillo JM (1997) Human Domination of Earth's Ecosystems. *Science* 277: 94–499, <https://doi.org/10.1126/science.277.5325.494>
- Winemiller KO, Rose KA (1992) Patterns of life-history diversification in North American Fishes: Implication for population regulation. *Canadian Journal of Fisheries and Aquatic Sciences* 49: 2196–2218, <https://doi.org/10.1139/f92-242>