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Long Term Resource Monitoring Element
Completion Report
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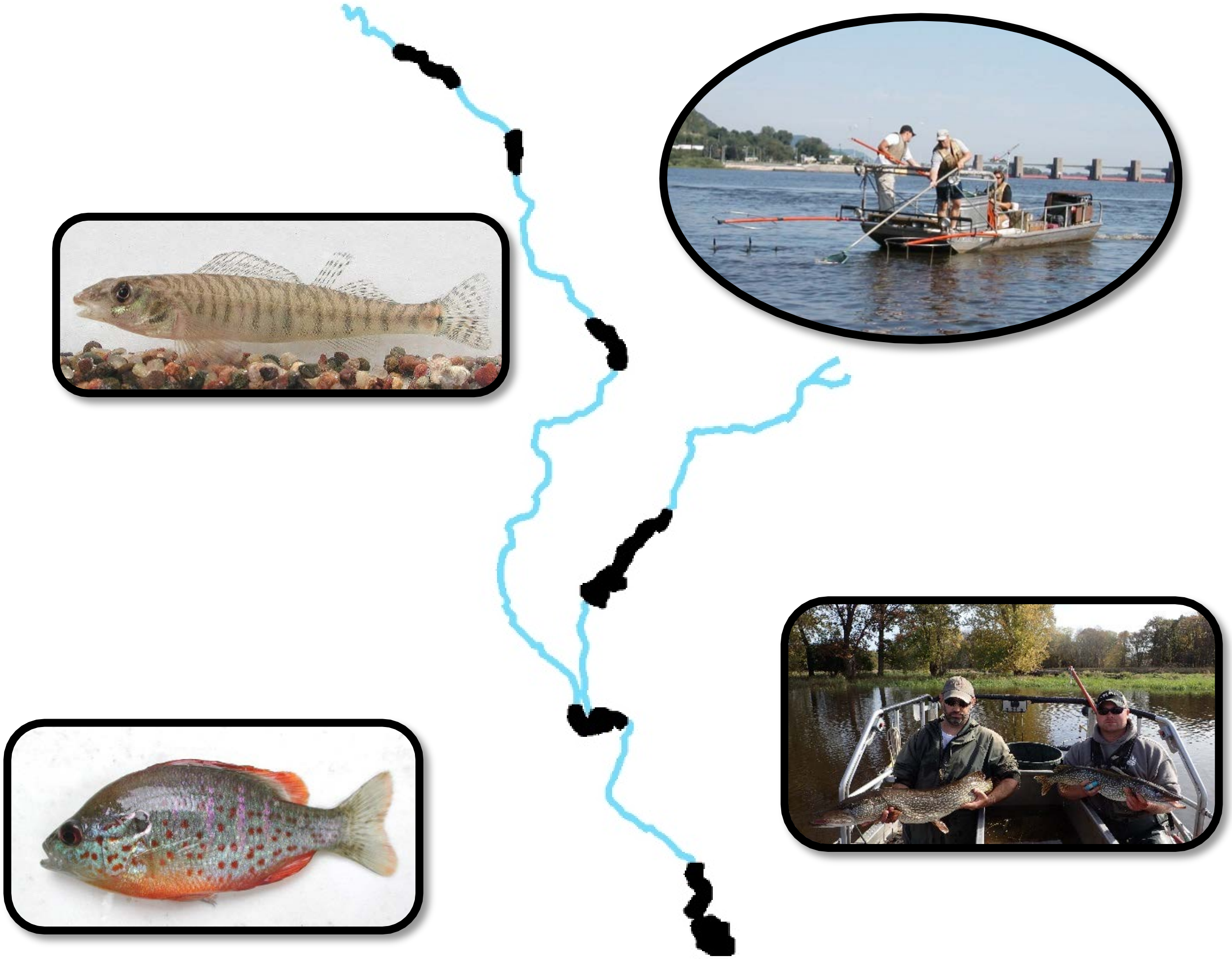
A framework for research and applied management technical support in the Fish Component of the UMRR LTRM



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A framework for research and applied management technical support in the Fish Component of the UMRR LTRM

Brian S. Ickes[1]

[1] Corresponding author, Fisheries Component Principal Investigator, Long Term Resource Monitoring element of the Upper Mississippi River Restoration Program, Upper Midwest Environmental Sciences Center of the United States Geological Survey, La Crosse, WI

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Preface

U.S. Army Corps of Engineers Upper Mississippi River Restoration Long Term Resource Monitoring (LTRM) element is implemented by the U.S. Geological Survey's Upper Midwest Environment Sciences Center, in cooperation with the five Upper Mississippi River System states of Illinois, Iowa, Minnesota, Missouri, and Wisconsin. The U.S. Army Corps of Engineers provides guidance and has overall program responsibility.

This report fulfills milestone 2018B14 from the FY18 UMRR LTRM scope of work.

Fish cover photos by Andy Bartels (WDNR) and Electroshocking boat photo by USGS

Executive Summary

The Long Term Resource Monitoring (LTRM) element of the U.S. Army Corps of Engineer (Corps) Upper Mississippi River Restoration (UMRR) program on the Upper Mississippi River System (UMRS) stands as the United States' largest river monitoring and research program and has amassed geospatial, hydrological, biological, and chemical databases unrivaled in other North American river systems. Presently, the LTRM is transitioning from a period of data banking, critical program evaluations, and data serving initiatives into a period of directed research and modeling to better understand ecosystem properties and dynamics in this heavily human-impacted river basin. Notably, the UMRS is managed as a multiple-use resource, resulting in rich research opportunities for conducting socially-relevant science.

This framework identifies several research topics and questions that can be addressed with existing data resources in the basin. A variety of topics is forwarded in an attempt to match research topics with individual interests, and to foster distributed, collaborative approaches to research across the basin (and beyond). In all, a "systemic UMRS" perspective is pursued. In addition, ideas are outlined for technically-supporting applied management actions in the UMRS basin.

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Topical Area: Habitat
Thematic area: Non-game species

The UMRS is a nexus of freshwater fish diversity in North America, with one-fifth of the entire conterminous United States freshwater ichthyofauna native to the basin; yet, fully 50 species presently possess either federal or state conservation status listing in the basin (see Table 1.3 in Ickes et al. 2005 for a listing of prospective study subjects). Most of these species are non-game species.

Nongame species, as a class of fishes in the basin, imperiled or otherwise, represent more than one-half of species found in the UMRS. Nongame species are often important components of food webs supporting other species valued by humans. Many nongame species are often fairly specific in their habitat requirements, making them excellent candidates for diagnosing changes in habitat conditions. In addition, nongame species, by definition, are not subject to exploitation, which may confound interpretation of status and trends data for recreationally and commercially exploited species, making them ideal candidates for scientific investigations, assessing UMRS environmental health, and measuring the effects/impacts of habitat rehabilitation actions throughout the basin.

It is critically important to develop an understanding of factors that limit at-risk nongame species so that conservation solutions can be identified, developed, and implemented. Exploratory analysis and hypothesis driven investigation of LTRM databases represents the best opportunity to identify and test factors presently constraining the abundance and distribution of many at-risk species in the basin.

Research can be conducted at a variety of spatial, temporal, and ecological scales and using any of a variety of methods and applied/theoretical models. For example, a researcher can investigate the distribution and abundance of a species within a particular aquatic habitat type, within a navigation pool, within a geomorphic reach, or within the entire UMRS. Factors associated with observed patterns in species distribution and abundance can be derived from monitoring data, previous research studies, or any of a variety of geospatial data sources. Theoretical foundations may be derived from population dynamics, metapopulation perspectives, community ecology, systems dynamics, or other areas of study depending on the investigator's interest and chosen topic. Prospective studies may include (1) determining species' ranges and distribution; (2) analyzing dynamics and trends in species abundance; (3) developing probability-based estimates of habitat occupancy; (4) forecasting estimates of extinction probabilities; (5) testing sympatric associations and interactions; (6) modeling environmental determinants of habitat selection; or (7) evaluating responses to management actions or on-going impairments. Investigators may choose to compare and contrast a species response within different portions of the river, using two or more different species in a single area, or by developing Geographic Information System (GIS) models. Some initial research tasks that may be common among many prospective projects include are listed below:

1. Identify one or more study subjects (species) and define a study area;
2. Develop a hypothesis and identify a theoretical framework within which it will be tested;
3. Assemble relevant data sources;

4. Conduct an exploratory analysis of assembled data;
5. Test hypothesis / build habitat model within the chosen theoretical framework;
6. Present results.

Some initial salient questions for using existing data to study non-game species in the UMRS include:

1. Are there observable differences in species size structure across the UMRS, and if so, are these differences the result of an exploitation effect, differential productivity potentials (owing to differences in food web structure, sympatric competitor interactions, or habitat quality), or zoogeographic/climatic zonal controls?
2. What are the habitat requirements of these species, how are those habitats distributed, and may they be limiting?
3. What are the sources of mortality for this class of species? What are the magnitudes of total annual mortality, and how do they vary across the UMRS?
   Is fishing mortality compensatory or depensatory?
4. Based on prevailing trends, is there any evidence that any of the species in this class of fishes will have a non-trivial probability (> 25%) of "functional extinction" within the next 50 years?
5. How does "habitat occupancy" vary for each species across the entirety of the UMRS? Which environmental covariates are most associated with these differences?

Ickes, B. S., M. C. Bowler, A. D. Bartels, D. J. Kirby, S. DeLain, J. H. Chick, V. A. Barko, K. S. Irons, and M. A. Pegg. 2005. 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. LTRM 2005-T005. 60 pp. + CD-ROM (Appendixes A–E). (NTIS PB2005-107572)

Topical Area: Habitat
Thematic area: Exploited species

Many fish species within the UMRS are subject to recreational or commercial exploitation. These species represent a significant portion of the economic value of fishery resources in the UMRS. Consequently, natural resource managers are interested in tracking trends in these species to ensure exploitation is sustainable over time. Changes in abundance or size structure can help diagnose over-exploitation and determine the effects of management actions initiated to improve populations. Moreover, many habitat improvement efforts within the UMRS are targeted at conserving these socially-valued species, so better understanding of how these species respond to habitat improvements should be a key scientific task in this topical and thematic area.

Many basic insights into exploited species' population dynamics can be gained from long-term fishery-independent observations available from LTRM (species status, trends in indexed abundance, size structure, frequency occurrence in the catch, etc…). Species may be investigated individually, in grouped fashion such as guilds, or even as socially-relevant classes of organisms (recreational species, commercial species). The highly standardized sampling protocols of LTRM, and the fishery-independent nature of its observations, eliminates most of the complexities of investigating trends, dynamics, and associations as may be common in creel or commercial harvest records, wherein effort, methods, and harvest efficiency may change over time due to market forces, technological advances, or regulatory circumstances.

A fully developed research framework is already generated for a UMRS fishes. This framework is centered on investigating over-winter habitat limitations across the UMRS. Interested readers/investigators are referred to that framework for more specific research questions and opportunities [see Appendix A herein].

Relevant background program information on exploited fish species in the UMRS includes Ickes et al. (2005) and Kirby and Ickes (2006). More generally however, some relevant questions that may be addressed with LTRM data sources for exploited fishes include the following:

1. Are there observable differences in species size structure across the UMRS, and if so, are these differences the result of an exploitation effect, differential productivity potentials (owing to differences in food web structure, sympatric competitor interactions, or habitat quality), or zoogeographic/climatic zonal controls?
2. What are the habitat requirements of these species, how are those habitats distributed, and may they be limiting?
3. What are the sources of mortality for exploited species? What are the magnitudes of total annual mortality, and how do they vary across the UMRS?
4. What is the contribution of exploitation (fishing mortality) to total annual mortality?
5. Is fishing mortality compensatory or depensatory?
6. Are observed differences in species abundance and size structure across the UMRS in any way related to differences in state harvest regulations, and if so, how so?
7. Based on prevailing trends, is there any evidence that any exploited species will have a non-trivial probability (> 25%) of "functional extinction" within the next 50 years?
8. How does habitat occupancy vary for each species across the entirety of the UMRS? Which environmental covariates are most associated with these differences?

Ickes, B. S., M. C. Bowler, A. D. Bartels, D. J. Kirby, S. DeLain, J. H. Chick, V. A. Barko, K. S. Irons, and M. A. Pegg. 2005. 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. LTRM 2005-T005. 60 pp. + CD-ROM (Appendixes A–E). (NTIS PB2005-107572)

Kirby, D. J., and B. S. Ickes. 2006. Temporal and spatial trends in the frequency of occurrence, length–frequency distributions, length–weight relationships, and relative abundance of Upper Mississippi River fish. U.S. Geological Survey, Upper Midwest Environmental Sciences Center, La Crosse, Wisconsin, July 2006. LTRM 2006-T002. 68 pp. (NTIS PB2006-114569)

Topical Area: Habitat
Thematic area: Nonnative/Invasive species

Nonnative fishes compose a sizeable fraction of the total fish mass in the UMRS and new introductions have occurred recently (Ickes et al. 2005; Irons et al. 2009; Ickes 2008 in Johnson and Hagerty eds. 2008). Once established, nonnative species are nearly impossible to control, and then only at great expense. The Mississippi River and its principal tributaries provide a highway for nonnative species to travel from areas as geographically disparate as the Atlantic Gulf Coast and the Laurentian Great Lakes to the interior of the North American continent, strengthening arguments for a systemic perspective on this thematic area. Recently established populations of silver carp (*Hypophthalmychthys molitrix*) and bighead carp (*H. nobilis*) in the southern portions of the UMRS are expected to increase in abundance (as evidenced by more recent data from the lower reaches) and expand their distribution within the UMRS. Additional species, including round goby (*Neogobius melanostomus*) and black carp (*Mylopharyngodon piceusare*), are poised to invade the UMRS from Great Lakes and down river sources, respectively. Because of the ability of many nonnative fish species to compete with and displace native species, nonnative species will remain a principal threat to native biodiversity in the foreseeable future in the Mississippi River drainage, home to nearly one-fifth of the entire North American freshwater fish fauna.

Earlier work in the LTRM fish component has synthesized information and data on extant nonnative fishes in the UMRS (Irons et al. 2009). Additionally, much non-program directed work has also occurred locally and regionally. LTRM's contribution to this topic should exploit its unique and unprecedented empirical assets (in spatial scope, rigor, and duration) to explore nonnative and invasive species questions not answerable by short-term directed field or laboratory study. The following initial and priority questions could serve as the foundation to a more systemic treatment of this issue in UMRS:

1. Why aren't viable populations of bigheaded carp established throughout the UMRS yet?
2. What are the habitat occupancy requirements for UMRS nonnative fishes and which environmental covariates are most closely associated with habitat occupancy?
3. How can environmental covariates associated with nonnative fish habitat occupancy best be managed to reduce the impacts and effects of nonnative fishes in the UMRS?
4. Can large scale ecosystem rehabilitation be enlisted in bigheaded carp control efforts?
5. LTRM data clearly show systemic declines in common carp abundance and occurrence. What factors are associated with these observed declines and how might that inform management of other nonnative fishes in the UMRS?
6. Is there evidence, systemically, that UMRS dams presently limit the distribution of bigheaded carp and other nonnative fishes?
7. What effects are bigheaded carp having on native sympatric species where they presently occur, and are there any density-dependent associations with regards to wider fish community responses?
8. Is there evidence that native fish mass is responding negatively to increases in bigheaded carp in the southern reaches of the UMRS?

9. Is there evidence that native fish assemblages are expressing decreased resilience owing to multiple concurrent stressors in the southern reaches of the UMRS (navigation, land use, invasive species, etc…).

Below, additional questions are provided that may be addressed, in part, with existing LTRM data sources, but also many of which would require new start-ups and directed studies. These questions are listed under the non-natives thematic area because of acute interest natural resource practitioners have concerning the effects of these non-native and invasive species on the diverse native UMRS fish community. However, it should be noted that these same questions, or their corollaries, may also apply to the exploited and non-game themes immediately above. They are presented once here to avoid redundancy:

1. What are the extant standing stocks of silver and bighead carps, their population demographics, and their fitness (pre-requisite for population dynamics modeling)?
    a. Size distributions?
    b. Length/weight at age?
    c. Sex ratios?
    d. Age/length at maturity?
    e. Fecundity?
    f. Growth rates?
    g. Longevity?

2. What are the recruitment processes, rates, and dynamics?
    a. Relationship of recruitment to spawning stock?
    b. Form of the relationship (Ricker vs. B-H form)?
    c. Sources of uncertainty in the stock:recruit relationship?
    d. Responses in recruitment to variation in the stock?
    e. Responses in recruitment to variation in environmental covariates?

3. What are the sources of immigration relative to existing assessment and/or management zones?
    a. Immigration rates?
    b. Seasonality in immigration?
    c. Demographics of immigration?
    d. Mode/triggers of immigration dispersal (passive vs. active)?

4. What are the sources of emigration relative to existing assessment and/or management zones?
    a. Emigration rates?
    b. Seasonality in emigration?
    c. Demographics of emigration?
    d. Mode/triggers of emigration dispersal (passive vs. active)?

5. What are the mortality sources and their magnitudes?
    a. Depensatory?
    b. Compensatory?

    c. Natural sources and rates?
    d. Fishing sources and rates?
    e. Age and/or size dependent (and if so, how)?
    f. Sexual dimorphism?

6. What are the growth rates, maturity rates, Gonadal Somatic Indices, Relative Weight, and differences/similarities among extant sub-stocks?

7. Can the populations be effectively managed under various possible exploitation strategies?
    a. Fixed exploitation rates?
    b. Growth overfish?
    c. Recruitment overfish?
    d. Population-based fishing strategies?
    e. Pulse vs. press exploitation?

8. What are the possible fisheries strategies (and their effect on stock)?
    a. Minimize immigration?
    b. Maximize emigration?
    c. Maximize harvest?
        i. Liberal quotas?
        ii. Liberal size limits?
    d. Minimize growth and/or recruitment?
    e. Total Individual Minimum Catch (estimable by [mass x F / participant number])?

9. Can the behavior of the fishery itself be described?
    a. Participation?
    b. Terms of entry and continuance?
    c. Economics thereof?
    d. Constraints to spatial dynamics?

10. Are other strategies for stock management possible?
    a. Integrated pest management strategies (diversify mortality sources; alter dispersal in favorable ways; etc…)?
    b. Short circuit production pathways?

Ickes, B. S., M. C. Bowler, A. D. Bartels, D. J. Kirby, S. DeLain, J. H. Chick, V. A. Barko, K. S. Irons, and M. A. Pegg. 2005. 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. LTRM 2005-T005. 60 pp. + CD-ROM (Appendixes A–E). (NTIS PB2005-107572)

Ickes, B.S. 2008. Fisheries indicators: Nonnative fishes. *in* Johnson, B.L. and K.H. Hagerty, editors. Status and Trends of Selected Resources of the Upper Mississippi River System. U.S. Geological Survey, Upper Midwest Environmental Sciences Center, La Crosse, Wisconsin,

Technical Report LTRM 2008-T002. pp. 73-74. Available online at: http://pubs.usgs.gov/mis/LTRM2008-T002/, accessed 3 January, 2012.

Irons, K.S., DeLain, S.A., Gittinger, E., Ickes, B.S., Kolar, C.S., Ostendorf, D., Ratcliff, E.N., and Benson, A.J. 2009. Nonnative fishes in the Upper Mississippi River System: U.S. Geological Survey Scientific Investigations Report 2009–5176, 68 p.

Topical Area: Habitat
Thematic area: Life History

Life history traits can be defined as a suite of characteristics particular to a species that describe its association to the environment in which it evolved or currently exists. These characteristics can be conceptualized as particular to the physiology, behavior, and general ecology of the species. Generally, species demonstrate physiological affinities and behavioral associations such that some combination of life history traits defines a suite of conditions that meet critical life history needs and that define the general association of a species to its environment. Because life history traits are fundamental determinants of population performance, the investigation of life history strategies is central to both theoretical ecology and natural resource management.

In ecosystem management, it is generally held that there is a direct relationship between habitat diversity and biotic diversity. Questions concerning this relationship are presently at the forefront of ecology (Tews et al. 2004). While ecosystem management paradigms largely embrace a “Habitat is key” perspective, scientific and empirical evidence assembled to date has resulted in a more mixed picture. Within the UMRS, the nature of the relationship between habitat and biotic diversity is especially prescient because ecosystem rehabilitation efforts are founded on the premise of habitat limitation. Earlier, research on Mississippi River fish communities found a relationship between fish diversity and geomorphic diversity (Koel 2004), which served as a surrogate for “habitat”, over large spatial extents (>1000 km river). This work, however, was based on species observations and measures of abundance that exhibit high degrees of variation. Potentially confounding factors, such as zoogeography, were not controlled for in the analysis.

One way to better control for potentially confounding factors and better test empirical relationships between biotic diversity and habitat diversity is to pursue a functional guild approach. Guilds pool species sharing similar observed life history traits and remove some potentially confounding effects associated with species distribution across large study areas (e.g., zoogeography). Recently, the LTRM has assembled a life history database for 230 fish species in the Central Basin of the United States (O’Hara et al 2006). This work proposes to recast LTRM fisheries observations into functional guild units using the life history database to investigate patterns in functional diversity of UMRS fish communities across 1960 km of river. Rather than basing diversity metrics on abundance, this research will recast individual fish observations into indexed mass units based on growth models coded into the LTRM fish life history database. In this way, all species are standardized to comparable mass-based units (e.g., issues such as equating one minnow to one sturgeon are fully addressed using mass measures rather than counts). Potential key research questions include:

1. Is the functional diversity of UMRS fish communities related to habitat diversity?
2. What are the spatial patterns in life history diversification within the UMRS and how do they relate to present and past patterns in UMRS aquatic environments?
3. What are the spatial patterns in indexed functional mass across the UMRS and is there evidence for counter-gradients in energy pathways (inferred by compositional differences in mass patterns among feeding guild classes)?

Koel, T. M., 2004, Spatial variation in fish species richness of the upper Mississippi River system: Transactions of the American Fisheries Society, v. 133, no. 4, p. 984-1003.

O'Hara, M., B. S. Ickes, E. Gittinger, S. DeLain, T. Dukerschein, M. Pegg, and J. Kalas 2007. Development of a life history database for Upper Mississippi River fishes. U.S. Geological Survey, Upper Midwest Environmental Sciences Center, La Crosse, Wisconsin. LTRM 2007-T001. 10 pp. + Appendixes A–B. (NTIS ADA470170)

Tews, J., U. Brose, V. Grimm, K. Tielborger, M.C. Wichmann, M. Schwager, and F. Jeltsch. 2004. Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. Journal of Biogeography. Vol 31(1): 79-92.

Topical Area: Fish passage
Thematic area: Longitudinal passage

Twenty seven dams on the UMRS mainstem allow for the management of water levels during low flows to permit commercial navigation. Most of these dams were authorized by Congress in 1930s to maintain a 9-foot navigation channel. Fish passage through these dams has been a long-standing concern (Ickes et al. 2001). Several studies have documented that some fish species can pass through UMRS dams, but the extent to which the locks and dams impede fish passage for most species remains unknown or controversial.

Previous efforts sought to define the current state of knowledge on fish passage in large floodplain rivers managed for commercial navigation, including a synthesis of prevailing river theory; species-specific behavior and physiological performance; engineering, design, and performance of alternative fish passage devices; and case history studies from around the world (Ickes et al. 2001). Additionally, freshwater mussels were given consideration in relation to longitudinal fish passage because mussel distribution and dispersal are directly related to movement of fish that act as hosts for the juvenile and parasitic stage of many freshwater mussel species.

LTRM data sources can provide unique systemic insights into the fish passage problem. Examples of questions that can be addressed include:

1. Using an index of ubiquity and theoretic models, can it be inferred whether locks and dams presently constrain the systemic distribution of a diverse fish fauna in the UMRS?
2. Do large floods increase the probability of UMRS lock and dam fish passage?

3. Do droughts decrease fish passage probabilities (inferred by changes in abundance [indexed or ranked] and/or occurrence probabilities in upstream reaches in each hydrologic circumstance, as observed over a 20 year period)?

Ickes, B. S., J. H. Wlosinski, B. C. Knights, and S. J. Zigler. 2001. Fish passage through dams in large temperate floodplain rivers: an annotated bibliography. U.S. Geological Survey, Upper Midwest Environmental Sciences Center, La Crosse, Wisconsin. An LTRM Web-based report available online at http://www.umesc.usgs.gov/LTRM_fish/fish_passage_biblio.html. (Accessed January 2014).

Topical Area: Fish passage
Thematic area: Lateral passage

Most Central Basin rivers in the United States have been intensively engineered (e.g., commercial navigation, agricultural development, flood control, etc…). As a consequence, dams, levees, bridges, roads, railways and ditches significantly affect hydrologic linkages between the main stem and lateral floodplain. On the Upper Mississippi River, present day floodplains represent a complex matrix of private and public lands managed for a wide array of goals and interests. The effect that such lateral fragmentation has had on native UMRS fishes is largely unknown; however, dozens of species are known to require floodplain and backwater environments for part or all of their life history requirements.

Earlier work produced the first systemic effort to identify the scope of lateral passage of fish in the UMRS, identify prospective applied and theoretical solutions, and to highlight data and information required to move a research program on this topic forward (Ickes et al 2005; Appendix B herein). Significant opportunities for improved management of lateral connectivity on the UMRS are available, mostly on public lands managed by the U.S. Fish and Wildlife refuge system or the Corps. However, present management paradigms (e.g., waterfowl production, flood control) pose severe physiological challenges to most native fish species requiring seasonal access to floodplain environments.

There are opportunities to better inform and study lateral fish passage in the UMRS. Existing LTRM fish community data can be analyzed and modeled to determine which areas are seemingly most impaired. For example, researchers may infer the faunal life histories requirements that are either being met or not in different regions of the UMRS; and habitat suitability and its environmental determinants may be modeled and quantified, which can be used in projects designed to restore, or otherwise manage, lateral connectivity in the UMRS. Examples of these types of analyses can be found in the citation provided below (Ickes et al. 2005). This publication presents an additional research framework and is attached to this document as Appendix B. Many of the “information assembly and discovery goals” laid out in the Appendix B report have been achieved since 2005, setting the stage for rapid advancement on lateral fish passage in the UMRS.

Ickes, B. S., J. Vallazza, J. Kalas, and B. Knights. 2005. 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.

Topical area: Basic Fisheries ecology
Thematic area: Management-relevant patterns in large river fish populations and communities

The UMRS possesses the richest fish fauna at temperate latitudes on the planet (Ickes et al. 2005). Since its inception in 1989, LTRM has observed 144 species and has tracked the status, trends, and dynamics of each species across 1900 km of river and for > 20 years of time. As such, the LTRM fisheries database represents perhaps the densest and largest fisheries database in existence upon large rivers in North America, if not the world.

Sub-theme: Community ecology (synecology)

Formerly, an inter-agency team of natural resource scientists explored and reported upon fish community patterns and their environmental covariates in the UMRS, and key findings are summarized and cited below. Because the LTRM makes observations in highly standardized, documented, and scientifically defensible ways, LTRM data sources provide a unique opportunity to explore non-random patterns and infer processes driving fish community dynamics at heretofore unprecedented scales of space and time. Research within this former team focused on multivariate spatiotemporal patterns in fish community dynamics at spatial scales ranging from ~1 km to 1960 km and temporal scales ranging from seasonal to decadal, based on greater than 5 million individual fish observations collected over 20 years by the LTRM. These initial pieces of work provide demonstrably non-random pattern determination in fish community responses across the UMRS, provide a spatial and temporal context for determining the status and trends of UMRS fish communities, provide insights into scaling issues in community responses, and identify environmental covariates associated to date with fish community dynamics.

Key findings to date can be summarized as follows: 1) spatial factors dominate fish community patterns at all scales investigated relative to temporal factors (Barko et al. 2004; Chick et al. 2005; Ickes et al. 2005); 2) community level responses to large disturbances such as floods vary in magnitude along a floodplain and channel disturbance gradient, but are only a minor component of overall community variation (Chick et al. 2005; Ickes et al. 2005); 3) community dynamics are substantially different between juvenile and adult community components (Barko et al. 2005; Ickes et al. 2005); 4) small scale habitat rehabilitation efforts (e.g., 1 - 10s km2) are unlikely to have measurable or detectable effects on UMRS fish community outcomes (Ickes et al. 2005); and 5) limnophilic and lentic guilds have responded significantly and strongly to substantial increases in aquatic macrophyte abundance and distribution in the northern reaches of the UMRS whereas there is a discernible concomitant decline in rheophilic species (Giblin 2017).

Discerning how entire fish communities respond to both natural and anthropogenic changes in river conditions is central to developing informed and impactful management alternatives for achieving a socially beneficial and sustainable fish fauna throughout the UMRS. Threats to the UMRS fish fauna are many and derive from a multitude of sources, ranging from habitat loss to exploitation, and from invasive species to impacts deriving from industrial uses of the Mississippi River. Past research on community ecology represents an important first step in crafting multi-species and community management objectives within the basin. To date, however, initial results from these studies have not been used by applied management practitioners to establish such objectives.

Relevant questions, derivable from LTRM fish component data sources, include the following:

1. Are observed fish community and functional guild shifts in northern UMRS study reaches likely to result in an alternate stable state?
2. What is the functional basis of observed shifts, as inferred by changes in functional feeding and reproductive guild classes?
3. What effects are invasive bigheaded carp having on functional community ecology in the southern reaches of the UMRS?
4. How resilient are southern UMRS fish communities to bigheaded carp invasion (using the north as a pseudo-control group)?
5. Disturbance theory in restoration ecology suggests that diversity is greatest at intermediate levels of disturbance. Is there evidence that the combined impacts of navigation, habitat impairment, and bigheaded carp invasion are beginning to suppress expressions of faunal diversity (richness and evenness) in the southern UMRS reaches?
6. What are the sympatric associations of extant fisheries fauna within different aquatic area classes across the UMRS, how do they vary north to south, and what might that say about the resilience of the respective communities/assemblages to existing and increasing stresses?
7. Is there evidence of directional trajectories in UMRS fish communities, to what factors are such trajectories attributable, and is there evidence of management effects/influences upon such trajectories?

Barko, V.A., M.W. Palmer, D.P. Herzog, and B. Ickes. 2004. Influential environmental gradients and spatiotemporal patterns of fish assemblages in the unimpounded Upper Mississippi River. American Midland Naturalist 152(4): 369-385.

Barko, V. A., B. S. Ickes, D. P. Herzog, R. A. Hrabik, J. H. Chick, and M. A. Pegg. 2005. Spatial, temporal, and environmental trends of fish assemblages within six reaches of the Upper Mississippi River System. U.S. Geological Survey, Upper Midwest Environmental Sciences Center, La Crosse, Wisconsin, February 2005. Technical Report LTRM 2005-T002. 27 pp.

Chick, J. H., B. S. Ickes, M. A. Pegg, V. A. Barko, R. A. Hrabik, and D. P. Herzog. 2005. Spatial structure and temporal variation of fish communities in the Upper Mississippi River System. U.S. Geological Survey, Upper Midwest Environmental Sciences Center, La Crosse, Wisconsin, May
2005. LTRM Technical Report 2005-T004. 15 pp.

Giblin, S. 2017. Identifying and quantifying environmental thresholds for ecological shifts in a large semi-regulated river. Journal of Freshwater Ecology, 32:1, 433-453, DOI: 10.1080/02705060.2017.1319431

Ickes, B. S., M. C. Bowler, A. D. Bartels, D. J. Kirby, S. DeLain, J. H. Chick, V. A. Barko, K. S. Irons, and M. A. Pegg. 2005. 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. LTRM 2005-T005. 60 pp. + CD-ROM (Appendixes A–E).

Kirby, D. J., and B. S. Ickes. 2006. Temporal and spatial trends in the frequency of occurrence, length–frequency distributions, length–weight relationships, and relative abundance of Upper Mississippi River fish. U.S. Geological Survey, Upper Midwest Environmental Sciences Center, La Crosse, Wisconsin, July 2006. LTRM 2006-T002. 68 pp. (NTIS PB2006-114569)

Sub-theme: Single species ecology (autecology)

Community dynamics are determined, in part, by population dynamics within species and interactions among species. Moreover, from a management perspective, fish communities are comprised of many species that are managed for different purposes (e.g., consumptive or recreational uses, biodiversity, threatened or endangered species conservation, and non-native species control). This sub-theme of autecology seeks to quantify and model single species dynamics (e.g., abundance, size structure, growth) for a majority of UMRS fish species using LTRM data sources. Specifically, this research investigates 1) spatial patterns in species prevalence over a 20 year period; 2) spatiotemporal patterns in growth responses; 3) spatial differences in size structure of exploited species; 4) spatiotemporal patterns in abundance; and (5) habitat suitability for species of acute management interest.

Key findings can be summarized as follows : 1) growth rates in Illinois River fishes were significantly greater than Upper Mississippi River fishes, suggesting differential geomorphic controls on productivity, different energy and tropic pathways, or some combination of these (Kirby and Ickes 2006); 2) recreationally-exploited species shared similar size structure throughout the UMRS but commercially-exploited species exhibited truncated size structure in southern reaches where exploitation is greatest (Kirby and Ickes 2006); 3) species size-structured abundance responses to several spatial and temporal scales innate to the LTRM sampling design have been elucidated and can be used to identify intelligent indicators for studying biological responses to habitat rehabilitation (Kirby and Ickes 2006; Ickes et al. 2005); and (4) spatially-explicit habitat occupancy models have been attempted/developed for 28 species across the entirety of the UMRS (AHAG; Ickes et al. 2014).

Results from this body of work are presently being used throughout the UMRS management community to refine specific research questions and to provide a “blueprint” for bio-indicator selection as part of habitat rehabilitation assessments by the Corps, the five upper Midwestern states of MN, WI, IA, IL, and MO, the Environmental Protection Agency, the US

Fish and Wildlife Service, and the Upper Mississippi River Basin Association. Results have also been integrated into the 10 year strategic management plan for the multi-state Upper Mississippi River Conservation Commission.

Additional research and application in this area should include the following:

1. Elucidate/investigate environmental determinants of juvenile as well as adult fish abundance and site occupancy. The basic science question is whether the environmental determinants of single-species biological responses vary as a function of ontogeny (life stage), and in what ways.
2. Further develop and refine habitat occupancy models (e.g, AHAG) as needed to assist habitat managers.
3. Estimate functional extinction probabilities for a variety of species across the UMRS to better inform management priorities and biological targets.
4. Seek to better understand the proximate causes of observed differences in prevailing growth rates across the UMRS, especially changes in growth rate responses associated with habitat rehabilitation efforts.
5. Use earlier results to intelligently inform biological indicator selection for habitat rehabilitation efforts throughout the UMRS.
6. Several species are demonstrating notable changes in their dynamics (e.g., recruitment failures in northern white bass populations; profound increases in weed shiner abundance and range expansion, bigheaded carp and native assemblages in the south). Such patterns can be observed within the LTRM Fish Component online browser utilities and visualization tools. Work is needed to model/study and understand the underlying mechanisms giving rise to these observed patterns.

Ickes, B. S., M. C. Bowler, A. D. Bartels, D. J. Kirby, S. DeLain, J. H. Chick, V. A. Barko, K. S. Irons, and M. A. Pegg. 2005. 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. LTRM 2005-T005. 60 pp. + CD-ROM (Appendixes A–E).

Ickes, B.S., Sauer, J.S., Richards, N., Bowler, M., and Schlifer, B., 2014, Spatially explicit habitat models for 28 fishes from the Upper Mississippi River System (AHAG 2.0) (ver. 1.1, July 2014): A technical report submitted to the U.S. Army Corps of Engineers' Upper Mississippi River Restoration-Environmental Management Program, Technical Report 2014–T002, 89 p., *http://pubs.usgs.gov/mis/ltrmp2014-t002/*.

Kirby, D. J., and B. S. Ickes. 2006. Temporal and spatial trends in the frequency of occurrence, length–frequency distributions, length–weight relationships, and relative abundance of Upper Mississippi River fish. U.S. Geological Survey, Upper Midwest Environmental Sciences Center, La Crosse, Wisconsin, July 2006. LTRM 2006-T002. 68 pp. (NTIS PB2006-114569)

Topical Area: Applied management technical support
Thematic area: Novel Ways to Communicate Monitoring and Science Information to Natural Resource Managers and the Public

Ecosystem management in large ecosystems is complicated by the size of the systems themselves, multiple jurisdictional agents, and multiple use doctrines. In such systems, in order for common data platforms to enter into management judgments, these problems need to be overcome. Ecosystem monitoring data are most useful when they are readily available in a variety of forms that can be used to inform management actions, develop research hypotheses, and engage the public in the resource being monitored. The LTRM has stood as a national leader in serving ecological data to diverse interests under an "open access" paradigm. For example, in 2003, the LTRM developed an on-line tool that allows natural resource managers, scientists, and the public to easily and intuitively investigate the status and trends of UMRS fish communities and the population dynamics of greater than >130 UMRS fish species. The tool is based on principles of data visualization and expert systems science and uses Java technology to provide an approachable graphical interface to exceedingly complex ecological databases compiled by the LTRM over the past 20 years. This tool has greatly enhanced the relevancy of LTRM databases in day-to-day management of UMRS fisheries, serves as scientific hypothesis generating mechanism for natural resource scientists throughout the basin, and also serves as a public outreach tool for the program. See the following links:
http://www.umesc.usgs.gov/data_library/fisheries/graphical/fish_front.html
http://www.umesc.usgs.gov/reports_publications/psrs/psr_2003_01.html

The next generation of this tool is to link it to the recently completed LTRM fish life history database. A primary goal would be to link life history attributes to species presented within this tool; portraying distribution maps, species descriptions, species photos, and interesting life history tidbits for >130 UMRS fish species. This project represents an opportunity for investigators with interests in computer programming, databases, and / or data visualization to develop skills within a natural resource science setting.

There are also several new data visualization tools under development, ones that permit insights into fish community and species dynamics through simple empirical animation and/or classification. Examples include the recent launch of the LTRM Fish Component's online Treemap application that permits not only compressed data visualization, but also higher end data mining of these compressed visualizations using LTRM's prodigious databases. This tool permits user-driven investigation of LTRM fish data by species and a variety of functional or thematic guilds, in either indexed abundance or indexed mass units, for all spatial and temporal domains of LTRM observations.
(see
http://www.umesc.usgs.gov/data_library/fisheries/graphical/treemap/LTRM_treemap.html).
Trends and variance benchmarks, pie charts reflecting compositional aspects of the full community or selected guild, and complex bar charts can all be easily gleaned from this tool in a distributed user environment.

Another example under consideration and development under this topic is predicated on GapMinder technology and permits dynamic animation of user-defined relationships (say rank abundance vs. frequency occurrence) for user-defined assemblages or communities. Beta versions of this tool have been shown in various recent talks in the basin (e.g., http://www.nps.gov/miss/naturescience/rf0518.htm, see presentation file and video slides 43 and 44).

Many additional distributed data user visualization tools can be conceived and created, and many ideas already exist. New tools need not be constrained to the fish component of the LTRM data. Because these tools are "user-driven", prospective users need to have/provide input before additional data visualization tools are developed.

Topical Area: Applied management technical support
Thematic area: Socio-Economic Indicators of UMRS Fisheries Resources

Increasingly, natural resource management is shifting towards "ecosystem system health" perspectives wherein health is ascribed based on indices of coupled ecologic, social, and economic systems. Most frequently, indices are compiled separately for numerous ecological, social, and economic outcomes so that policy trade-offs among ecological, social, and economic interests can be explored, modified, or otherwise accommodated (Gundersen and Holling, eds. 2002). Often, however, it is difficult to ascribe relative valuation criteria to many ecological outcomes of interest. For example, how does one ascribe a "value" to rare species in a quantitatively rigorous way? One way is to express value in monetary units. From a policy perspective, indices valued in such a way permit policy makers to explore "utility optimization" perspectives in the management of coupled ecologic, social, and economic systems.

Work proposed under this thematic area ascribes economic valuations to UMRS fishes to investigate several questions related to habitat quality and ecosystem restoration. LTRM fish observations (N > 5 million fish) can be ascribed an economic replacement value based on data published by the American Fisheries Society. Recasting these data can lead to several achievements: statistical description of "standing indexed fish value (e.g., $PUE)" in each of 6 river reaches, trends determination over time in economic value, and testing relationships between total economic value of UMRS fishes and expenditures in habitat rehabilitation within the basin. Specific questions include:

1. Is there a positive relationship between habitat diversity and the indexed economic value of UMRS fishes?
2. Is there a positive relationship between habitat rehabilitation expenditures and the indexed economic value of UMRS fishes?

Gundersen, L.H and C.S. Holling, eds. 2002. Panarchy: understanding transformations in human and natural systems. Island Press, Washington D.C. xxiv + 507 pages.

Topical Area: Applied management technical support
Thematic area: Status and Trends Indicators of UMRS Fisheries Resources

Partnering federal and state agencies within the UMRS, that are parties to the UMRR, must periodically assess and report on the Status and Trends of the ecological health of the UMRS. Developing a framework within which to conduct Status and Trends assessments remains an ongoing process. Previous reports have 1) laid the conceptual foundation for conducting assessments; and 2) brought unprecedented empirical resources to bear on the assessments. Still remaining are the tasks of establishing reference conditions, selecting responsive indicators, and stating long-term management objectives against which progress towards a healthier UMRS can be measured and charted.

In March 2010, the A-Team of the Upper Mississippi River Restoration Coordinating Committee (UMRRCC) established a special committee on fish indicators to address the following three objectives: (1) define what constitutes a healthy UMRS ecosystem (from a fisheries point of view); (2) make recommendations for indicating fish community health attributes and for making data-informed judgments on their status and trends in the future; and (3) make recommendations for additional indicators to consider and/or additional analytic work that may be needed in either selecting additional indictors or optimizing their implementation. This team's report is presented in three chapters that align with each committee objective (Ickes et al. 2010; see report for priority work/research topics).

Ickes, B.S. and 8 others. 2010. Upper Mississippi River Restoration Coordinating Committee Analysis Team Indicators Ad hoc Committee, Special Committee on Fish Indicators for Status and Trends Assessments. U.S. Geological Survey, Upper Midwest Environmental Sciences Center, La Crosse, Wisconsin, June 2010. Long Term Resource Monitoring Program Report submitted to the US Army Corps of Engineers, Rock Island, Illinois. 48 pp.

Appendix A: A research framework for aquatic over-wintering issues in the Upper Mississippi River Basin (Published 2005)

1. Executive summary

This document details a framework for research into an over-arching hypothesis of winter habitat limitation on the production of fishes in the Upper Mississippi River System (UMRS). The goal of this document is to lay a foundation of background material, outline a sequence of pertinent research questions, and identify approaches and methodologies for study. This framework is expected to direct research into this topic through the auspices of the Long Term Resources Monitoring (LTRM) element of the Upper Mississippi River Restoration (UMRR) program.

The geographical setting for the research outlined in this program is the Upper Mississippi River System (UMRS), legislatively defined as the commercially navigable reaches of the Upper Mississippi River (UMR) as well as the Illinois River (ILR) and navigable portions of the Kaskaskia, Black, St. Croix and Minnesota Rivers. Under the UMRR, significant resources are expended to rehabilitate riverine landscapes in an adaptive management framework. Such management actions offer unique opportunities to conduct both basic and applied research for the purpose of improving rehabilitation efforts as well as to better understand large river ecosystems.

As conceived and drafted **the principal question this research program seeks to answer is whether over-winter habitat limits fish production in the UMRS**.

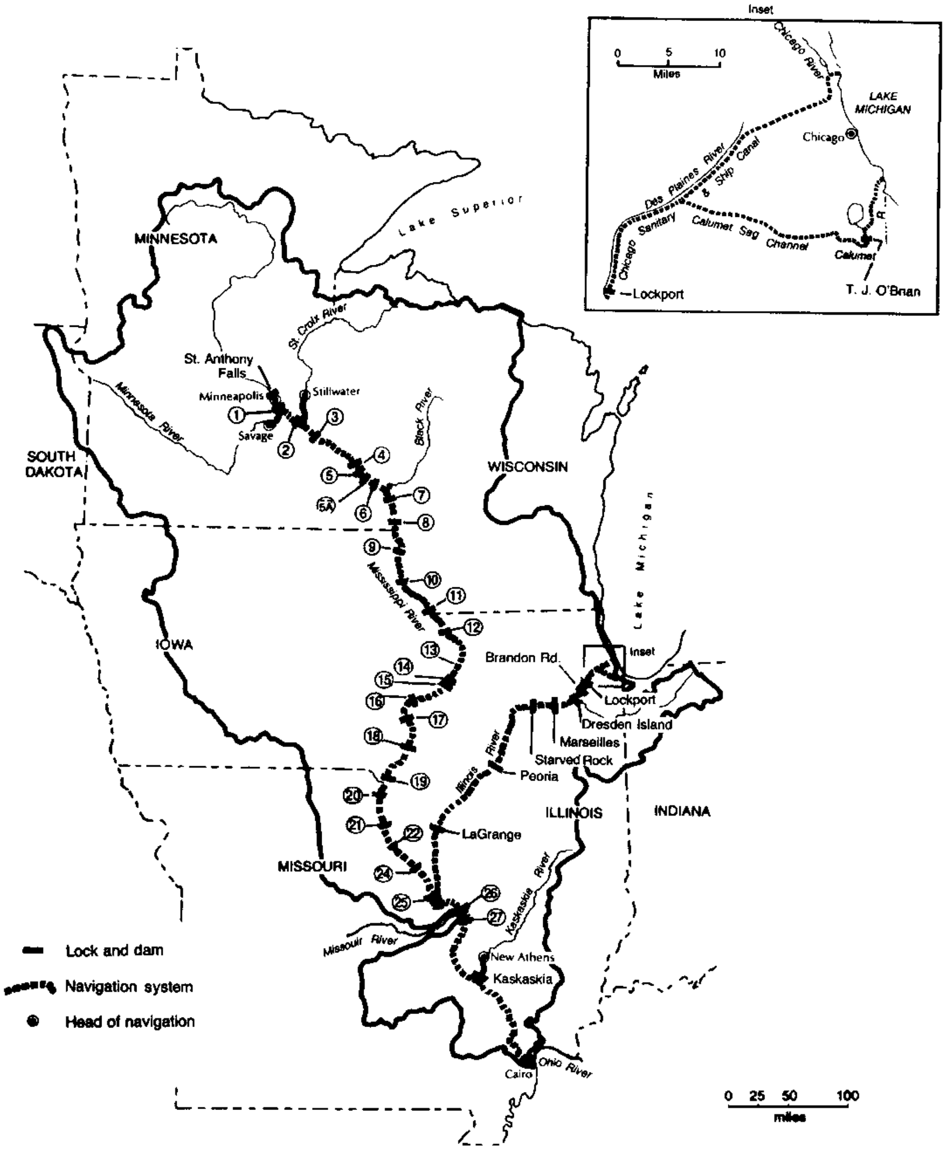
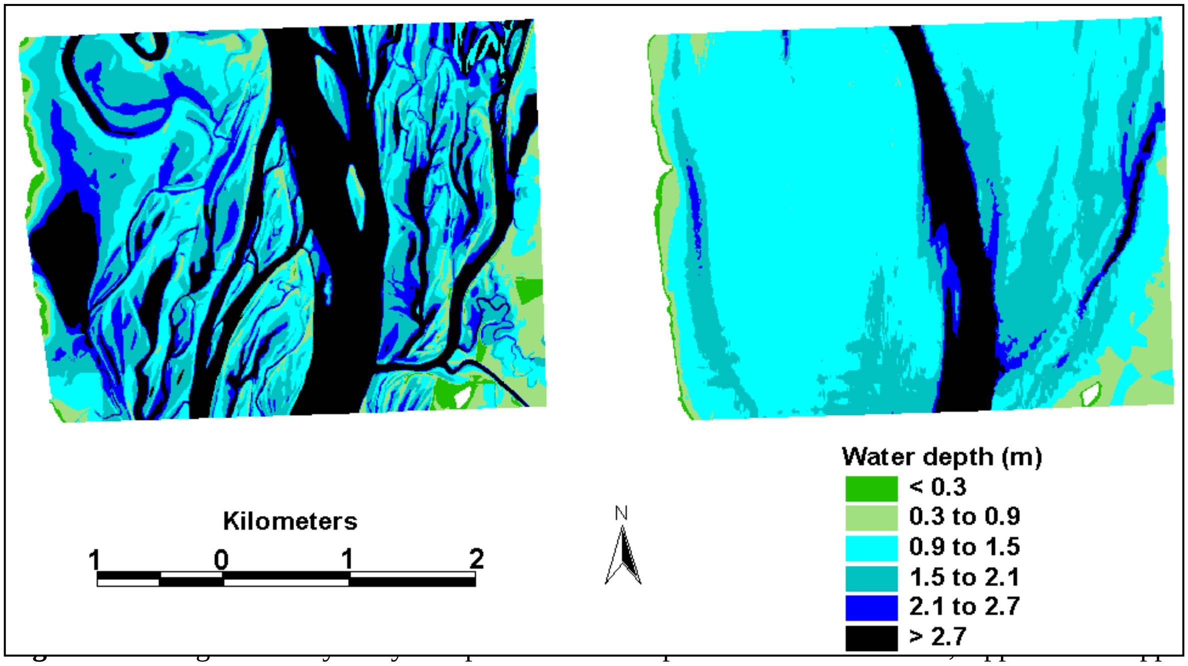


Figure 1. The Upper Mississippi River System.

1.1 Background

The Upper Mississippi River System (UMRS) was impounded in the 1930's by a series of 29 low-head navigation dams from St. Louis, MO to Minneapolis, MN (Figure 1). Impoundment fundamentally altered river morphology and key fluvial processes that maintained diverse river environments in the pre-impoundment era. Some of the most notable changes have occurred in backwater environments of the UMRS. For example, impoundment artificially raised and stabilized water levels, reduced flow velocity, and increased sediment deposition rates in backwater environments (U.S. Geological Survey 1999; McGuiness 2000; River Resources Forum 2004). Backwater environments are currently accumulating sediment at a rate of 0.12 cm to 0.80 cm per year (Rogala and Boma 1996). Increased aquatic surface area following impoundment also resulted in greater wind fetch and wave-induced erosion rates (River Resources Forum 2004). The process of erosion in shallow areas and sediment deposition in deeper areas has led to dramatic declines in morphometric diversity within many UMRS navigation pools (Figure 2). Loss of geomorphic diversity and the resulting changes in biogeochemical processes are often cited as causes of habitat degradation in backwaters (Bodensteiner et al. 1990; Sheehan et al. 1990; Pitlo 2001; Knights et al. 1995; Gent et al. 1995; Raibley et al. 1997).



River, from 1940 (left) to 1990 (right).

From 1988-2003, about US$146M were spent on Habitat Rehabilitation and Enhancement Projects (HREPs) on the UMRS. HREPs have restored, protected, or enhanced over 67,000 acres of habitat and projects encompassing 74,000 additional acres are in progress. Many of these projects focus on backwaters, largely by re-engineering the morphology of these environments. Management tools include backwater dredging, island construction, and pool-scale drawdowns; each designed in some way to increase and recover lost morphometric diversity.

Implicit in backwater rehabilitation efforts is an assumption that habitat limits the production of target biota. However, such limitation has not been adequately demonstrated (Gutreuter 2004). Determining if, and how, habitat limits biotic production will have numerous benefits. First, effective use of finite resources for rehabilitation will benefit significantly from knowing where and when habitat limits biota. Second, rehabilitation efforts are management experiments that can enhance scientific understanding of how the UMRS functions. Finally, research into habitat limitations must address the physiochemical UMRR template that defines habitat for any given species or assemblage. Such research will provide insights into a host of biogeochemical relationships, as well as water quality dynamics, small scale hydrology and bathymetry, and pathways of overall system productivity.

There are many alternative hypotheses regarding what limits fish production in the Upper Mississippi River System. Four possible hypotheses are:

1) Availability, quantity, and / or quality of winter habitat limits biotic production,
2) Excessive exploitation limits biotic production,
3) Energy (food) availability limits biotic production, and
4) Predatory cropping limits biotic production.

The most salient question thus becomes, which alternative hypothesis appears most reasonable to tackle first? The next most important question then becomes, which species would be expected to demonstrate differences in winter habitat quantity and quality and how do we proceed?

1.2 Winter habitat as a possible limiting factor

Research suggests that winter habitat limitation is a reasonable hypothesis to explore first. Several studies (Knights et al. 1995; Bodensteiner et al. 1990; Sheehan et al. 1990; Pitlo 2001; Raibley et al. 1997) suggest that winter habitat may limit fish production in the UMRS. Reasons cited include high sedimentation rates in backwaters and attendent reductions in depth and dissolved oxygen; observations that largemouth bass (*Micropterus salmoides*) move long distances to reach over-wintering location; high concentrations of fish in a small number of locations during winter as compared to summer; suspected over-exploitation of fish in winter when they are concentrated; and suspected high size-related, over-winter mortality of age-0 fish. Habitat models developed at the Upper Midwest Environmental Sciences Center using data from the LTRM [Jim Rogala, Upper Midwest Environmental Sciences Center; and Jim Fischer, Wisconsin Department of Natural Resources, personal communication], also suggest that suitable over-wintering conditions for many fishes are uncommon in UMRS navigation reaches (Figure 3). Additionally, many HREPs are designed to improve over-winter conditions, thus providing opportunities to test a hypothesis of over-winter habitat limitation.

This proposal suggests a framework to explore a hypothesis of over-winter habitat limitation on fish production across the full UMRS. It outlines key research areas and questions, and discusses relevant approaches and techniques to initiate and guide this research. Individual investigators will still need to define precise questions, methods, and analyses for specific projects. Future projects are expected to build on initial results and modify their approach, if needed, as research progresses.

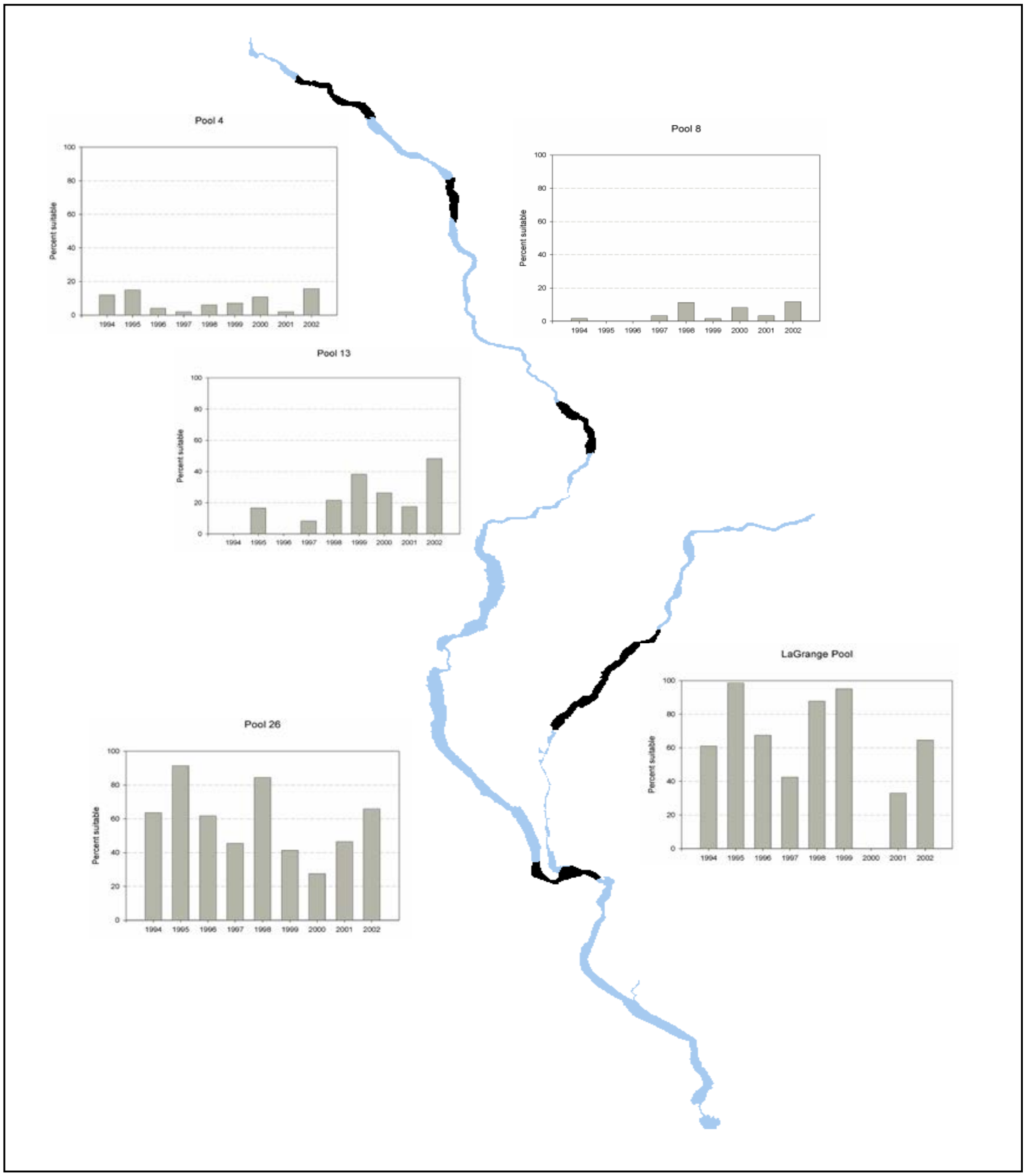


Figure 3. Percent of backwater area presumed suitable for limnophilic fishes during winter periods from 1994 to 2002. Suitability was assessed based on published physiologic tolerance thresholds during winter for several Centrarchidae species (Sheehan et al. 1990) and the spatial distribution of suitable morphologic and limnologic variables during winter periods, as measured by LTRM on the Upper Mississippi River System.

1.3 Responses to measure and potential confounding factors

The most appropriate ecological unit for gauging fish responses to habitat limitations is the population. Thus, production responses should include key demographic parameters such as population abundance, individual biomass, growth rates, and mortality rates; key parameters in a large family of population dynamics models.

Measuring and modeling population level responses to habitat limitation will present many challenges and should be a focal area for research. One such challenge is the open-system nature of the UMRS. Factors such as immigration and emigration may cloud studied responses. This has been a criticism of previous studies of biotic response that could not determine whether a response was due to additional production or only local attraction. Research proposals should try to minimize these confounding effects. Scale will also present challenges. Most studies of habitat limitation on large river fishes have focused on small spatial scales (e.g., < 100 ha) and short temporal scales (< 4 years). However, the consequences of habitat limitation on large river fish populations likely manifest at larger spatial scales (e.g., 10s – 100s of km^2) and decadal temporal scales; scales required to complete full life cycles (see Gutreuter 2004).

Another potential confounding factor is density-dependent mechanisms. At small (e.g., < 10km^2), and perhaps intermediate, spatial scales, intraspecific and interspecific interactions among individuals may influence key population parameters. Examples include intraspecific competition for food, predator-prey interactions, and human exploitation. Research proposals should address how the potential effects of such confounding factors will be handled (e.g., through experimental controls, synoptically measuring and then adjusting for confounding factors in the analysis, etc…).

2. Approaches and methodologies

Due to the size, spatial complexity and temporal dynamicism of the UMRS, no single line of research will fully address the habitat limitation hypothesis,. A "multiple lines of evidence" approach will be needed that uses physical and ecological gradients in the UMRS, existing data sources, laboratory and field experiments, and observational studies to fill data and information gaps. Modeling will also play a key role in integrating data and information and for developing and exploring additional research questions. In Section 2, several research approaches and key methodologies for carrying out this research plan are outlined. Research questions presented within five key research areas in Section 3 are cross referenced to approaches and methodologies presented here in Section 2. This is intended to help guide research proposal development.

2.1 Exploit existing observational data

Large rivers are less well studied than other aquatic environments. However, the UMRS is perhaps the best studied large river in the world. Abundant data are available from a variety of state and federal agencies covering biological components (e.g., fish, aquatic vegetation, limnology, and aquatic invertebrates), hydrology, land use and land cover, and bathymetry, among many others. **Existing data represent a potentially rich source of information for investigating many of the research questions within this program and should be exploited to the extent possible.** Observational data will be best applied in exploratory analyses designed to refine research hypotheses and develop study designs (Ickes et al. 2005). Observational data will be instrumental in recognizing and testing patterns and trends, developing and testing spatial contrasts, and estimating key biological and physical parameters. However, observational data will be insufficient for carrying out a full research program because they are limited in spatial density, scale, and time.

2.1.1 Pattern recognition

Observational data are best suited to answer the “what”, “where”, and “how” questions that must precede studies designed to answer the “why” questions. For example, what are the trends in fish abundance, where is winter habitat most and least abundant, and how is winter habitat distributed? These questions focus on pattern recognition, which is an important precursor for developing research to answer process-oriented questions, such as why is abundance declining, why are habitats abundant in some places and scarce in others, and why are habitats distributed in various manners?

Observational data are useful for describing patterns, but generally cannot explain why the patterns exist. Evidence derived from observational data is typically circumstantial, because no *a priori* expectation for the patterns is proposed and potential confounding factors are not controlled in the observations or analysis. For example, a difference in fish abundance among two or more areas may be correlated with the abundance of over-winter habitat. However, over-winter habitat is not necessarily the cause for the observed difference because other factors not tested, such as gradients in exploitation, could also explain the pattern. However, such correlations are important for defining the direction of future research and identifying relevant research questions.

Methods for analyzing observational data range from various forms of univariate statistical tests (e.g., Analysis of Variance, generalized linear models, non-parametric tests, etc…), multivariate ordination (e.g., non-metric multidimensional scaling, canonical correspondence analysis, cluster analysis, etc..), data mining models (e.g., decision trees, categorization and regression trees, etc..), Geographical Information System modeling (e.g., spatial analyst, model builder, etc…) and complex modeling based on theoretical foundations (e.g., are observations consistent with predictions arising from theory). Many other methods are available and it is highly recommended that investigators consult a statistician and carefully consider appropriate methods. The strength of inference derived from observational study will depend on a clear description of the research question, the relative ability of existing data to inform the question, and the assumptions of the analytical method used.

2.1.2 Spatial contrasts

A second approach to analyzing observational data compares responses from different areas. These analyses can proceed under different levels of rigor. The least rigorous analysis produces probabilistic statements about differences among areas. For example, a study may find that fishes are twice as abundant in area A as in area B, or that the surface area of suitable over-winter conditions is twice as much in area X as in area Y, and that these differences are statistically significant. Such comparisons can describe the range of conditions and the relative magnitudes of study responses, but typically cannot answer what limits fish production because confounding factors remain embedded in the responses.

A more rigorous approach is the use of spatial contrasts to determine if potential confounding factors are similar among study areas. For example, exploitation rates were proposed as a potential confounding factor in Section 2.1.1, but if creel survey data show that study areas are similar in exploitation rates, then tests for differences in fish abundance among study areas can be considered "independent" of exploitation and more likely to reflect differences in winter habitat. This more rigorous approach uses "planned" or "quasi-experimental" recasting of observational data to control for potential confounding factors. As such, hypothesized responses are explicitly stated *a priori* and potential confounding factors are controlled to the extent possible within the analysis.

Such spatial contrasts are possible because strong longitudinal and lateral gradients exist in the UMRS (Ickes et al. 2005). Investigators should exploit such gradients in their analysis of observational data. Methodological considerations should be similar to those for Section 2.1.1,"Pattern recognition".

2.1.3 Estimating key parameters

A third approach to analyzing observational data is estimating key parameters for use in modeling and analyses. In some cases, existing data may not provide highly accurate estimates but can provide useful first order estimates. For example, catch curve analysis can be applied to LTRM fisheries data to estimate total mortality. Length frequency data can be used to estimate recruitment rates and year class strength. Growth models can be applied to LTRM fish counts and length-weight data to estimate biomass. LTRM water quality data can be used to identify winter conditions in backwaters and to parameterize habitat suitability models. These parameter estimates can be used in analyzing spatial contrasts (Section 2.1.2). They may not explicitly test the primary hypothesis, but will be crucial for developing population and habitat models that can help distinguish among competing factors. Studies using this approach should carefully consider alternative methods and their assumptions, and the quality and potential biases of existing data. Consultation with a statistician is highly recommended. Methodological considerations should be similar to those for Section 2.1.1, "Pattern recognition".

2.2 Experimentation and new observation

Analyses of existing data can be very useful, but will be insufficient to fully address habitat limitation. New research will be needed, including field experiments, laboratory experiments, and additional observational work.

2.2.1 Field experiments

Habitat rehabilitation efforts present enormous potential for studying the effects of habitat limitation on biological production. HREP's are essentially field experiments and investigators should seek to capitalize on the learning potential they present. Although simple monitoring of bio-responses to habitat rehabilitation affords some data and information relevant to the central hypothesis, such observational information suffers from many of the same problems highlighted in Section 2.1 above. It would be better to adopt an adaptive management framework that incorporates key features of experimental design that can test specific questions and reduce uncertainty. These key features include well-defined test and control treatments, randomization, and replication. Careful coordination with HREP planners will be crucial for designing these key features into HREPs to realize their learning potential. For example, replication can significantly strengthen inferences, but would require that two or more similar rehabilitation efforts (e.g., backwater dredging) be performed simultaneously. This would require close coordination among HREP planners and contractors, and flexibility in budgets and monitoring efforts.

A second type of field experiment uses mesocosms. Mesocosms are simply various forms of experimental units (e.g., net pens) placed in the river. Mesocosm studies are analagous to laboratory aquarium studies where different treatments are prescribed randomly among mesocosms. Such experiments may prove most useful for testing the effects of confounding factors on production within large habitat rehabilitation experiments. For example, investigators could collect fish to measure abundance and growth in both a control site and a test (rehabilitated) site. However, as we noted earlier, this is an open system with no control on fish movements. Using mesocosms within both study areas, investigators can control for confounding factors such as immigration, emigration, and density-dependent growth.

Methods for designing and analyzing field experiments are numerous and are discussed in detail in a number of excellent books (Quinn and Keough 2002; Scheiner and Gurevitch 1998; Underwood, A.J. 1996). Designing field experiments and selecting appropriate analytical methods will require close coordination among investigators, HREP planners, and statisticians and my require substantial lead time.

2.2.2 Laboratory experiments

Laboratory experiments will prove useful for defining model parameters not easily derived from field studies. For example, physiological thresholds to various limnologic or hydrologic parameters can be precisely manipulated in the laboratory and established. Such studies have been performed for some species (e.g., Sheehan et al. 1990), however, others may be required for additional species. Clearly defined physiological thresholds permit determination of suitable winter conditions. Similarly, laboratory studies are frequently critical for determining parameters for theoretical models such as bioenergetics models (see section 2.3.2) and for diagnosing potentially confounding density-dependent effects. Methods for designing and analyzing laboratory experimental studies are discussed in detail in a number of excellent books (Quinn and Keough 2002; Scheiner and Gurevitch 1998; Underwood, A.J. 1996). Consultation with statisticians and researchers with previous experience is recommended when selecting appropriate analytical methods.

2.2.3 New observation

Existing data will prove insufficient for the full needs of this research framework. In particular, basic limnologic and fisheries data are largely lacking from most reaches of the UMRS. Additionally, fisheries observations within six LTRM study reaches are not made in winter periods. Thus, it will be necessary to develop new observational studies that define basic system conditions for many locations. New projects will be needed to map the prevalence, location, and extent of over-winter habitat and to evaluate fish use of habitats during winter, especially relative to model predictions.

2.3 Conceptual and numerical model development

Models can and should play a key role in this research program. In this section, I dichotomize models into two general classes, describe their respective utility within the research program, and identify key features that should be accomodated by each modeling framework.

2.3.1 Conceptual models

Conceptual models are largely descriptive and frequently used to describe the scope and relationships of a problem. They are a starting point toward increased understanding, rather than the final word on how the system works, and should evolve as more data and knowledge are obtained. Conceptual models can be very helpful in applied studies where the objective is to predict the direction of a system's response to a particular stressor or a rehabilitation effort. Conceptual models are useful for identifying the linkages between information and data, generating hypotheses about relationships among system components, and may ultimately be used to help develop numerical models (Section 2.3.2). Ideally, a conceptual model should help to (1) identify the processes and factors that need to be considered to predict the response of fish populations to a restoration action, (2) design restoration projects that alleviate limiting conditions, (3) develop process-based monitoring for restoration projects, (4) formulate research studies and experiments to address poorly understood elements of population production limits, and (5) evaluate underlying assumptions of restoration proposals. **It is recommended that a conceptual model of winter habitat limitation on UMRS fishes be developed early in the research program.**

The conceptual model framework should have several important characteristics:

1. It should be hierarchical and describe detailed as well as general interactions.

2. It should incorporate both spatial and temporal variation.

3. It should consider landscape relationships and variability.

4. It should explain and predict qualitative changes.

5. It should be feasible to translate it from a descriptive model into a computational model.

The model should be organized in five levels of increasing complexity:

Level 1: *domain;* Identify all interacting links between winter habitat availability, physiochemical predictors, and production responses.

Level 2: *process;* Identify the major processes linking ecosystem elements.

Level 3: *action scenario sub-model;* Describe predictable interactions resulting from restoration or other actions directed toward alleviating production limits on UMRS fishes.

Level 4: *spatial scales and landscape context;* Identify relevant spatial scales for responses and restoration activities, including variability and landscape context.

Level 5: *time variability;* Identify relevant temporal scales (daily, seasonal, interannual); long-term processes; and rare events that are relevant to the desired response and restoration efforts.

2.3.2 Numerical models

Numerical models will be critical components of this research program. They provide an analytical framework for incorporating key units of smaller research and for developing quantitative predictions that derive from conceptual models. Numerical models represent a diverse class of models that attempt to mathematically model key system components based on various simplifying assumptions, logic, and mathematical relationships. Numerical models can range from deterministic to dynamically stochastic. Various statistical approaches are often adopted to account for uncertainty in modeled outcomes and models that explicitly account for uncertainty have gained prominence in natural resource management (Hilborn and Walters 1992).

Several types of numerical models should be useful for addressing winter habitat limitation. Generally, these models include population dynamics models, bioenergetic models, habitat suitability models, meta-population models, and various types of coupled dynamic models that link components of classic numerical models together.

Population dynamics models represent a diverse family numerical models that predict production response (e.g., abundance, biomass, etc..) over time (typically annually) as a function of standing stock, growth potential, and mortaility. Simple models estimate future population size based on current population plus births over time, minus deaths over time. More realistic models require information on population demographics, recruitment, various components of mortality, and growth. Additional complexity can be added by considering predator-prey dynamics, exploitation dynamics, and other forms of inter- and intra-specific interactions. **Properly developed, population dynamics models are a powerful framework for modeling and predicting production responses to changes in key population parameters, such as those that may be predicted to respond to habitat improvements (e.g., mortality parameters).** Hilborn and Walters (1992) provide an excellent review of fish population dynamics models.

Bioenergetic models attempt to model growth responses as mass balance functions using thermodynamics principles. Applications of bioenergetic models to fishes have included estimates of the intensity and dynamics of predator-prey interactions, estimation and modeling of prey consumption by individuals and populations, and estimation of growth potential of populations. **Most commonly, bioenergetic models are used to assess the way changes in habitat, such as temperature, dissolved oxygen, water velocity, and contaminants, may be expressed in terms of production.** Potential uses of bioenergetics models for investigating over-winter habitat limitation include estimating over-winter size-selective mortality of fishes, investigating energetic expenditures associated with migrations to and from over-wintering habitats (as a tax on production), estimating energy available for reproduction in spring, and estimating the intensity and importance of predator-prey interactions (a potential confounding factor to the primary hypothesis). Bioenergetics modeling is theoretically well-founded and a review of previous applications can be found in Hansen et al. (1993).

Habitat suitablilty models have been widely used to assess the quantity and quality of habitat for fish and wildlife species. Habitat suitability models typically ascribe a habitat quality index value based on physiochemical parameters relevant to the modeled species and a series of theoretical ideal conditions for each habitat parameter. Existing models are readily available through the US Fish and Wildlife service for many game species, but few non-game species. **The potential utility of habitat suitability models in this research program includes identifying, quantifying, and ranking the relative quality of available habitat for study subjects.** However, few of these models have been evaluated in the field. Their use in this research should include attempts to validate their predictions with empirical data.

Metapopulation models view high quality habitats as patches in space, with areas between patches representing lower habitat quality that must be traversed by biota to move among high quality patches. Biota occupying patches are viewed as sub-populations, and the total of all sub-populations represents a metapopulation. Spatial interactions among sub-populations can be modeled as a consequence. Metapopulations should occur naturally due to heterogeneity in habitat quality, as well as from anthropogenic influences (e.g., barriers to dispersal, such as dams). Metapopulation models are typically spatially-explicit and implemented using a Geographical Information System (GIS). **Because UMRS limnophilic habitats are fragmented both longitudinally (along the river corridor) and laterally (across the floodplain), metapopulation models should be useful for modeling the effects of such fragmentation on fish production under this research framework.**

Dynamic models attempt to integrate one or more classic numerical models together, either to address assumptions more realistically or to extend the usefulness of simpler models. The output of such models can be highly variable over time because non-linearities embedded within each sub-model interact in dynamic ways. Such variation often produces more realistic system behavior, but often at the expense of predictive ability. **Dynamic models are particularly suited for investigating functional relationships among parameters or system components and may prove useful in investigating such things as population level effects of dispersal barriers.**

3. Key research areas

In addition to conceptual model development outlined in section 2 above, five key areas for initial investigation within the research program are identified. Generically, these five areas include quantifying and modeling suitable winter habitat availability, validating habitat availability observations and models, estimating production potential, identifying and quantifying key components of mortality, and determining the role of population distribution and dispersal in biotic production. Below, each of these key research areas is outlined in greater detail, general approaches are recommended when possible, and a series of pertinent research questions is presented. It is expected that subsequent proposals focusing on one or more of these key research areas will consider approaches and methodologies outlined in the previous section and address potential confounding factors within their study plans.

3.1 Quantifying and modeling habitat availability

Indirect evidence presently suggests that over-winter habitat may be limiting some fishes in the UMRS, but the quantity, quality, and distribution of such habitat is poorly known. Because of the vast extent of the UMRS, its spatial complexity, and temporal dynamism, research efforts in this focal area should principally focus on measuring, quantifying, and mapping presumptive winter habitat suitability. Efforts should focus on determining the spatial extent, distribution, and configuration and temporal dynamics of winter habitat. Furthermore, efforts should be directed at developing and implementing methods that permit modeling and mapping presumptive winter habitat based on physiochemical predictors (e.g., hydrology, limnology, geomorphology, and morphoedaphic features) over large spatial expanses. New observational study will be required in areas presently lacking sufficient physiochemical information. New observational approaches and GIS methodologies will be central to this research task.

3.1.1 What constitutes lethal winter conditions for fishes in the UMRS?

Elaboration: Quantification of physiologic thresholds to winter physiochemical conditions – determinations need to be made on all study subjects (e.g., species) considered or assumed similar

among study subjects. Some determination has previously been accomplished (see Sheehan et al. 1990).
Approach: Laboratory experimentation (Section 2.2.2) validated with *in situ* New observation (Section 2.2.3).
Methodology: Experimental design and appropriate statistical tests.
Potential confounding Factors: None – should be controlled for in experimental design.

3.1.2 Which physiochemical parameter(s) is/are most limiting in spatial extent?
Elaboration: Quantification and mapping of key physiochemical parameters associated with over-winter mortality of UMRS fishes – which is most limited spatially (e.g., current velocity, temperature, dissolved oxygen, etc…)
Approach: Pattern recognition (Section 2.2.1), New observation (Section 2.2.3)
Methodology: GIS mapping of existing or new observational habitat data and appropriate statistical summaries and tests.
Potential confounding Factors: None.

3.1.3 How much suitable winter habitat is available?
Elaboration: Quantification of the areal extent of presumptive winter habitat.
Approach: Pattern recognition (Section 2.2.1), New observation (Section 2.2.3)
Methodology: GIS analysis of existing or new observational habitat data and appropriate statistical summaries and tests.
Potential confounding Factors: None.

3.1.4 How is suitable winter habitat distributed?
Elaboration: Measurement of landscape parameters that describe the distribution of presumptive winter habitat – such as frequency histograms of size classes, proximity measures, etc…
Approach: Pattern recognition (Section 2.2.1), New observation (Section 2.2.3)
Methodology: GIS analysis of existing or new observational physiochemical data and appropriate statistical summaries and tests.
Potential confounding Factors: None.

3.1.5 Are there differences in winter habitat suitability across space (e.g., among pools and reaches) or over time (e.g., has suitable winter habitat changed over years within or among pools)?
Elaboration: Comparisons among areas or over time in presumptive winter habitat quantity and quality.
Approach: Spatial contrasts (Section 2.1.2), New observation (Section 2.2.3)
Methodology: Inferential statistical models and tests.
Potential confounding Factors: Model assumptions and biases.

3.1.6 How can suitable winter habitats best be modeled?
Elaboration: Identify and evaluate alternative modeling frameworks for predicting presumptive winter habitat based on key physiochemical parameters (existing or new observations).
Approach: Estimating key parameters (Section 2.1.3), Conceptual models (Section 2.3.1), and Numerical models (Section 2.3.2).
Methodology: To be determined, but potential methods include spatially explicit regression modeling, various spatial statistics methods, and GIS modeling.
Potential confounding Factors: Model biases and inherent assumptions.

3.2 Validation of habitat availability observations / models

Models based on physiochemical and species tolerance data are necessary to define the spatial and temporal extent of suitable winter habitats, but are insufficient for testing a hypothesis of habitat limitation. Such models require validation with data on fish use to evaluate how well fish use corresponds with predicted habitat availability and suitability. Methodologies for measuring fish use will vary, but may include observation and measurement using standard sampling gear, mark-recapture methods, telemetry methods, hydroacoustic profiling, and creel surveys. Different methods have associated biases, as well as utility for informing other research areas. For example, mark-recapture studies have the potential to provide information on fish distribution and dispersal, population size, and mortality components. However, the utility of such estimates entirely depends on the ratio of recaptures to tagged fish in the population. Logistically, it may prove difficult to mark and recapture enough individuals to provide reliable estimates of such population parameters, at least at spatial scales approaching a river reach. Such methodological tradeoffs should be carefully considered by prospective investigators and sufficient rationalization for any chosen methodology should be made.

3.2.1 How can suitable winter habitats best be modeled?

Elaboration: Identify and evaluate alternative modeling frameworks for predicting presumptive winter habitat based on key physiochemical parameters (existing or now observations).
Approach: Estimating key parameters (Section 2.1.3), Conceptual models (Section 2.3.1), and Numerical models (Section 2.3.2).
Methodology: To be determined, but potential methods include spatially explicit regression modeling, various spatial statistics methods, and GIS modeling.
Potential confounding Factors: Model biases and inherent assumptions.

3.2.2 Do UMRS fishes preferentially select for winter habitats deemed suitable by habitat models?

Elaboration: Identify or otherwise measure fish use among presumptively suitable winter habitats.
Approach: New observation (Section 2.2.3), Numerical models (Section 2.3.2).
Methodology: To be determined, but prospective investigators should carefully weigh the benefits and limitations of alternative fish sampling methodologies.
Potential confounding Factors: Sampling biases.

3.2.3 Do the home-range areas of UMRS fishes match the spatial scale at which over-wintering habitats are distributed?

Elaboration: Describe and quantify how the spatial arrangement of suitable winter habitats coincide with the home-range or dispersal requirements of fish populations.
Approach: New observation (Section 2.2.3), Pattern recognition (Section 2.1.1), Spatial contrasts (Section 2.1.2), Numerical models (Section 2.3.2).
Methodology: GIS modeling, spatial statistics models, mark-recapture, telemetry, or hydroacoustic profiles of limnophilic dispersal.
Potential confounding Factors: Model biases and inherent assumptions, sampling biases.

3.2.4 Within a winter, how long of a period of sub-optimal conditions can UMRS fishes endure with no persistent effects (e.g., mortality)?

Elaboration: Identify and quantify accute effects of sub-optimal winter habitat conditions.

Approach: New observation (Section 2.2.3), Laboratory experimentation (Section 2.2.2)
Methodology: Controlled laboratory experimentation coupled with *in situ* validation..
Potential confounding Factors: Experimental – none (control for confounding effects). *In situ* – dispersal away from stressful conditions.

3.2.5 Do the relations of UMRS fishes to modeled suitable winter habitat vary longitudinally?
Elaboration: Do fish use observations within modeled winter habitats among UMRS reaches support broad application of winter habitat suitability models (Yes if no variation) or not (No if fish use varies among study reaches). This constitites a validation on the application of habitat suitability model(s) generated under reasearch area 1 above.
Approach: New observation (Section 2.2.3), Pattern recognition (Section 2.1.1), Spatial contrasts (Section 2.1.2), Numerical models (Section (2.3.2).
Methodology: To be determined, but potential methods include regression modeling, various spatial statistics methods, and GIS modeling.
Potential confounding Factors: Model biases and inherent assumptions.

3.2.6 What winter habitat features are most closely associated with fish use measures (e.g., presence, abundance, etc..)?
Elaboration: Do characteristics of different winter habitats result in different degrees of fish use (e.g., what makes good over-winter habitat – size, location, proximity to other sites, etc…)?
Approach: New observation (Section 2.2.3), Numerical models (Section 2.3.2), Pattern recognition (Section 2.1.1), Spatial contrasts (Section 2.1.2).
Methodology: GIS modeling, descriptive and simple inferential statistical tests, various methods for observing fish use (carefully consider alternatives).
Potential confounding Factors: Model biases and inherent assumptions, sampling biases.

3.2.7 Are patterns in UMRS fish abundance within the UMRS consistent with differences in the availability of suitable winter habitat either spatially (i.e., among reaches) or temporally (i.e., has winter habitat declined over time within or among UMRS reaches)?
Elaboration: Correlated responses between abundnace dynamics and winter habitat availability would be consistent with a hypothesis of winter habitat limitation. However, results are correlative and not causative.
Approach: Pattern recognition (Section 2.1.1), Spatial contrasts (Section 2.1.2).
Methodology: GIS modeling, descriptive and simple inferential statistical tests, inferential models (see Gutreuter 2005).
Potential confounding Factors: Model biases and inherent assumptions, potential confounding factors likely not controllable in the analysis.

3.3 Estimation of production potential

Ultimately, inference on habitat limitation is best achieved if the production potential of the population under study is known. By definition, observed production below potential represents limitation. Evaluations of and investigations into the production potential of UMRS fish populations can proceed in either of two principal ways. The first is to estimate potential production based on numerical or empirical models. Such models attempt to estimate productive capacity of consumers based on primary production precursors, such as morphometric attributes and nutrient concentrations (e.g., morphometric indices, morphoedaphic models, or empirical yield models; see Appendix A.1 for some relevant citations). The second approach is to relativise production potential based on “maximum observed production” in an area of the system under study. Ideally this reference area would constitute an area that is widely deemed to have excellent production. LTRM data will prove useful in relativising potential production if this approach is adopted by prospective investigators.

3.3.1 Based on morphoedaphic metrics and yield models, how much fish production is expected in UMRS pools?
Elaboration: Establish a (crude?) theoretical benchmark for fish production potential in UMRS reaches.
Approach: Numerical models (Section 2.3.2).
Methodology: Application of existing or modified morphoedaphic and yield models (see Appendix A.1). Morphoedaphic features can be derived from existing GIS coverages and LTRM data sources.
Potential confounding Factors: Model biases and inherent assumptions (e.g., river reaches considered independent from one another).

3.3.2 Does estimated production potential vary among UMRS pools?
Elaboration: How similar or different is modeled production potential among UMRS reaches and what factors are associated with these differences (e.g., climate measured as growing degree days, geomorphic diversity, primary production precursors, etc…).
Approach: Pattern recognition (Section 2.1.1), Spatial contrasts (Section 2.1.2).
Methodology: GIS modeling, descriptive and simple inferential statistical tests.
Potential confounding Factors: Model biases and inherent assumptions.

3.3.3 Which UMRS pools have the highest observed fish production, which have the least, and what factors are associated with these differences?
Elaboration: Exploratory analysis of existing data. Goal is to relativise observed production among UMRS reaches and attempt to correlate differences to factors suspected for these differences. Should include factors associated with alternative hypotheses (e.g., predator density, relative exploitation intensity, etc..) as well as habitat metrics (e.g., morphometric diversity, quantity of winter habitat, etc…).
Approach: Pattern recognition (Section 2.1.1), Spatial contrasts (Section 2.1.2).
Methodology: Statistical tests and models, GIS models – if possible attempts should be made to control confounding factors using spatial contrast approaches.
Potential confounding Factors: Model biases and inherent assumptions, likely not able to control confounding factors in the analysis, so results will be correlative, not causative.

3.3.4 Is inter-annual variation in fish abundance/biomass correlated with inter-annual differences in winter habitat suitability?
Elaboration: Covariation in summer abundance/biomass, as measured by the LTRM, with winter habitat availability/suitability, as determined from habitat models, would provide correlative evidence of potential winter habitat limitations.
Approach: Pattern recognition (Section 2.1.1), Spatial contrasts (Section 2.1.2).
Methodology: Inferential statistical models.
Potential confounding Factors: Model biases and inherent assumptions, other factors may explain patterns and are unlikely to be controlled in the analysis of existing observation data – results would be correlative, not causative.

3.3.5 Do habitat rehabilitation projects that increase over-winter habitat quantity and/or quality result in greater fish production?
Elaboration: If winter habitat is limiting, habitat rehabilitation efforts should produce a production response, *sensu stricto*.
Approach: *In situ* experimentation (Section 2.2.3), Conceptual models (Section 2.3.1), Spatial contrasts (Section 2.1.2), New observation (Section 2.2.3).
Methodology: Coordinated *in situ* experimental approaches, controlling potential confounding factors with complimentary mesocosm studies, inferential statistical tests.
Potential confounding Factors: Attempts should be made to provide for control and treatment effects, randomization, and insofar as possible, replication. Confounding factors should be addressed through the use of mesocosm studies in proximity to the *in situ* management experiment.

3.4 Identification and quantification of mortality components

The issue of habitat limiting production is fundamentally a population level question, yet little is known about key population dynamics of fishes in the UMRS.
Mortaility represents the key process that determines population demographics and ultimately the productive capacity of a population, particularly under a hypothesis of winter habitat limitation as no growth or recruitment is expected during winter. Yet mortaility components within populations represent key uncertainties in population dynamics and attendant production. Several components of mortality need to be elucidated. Total annual mortality is the instantaneous mortality rate acting on a population. Total annual mortality is a function of natural mortality and fishing mortality, two principal mortality components. Natural mortality is the rate of mortality that would occur under natural conditions (e.g., winter mortality would be a component of this) while fishing mortality is that portion of total annual mortality attributable to exploitation. Mortality estimation in UMRS fish populations must address each of these mortality components because most common species are exploited to lesser or greater extents. Such exploitation effects represent potential confounding factors to our primary hypothesis of habitat limitation and must be diagnosed or otherwise controlled in prospective studies in this area of research.

3.4.1 What is the total annual mortality of UMRS fish populations, does it vary among UMRS reaches, and how does it compare to other systems?
Elaboration: Is mortality high or low and does it differ among areas? Low total annual mortality, relative to other systems, would suggest habitat is not limiting.
Approach: Spatial contrasts (Section 2.1.2), New observation (Section 2.2.3), Pattern rocognition (Section 2.1.1), Numerical models (Section 3.3.2).
Methodology: Catch curve analysis using LTRM data, estimates of total mortality from tagging studies, estimates from population dynamics models.
Potential confounding Factors: Not clear what constitutes a population. On a per river reach basis, an assumption that the population is closed to immigration and emigration would need to be made.

3.4.2 Do spatial patterns in total annual mortality estimates correlate with spatial differences in winter habitat quantity / quality?
Elaboration: Positive correlations would support, but not prove, a hypothesis of winter habitat limitation..
Approach: Spatial contrasts (Section 2.1.2), New observation (Section 2.2.3), Pattern rocognition (Section 2.1.1).
Methodology: Inferential statistical tests, GIS models.

Potential confounding Factors: Other hypothetical mechanisms are possible (i.e., exploitation). Results would be correlative, not causative

3.4.3 Are certain size or age classes more vulnerable to winter mortality?
Elaboration: How is winter mortality realized among various population demographics? Do individuals need to reach a certain size threshold to persist? Is mean size or condition factor of a year class in fall related to winter mortality rate?.
Approach: New observation (Section 2.2.3).
Methodology: Comparison of size or age structure preceding winter and immediately following winter.
Potential confounding Factors: None.

3.4.4 What are the natural and fishing mortality rate components of UMRS fish species, is fishing mortality an additive or compensatory component to natural mortality, and how do mortality component estimates vary among UMRS pools?
Elaboration: How important is exploitation to total annual mortality, does is cull production that would otherwise perish (compensatory) or compound natural mortality (additive), and are spatial patterns consistent with gradients in winter habitat, exploitation, or a combination of both?.
Approach: Spatial contrasts (Section 2.1.2), New observation (Section 2.2.3), Pattern rocognition (Section 2.1.1), Numerical models (Section 3.3.2).
Methodology: Catch curve analysis using LTRM data, estimates of total mortality from tagging studies, estimates from population dynamics models, creel surveys for fishing mortality components..
Potential confounding Factors: On a per river reach basis, an assumption that the population is closed to immigration and emigration would need to be made.

3.4.5 Do habitat rehabilitation efforts reduce winter mortality rates?
Elaboration: If habitat is limiting, habitat rehabilitation efforts should reduce winter mortality, *sensu stricto*.
Approach: *In situ* experimentation (Section 2.2.1), New observation (Section 2.2.3), Numerical models (Section 3.3.2).
Methodology: Coordinated *in situ* experimental approaches, controlling potential confounding factors with complimentary mesocosm studies, inferential statistical tests.
Potential confounding Factors: Attempts should be made to provide for control and treatment effects, randomization, and insofar as possible, replication. Confounding factors should be addressed through the use of mesocosm studies in proximity to the *in situ* management experiment. A positive finding does not result in a clear conclusion that habitat limits production. Other factors could still limit production (e.g., summer forage resources). Mortality in this scenario would be conserved during winter, but realized at another point in time, perhaps in another place.

3.5 Population distribution and dispersal

Movements of fishes in large-river floodplain systems are poorly understood, yet such movements or migrations require energetic expenditures and mortality risks that may influence population production.

3.5.1 Is observed or predicted production related to measures of winter habitat quantity, size, distribution, or spatial organization?
Elaboration: Are many small winter habitat areas better than a few large ones or *vice versa*?.
Approach: New observation (Section 2.2.3), Numerical models (Section 3.3.2).
Methodology: Inferential statistical models, GIS models based on observed response (e.g., abundance, biomass, mortality, etc..) and landscape association metrics derived from habitat models.
Potential confounding Factors: ????

3.5.2 How far must fishes migrate to find suitable winter habitat and are there longitudinal or lateral barriers to such migrations??
Elaboration: Estimation of how "fragmented" a study reach is in regards to winter habitat. Precursor to estimating production implications.
Approach: New observation (Section 2.2.3)
Methodology: Tagging, mark-recapture, telemetry.
Potential confounding Factors: Methodological biases.

3.5.3 Do energetic expenditures or mortality risks associated with fish dispersal towards or away from winter habitats affect production?
Elaboration: Does migration in a fragmented environment impart undue energetic expenditures or mortality risks upon fish populations that may serve to limit production?
Approach: New observation (Section 2.2.3), Numerical models (Section 2.3.2).
Methodology: Bioenergetics modeling, Population dynamics modeling, Metapopulation modeling.
Potential confounding Factors: Mortality risks could be associated with either natural sources (e.g., predation) or fishing mortality. Prospective investigators should seek to control for mortality sources in their studies.

References

Bodensteiner, L.R., W.M. Lewis, and R.J. Sheehan. 1990. Differences in the physical environment of the Upper Mississippi River as a factor in overwinter survival of fish. Pages 109-117 *in* The Restoration of Midwestern Stream Habitat. North-Central Division, American Fisheries Society, Bethesda, MD.

Chapman, D.W. 1978. Production in fish populations. Pages 5-25 *in* S.D. Gerking, ed., *Ecology of Freshwater Fish Production*. Wiley and Sons, New York.

Costanza, R. 1992. Toward an operational definition of ecosystem health. Pages 239-256 *in* Costanza, R., B. Norton, and B. J. Haskell, eds. *Ecosystem Health: New Goals for Environmental Management*. Island Press, Washington DC.

Gent, R., J. Pitlo, Jr., and T. Boland. 1995. Largemouth bass response to habitat and water quality rehabilitation in a backwater of the Upper Mississippi River. North American Journal of Fisheries Management 15:784–793.

Gutreuter, S. 2004. Challenging the assumption of habitat limitation: An example from centrarchid fishes over an intermediate spatial scale. River Research and Applications 20: 413-425.

Hansen, M.J., and 6 co-authors. 1993. Application of bioenergetics models to fish ecology and management: Where do we go from here? Trans. Am. Fish. Soc. 122: 1019-1030.

Hilborn, R., and C. J. Walters. 1992. Quantitative Fisheries Stock Assessment: Choice, Dynamics and Uncertainty. Chapman and Hall, New York. 570 p.

Ickes, B.S., M.C. Bowler, A.D. Bartels, D.J. Kirby, S. DeLain, J.H. Chick, V.A. Barko, K.S. Irons, and M.A. Pegg. 2005. 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. LTRM 2005-T005. 60 pp. + CD-ROM (Appendixes A–E).

Kirby, D.J., and B.S. Ickes. In press. Temporal and spatial trends in the frequency occurrence, length-frequency distributions, rate of gain, and relative abundance of Upper Mississippi River fish. A report of the Long Term Resources Monitoring Program. U. S. Geological Survey, Upper Midwest Environmental Sciences Center. La Crosse, WI.

Knights, B.C., B.L. Johnson, and M.B. Sandheinrich. 1995. Responses of bluegills and black crappies to dissolved oxygen, temperature, and current in backwater lakes of the Upper Mississippi River during winter. North American Journal of Fisheries Management 15(2): 390-399.

Krebs, C.J. 1985. Ecology, 3rd ed. Harper and Row Publishers. New York.

McGuiness, D. 2000. A river that works and a working river: A strategy for the natural resources of the Upper Mississippi River System. Report of the Upper Mississippi River Conservation Committee. Rock Island, IL. 40 pp.

Odum, E.P. 1971. Fundamentals of Ecology, 3rd ed. W.B. Saunders. Philadelphia, PA.

Pitlo, J. Jr. 2001. An evaluation of winter habitats used by bluegill, black crappie, and white crappie in pool 13 of the upper Mississippi River. Iowa Department of Natural Resources, Federal Aid in Sportfish Restoration, Project F-160-R, Study 7021, Annual Performance Report, Des Moines.

Quinn, G.P., and M.J. Keough. 2002. Experimental design and data analysis for biologists, 1st ed. Cambridge University Press. 556 pp.

Raibley, P.T., K.S. Irons, T.M. O'Hara, K.D. Blodgett, R.E. Sparks. 1997. Winter habitats used by largemouth bass in the Illinois River, a large river-floodplain ecosystem. North American Journal of Fisheries Management 17: 401-412.

Randall, R.G., and C.K. Minns. 2000. Use of fish production per unit biomass ratios for measuring the productive capacity of fish habitats. Can. J. Fish. Aq. Sci 57: 1657-1667.

Rissotto, S.P., and R.E. Turner. 1985. Annual fluctuation in abundance of commercial fisheries of the Mississippi River and tributaries. North American Journal of Fisheries Management 5: 557-574.

River Resources Forum. 2004. Environmental Pool Plans: Mississippi River, Pools 1-10. U.S. Army Corps of Engineers, St. Paul District, St. Paul, Minnesota. 156 pp.

Rogala, J. T., and P. J. Boma. 1996. Rates of sedimentation along selected backwater transects in Pools 4, 8, and 13 of the Upper Mississippi River. U.S. Geological Survey, Environmental Management Technical Center, Onalaska, Wisconsin, October 1996. LTRM 96-T005. 24 pp. (NTIS PB97-122105).

Scheiner, S.M., and J. Gurevitch (eds.) 1998. Design and analysis of ecological experiments. Chapman and Hall. 415 pp.

Sheehan, R.J., W.M. Lewis, and L.R. Bodensteiner. 1990. Winter habitat requirements and overwintering of riverine fishes. Federal Aid Completion Report, project F-79-R, Fisheries Research Laboratory, Southern Illinois University, Carbondale, IL.

Underwood, A.J. 1996. Experiments in Ecology: Their Logical Design and Interpretation Using Analysis of Variance. Cambridge University Press. 522 pp.

U.S. Geological Survey. 1999. Ecological status and trends of the Upper Mississippi River System 1998: A report of the Long Term Resource Monitoring Program. U.S. Geological Survey, Upper Midwest Environmental Sciences Center, La Crosse, Wisconsin.

West Consultants, Inc. 2000. Final report Upper Mississippi River and Illinois Waterway cumulative effects study Volume 2: Ecological assessment. Department of the Army. Corps of Engineers, Rock Island District. Contract Completion Report No. DACW25-97-R-0012. 295 pp.

Appendix A.1. Some relevant references on Empirical yield models.

Hanson, J.M. and W.C. Legget, 1982. Empirical prediction of fish biomass and yield. Can. J. Fish. Aquat. Sci., 39(2): 257–263.

Henderson, H.F. and R.L. Welcomme, 1974. The relationship of yield to Morpho Edaphic Index and number of fishermen in African inland fisheries. Relation entre la production, l'indice Morpho-Edaphique et le nombre de pêcheurs des pêcheries des eaux continentales d'Afrique. CIFA Occas. Pap./Doc. Occas. CPCA, (1): 19 p.

Jackson, D.A., H.H. Harvey and K.M. Somers, 1990. Ratios in Aquatic Sciences: Statistical Shortcomings with Mean Depth and the morphoedaphic Index. Can. J. Fish. Aquat. Sci., 47: 1788–1795.

Kapetsky, J.M., 1984. Coastal lagoon fisheries around the world: some perspectives on fisheries yields, and other comparative fishery characteristics. In: J.M. Kapetsky and G. Lasserre (eds.), Management of Coastal Lagoon Fisheries. Stud. Rev. GFCM, 61(1):97–140.

Marshall, B.E., 1984. Towards predicting ecology and fish yields in African reservoirs from pre-impoundment physico-chemical data. CIFA Tech. Pap., (12): 36 pp. Rome: FAO.

Melack, J.M., 1976. Primary productivity and fish yields in tropical lakes. Trans. Am. Fish. Soc., 105:575–580.

Oglesby, R.T., 1977. Relationships of fish yield to lake phytoplankton standing crop, production and morpho-edaphic factors. J. Fish. Res. Board Can., 34(12): 2271–2279.

Quiros, R., 1990. Predictors of Relative Biomass in Lakes and Reservoirs of Argentin a. Can. J. Fish. Aquat. Sci., 47: 928–939.

Rawson, D.S., 1952. Mean depth and fish production of large lakes. Ecology, 33:513–521.

Ryder, R.A., 1965. A method for estimating the potential fish production of north-temperate lakes. Trans. Am. Fish. Soc., 94: 214–218.

Schlesinger, D.A. and H.A. Regier, 1982. Climatic and Morphoedaphic Indices of Fish Yields from Natural Waters. Trans. Am. Fish. Soc., 111: 141–150.

Welcomme, R.L., 1974. Some general and theoretical considerations on the fish production of African rivers. CIFA Occas. Pap. (3): 26 p.

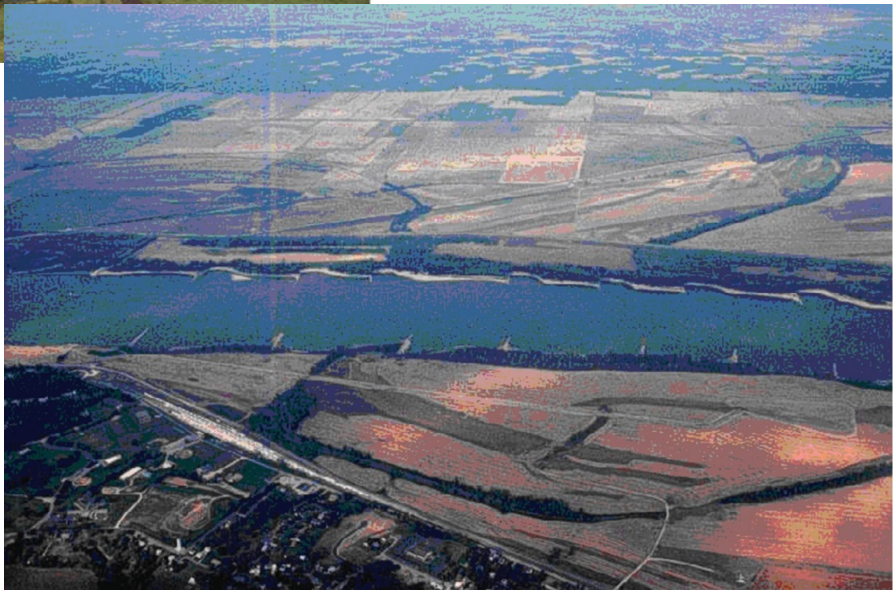
Welcomme, R.L., 1985. River fisheries. FAO Tech. Pap., 262: 330 pp.

Youngs, W.D. and D.G. Heimbuch, 1982. Another consideration of the Morphoedaphic Index. Trans. Am. Fish. Soc., 111: 151–153.

Appendix B: A research framework for fisheries-relevant lateral connectivity issues in the Upper Mississippi River Basin

Appendix B: A research framework for fisheries-relevant lateral connectivity issues in the Upper Mississippi River Basin

River Floodplain Connectivity and Lateral Fish Passage



Cover: (*top left*) An example of the effects of levee construction on lateral connectivity. (*bottom right*) An example of isolated floodplain environments.

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River Floodplain Connectivity
and Lateral Fish Passage

Abstract: Floodplains play a key role in the ecology of the Upper Mississippi River; however, humans have significantly affected the ecological function of floodplains by isolating them from the main stem of the river with levees. Impoundment and channel training within the main stem also influence floodplain function by altering the flow of water through the system. Because of the key role hydrology plays in floodplain ecosystem function, such effects are frequently conceptualized as decreases in lateral connectivity, or the hydrologically mediated lateral exchange of energy, material, and organisms between fluvial and floodplain system components. Some management practices attempt to reestablish periods of lateral connectivity to mitigate functional losses associated with isolation and an altered hydrograph. This report presents a review of scientific literature and synthesis of lateral connectivity as a theoretical and an applied management topic using fish as a point of focus. On the basis of our review of the literature, we recommend a framework for adaptive management of lateral connectivity at several scales within the system and identify data sources that can be used to develop this framework. Specifically, we recommend the development of a time-sequenced geospatial inventory of Upper Mississippi River floodplains. Such an inventory is presently being developed by university researchers investigating changing flood risks in the Mississippi and Missouri River basins. In addition, we highlight the need for high-resolution floodplain elevation data and the development of a detailed life-history database for Upper Mississippi River fishes. Finally, we believe that adaptive management techniques will be critical for developing applied management alternatives for enhancing lateral connectivity and biotic responses in the Upper Mississippi River Basin.

Key words: altered hydrology; fish habitat; floodplains; floodplain elevation; lateral connectivity; lateral fish passage; levees; Mississippi River

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Introduction

The lateral components of alluvial river systems, known as floodplains, are viewed as critical for maintaining river productivity (Junk et al. 1989), biotic diversity (Connell 1978; Wellborn et al. 1996; Wootton et al. 1996; Wootton 1998; Amoros and Bornette 2002), and for providing many ecosystem services of direct benefit to humans (Mitsch and Grosselink 2000). By definition, floodplains are transitional environments between terrestrial and aquatic ecosystems and hydrology is a key factor in determining the type and functional nature of floodplains. The dynamic interplay that exists between terrestrial and aquatic components in floodplain ecosystems lead to spatially complex and interconnected environments. Correspondingly, floodplains are widely regarded as one of the most productive and diverse ecosystems on Earth (Tockner and Standford 2002).

While floodplains are acknowledged for their diversity and productivity, they are also frequently described as one of the most imperiled ecosystems on Earth (Welcomme 1979), principally owing to human activities. Many factors are attributed to degraded floodplain environments and include floodplain sequestration (e.g., flood control levees to reduce flooding for urban development, or more prominently, for agricultural development), and altered hydrology (e.g., impoundment, channel-training measures to facilitate river navigation, and snag removal). These changes have greatly altered the magnitude, duration, and frequency where flood waters interact with the floodplain in many floodplain river systems. This “loss of interaction” is most frequently conceptualized as “altered lateral connectivity.”

Today, levees, culverts, roads, and bridges along more than 800 miles of the Upper Mississippi River (UMR; Figure 1) have restricted lateral fish passage onto the floodplain for feeding and reproduction. Land managers use a variety of habitat restoration techniques to reduce backwater sedimentation and recreate historical water-level regimes for the benefit of fish and wildlife, but structures associated with those habitat restoration efforts could also be limiting seasonal fish passage. Although increased movement of indigenous species is desirable, methods to restrict passage of destructive exotics, such as common carp (*Cyprinus carpio*), silver carp (*Hypopthalmichthys molitrix*), and bighead carp (*H. nobilis*) are also needed.

This report presents a review of scientific literature and a synthesis of information on lateral connectivity and fish passage in large floodplain rivers, but focusing on the Upper Mississippi River. Specific objectives include (1) a review of the scientific literature and compilation of relevant literature into an annotated bibliography, (2) a synthesis of the literature relevant to lateral fish passage and floodplain water-level management on the UMR, and (3) the identification of information and research needs required to advance applied management of fisheries resources within the UMR.

In preparing this report, we reviewed more than 3,000 papers. Our search included a review of Aquatic Sciences and Fisheries Abstracts (1978–2002), Conference Papers Index (1982–2002), Water Resources Abstracts (1967–2002), and Fish and Fisheries Worldwide (1971–2002) as well as various other sources housed at the U.S. Geological Survey Upper Midwest Environmental Sciences Center, La Crosse, Wisconsin.

All potential sources were not included in the bibliography. Synthesis papers, proceedings, and papers with a UMR focus were included whenever possible. Papers of local interest were largely excluded because other bibliographic sources exist for these works (e.g., *http://www.mississippi-river.com/umrcc/catalog.html*, accessed May 2005). Papers with relevance to engineered control structures and biological performance indicators were not included because many of the most pertinent sources can be found in an earlier report (Ickes et al. 2001). Papers from outside the geographical focus of this report were included if they added significantly to topical understanding within the UMR.

A total of more than 400 annotated citations were considered relevant

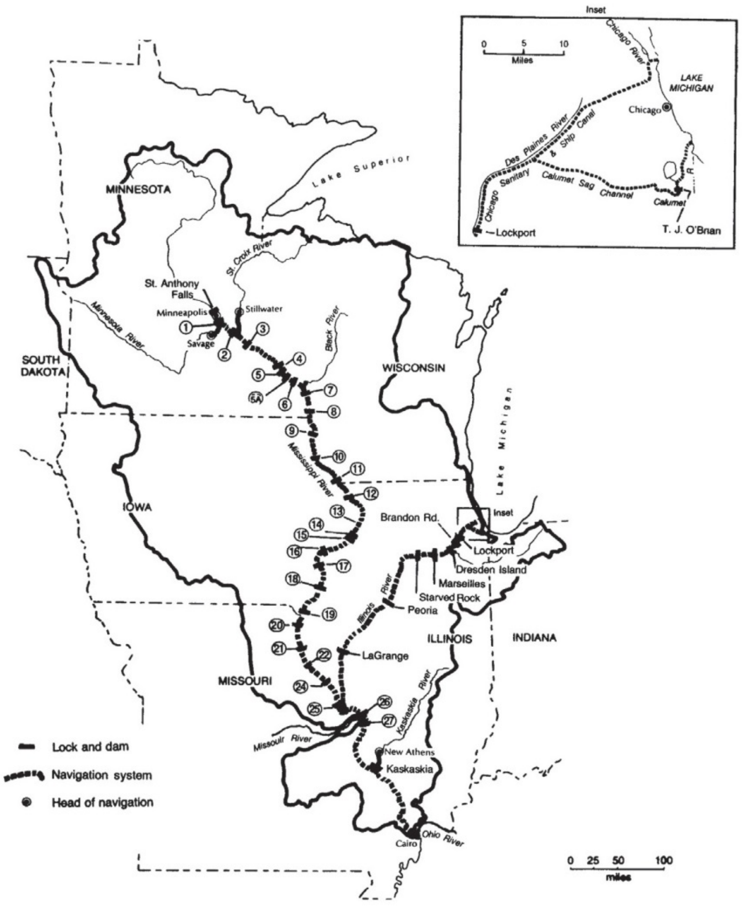

Figure 1. The watershed and major tributaries of the Upper Mississippi River System. Numbers in circles identify dams on the Mississippi River.

and included in the bibliographic database. Abstracts within this database are those of the original author. The database is served as a searchable electronic document on the Upper Midwest Environmental Science Center's Web site (*http://www.umesc.usgs.gov/LTRM_fish/fish_passage_biblio.html*, accessed May 2005).

A summary of many of the major ideas contained within the annotated bibliography is provided within this report. However, a thorough review of the ecology of the UMR, its history of modification, and an accounting of the diversity of management challenges as they pertain to floodplain environments is beyond the scope of this summary, although we do touch upon these subjects to build sufficient context. In the final section of this report, we identify several general, yet key information needs. We believe that addressing these needs could provide many applied management and research benefits on issues concerning floodplain management practices within the UMR.

Defining Lateral Connectivity in Floodplain Systems

Conceptual Development

Connectivity, generally defined by Pringle (2003), is the water-mediated transfer of energy, materials, and organisms across a hydrologic landscape. Thus defined, "connectivity" can be invoked and subsequently modified to focus on different components of a system (Ward 1989). For example, the term "longitudinal connectivity" is frequently invoked to describe changes along a river's primary axis of flow following impoundment (Ickes et al. 2001; Knights et al. 2002*b*). Similarly, "vertical connectivity" is invoked to describe fluxes between thermally stratified bodies of water in lakes, or between groundwater or hyporheic zones and flowing surface waters in rivers. Correspondingly, "lateral connectivity" is invoked to provide a conceptualization of the interaction between fluvial river segments and their corresponding lateral (e.g., perpendicular to the main axis of flow) floodplain environments. A graphical depiction of these forms of connectivity is presented in Figure 2.

While the term "lateral connectivity" implies a spatial or structural relation between a river and its floodplain, the degree to which lateral connectivity exists is a time-dependent phenomenon (Tockner et al. 1999*a*). This happens because rivers are hydrologically dynamic. At any time, whether a floodplain or some portion of it is connected depends on prevailing hydrologic conditions within the river and the corresponding surface elevation of the floodplain. As river stage exceeds floodplain elevation thresholds on the ascending limb of a hydrograph, connection occurs and floodplains are inundated (Figure 3). This conceptualization

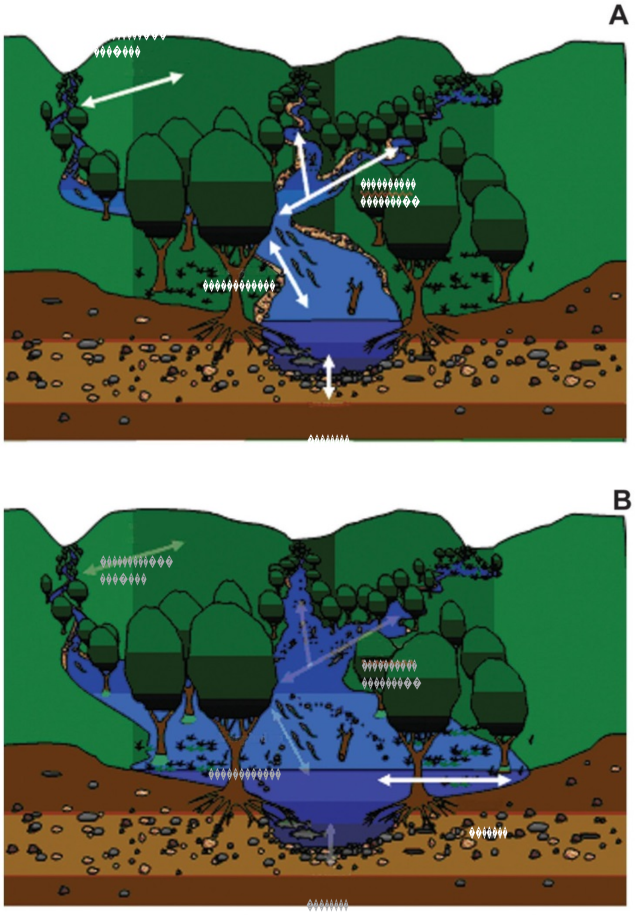

Figure 2. Conceptualization of the multiple dimensions of hydrologic connectivity. Panel A presents "in channel" definitions of connectivity (e.g., vertical and longitudinal). Panel B highlights lateral connectivity, the subject of this report. Figures are adapted from Luther Aadland (Minnesota Department of Natural Resources, personal communication).

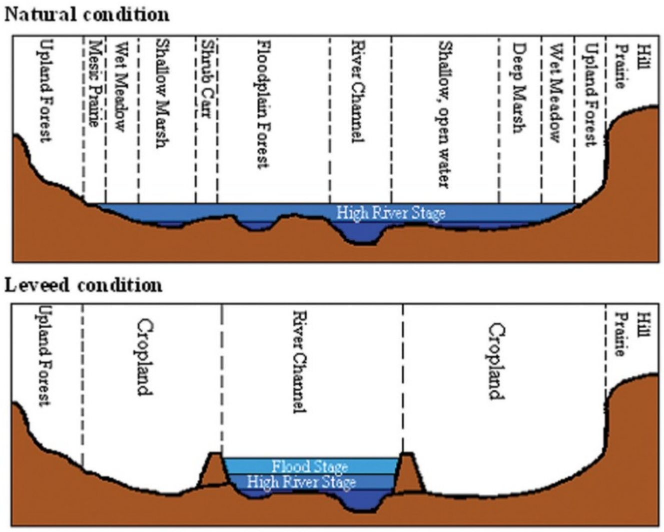

Figure 3. Cross sections of an idealized floodplain river depicting natural (*top*) and leveed (*bottom*) conditions.

simplifies this dynamic process, but captures the main idea. In northern temperate rivers such as the UMR, lateral connectivity events have a strong seasonal signature that coincides with seasonal precipitation patterns. Thus, flood events are often classified on the basis of their magnitude, duration, timing, and frequency.

Human activities on and around floodplains can greatly alter lateral connectivity (Figure 4). Most obvious are the effects of levee construction on lateral connectivity (Figure 5). Levees are regionally extensive in the UMR (Table 1) and serve to increase the effective elevation of floodplain landscapes, principally in support of flood control and agriculture development on UMR floodplains. Thus, river elevations must exceed local levee heights to inundate the floodplain. This has resulted in a decrease in the probability of lateral connectivity events (Figure 4). Because of the dynamic nature of lateral connectivity in floodplain river systems, scientists have yet to develop reliable methods for measuring lateral connectivity, although there is growing recognition that any means of measurement should be based on a mechanistic understanding of how physical and biological systems interact and how human activities influence these interactions (Johnson et al. 1995; Power et al. 1995). Moreover, it is becoming apparent that connectivity as a concept would benefit operationally from nonambiguous definitions (Pringle 2003). In other words, it does one little good operationally to talk about the lateral connectivity of the Mississippi River, as this is too ambiguous to be operational. Modifying Pringle's definition, connectivity needs to be defined as the transfer of energy, materials, and organisms between specific locations on the river and floodplain.

Figure 4. An example of the effects of levee construction on lateral connectivity by Trempeleau National Wildlife Refuge, Wisconsin. This aerial photograph demonstrates the lack of hydrologic connectivity that exists following levee development. Water in the Mississippi River (*left side* of photo) is clearly darker than water on the refuge side of the levees, suggesting no hydrologic mixing. Correspondingly, water, nutrient, energy, and biotic exchange between the main channel and the floodplain are severed.

Theoretical Development

Large rivers and particularly floodplain rivers remain little studied until the 1970s-1980s (Johnson et al. 1995) because of difficulties in sampling these systems. Since the 1980s, however, large river research has opened new insights into the physical, biological, and human forces that shape rivers. Today, physical and biological concepts have been combined into a more holistic framework that views river systems as interdependent, hierarchically structured combinations of aquatic and terrestrial landscapes. This perspective draws heavily from theory

Figure 5. An early photograph of snag removal in the Mississippi River. Snag removal conducted in concert with sandbar dredging represents the earliest attempts to improve navigation on the Upper Mississippi River and served as a precursor to more highly engineered channel development measures. Improved navigability lead to expanded floodplain development and sequestration of floodplain environments from the main channel of the river. (Photograph from N. Moore [1972].)

in fields as diverse as fluvial geomorphology, fractal geometry, network theory, hydrology and hydrodynamics, fisheries science, landscape ecology, chaos theory, and theories of self-organization (Tockner et al. 1998; Ward and Tockner 2001; Church 2002; Tockner and Standford 2002; Benda et al. 2004). While a full and cohesive theory has yet to emerge, there are two prevailing hypotheses of how lotic systems function: the river-continuum concept (Vannote et al. 1980) with several corollaries (Elwood et al. 1983; Ward and Stanford 1983) and the flood-pulse concept (Junk et al. 1989).

Table 1. Total acres of floodplain and percent of floodplain surface area sequestered behind levees in different segments of the Mississippi River.

		Percentage of floodplain
	Floodplain	**behind levees**
River segment	**acres**	**(%)**
Headwaters	328, 000	<0.01
Upper Mississippi-north[a]	496, 000	3
Upper Mississippi-south[a]	1,006,000	53
Middle Mississippi[a]	663,000	82
Lower Mississippi	25,000,000	93
Deltaic Plain	3,000,000	96
Total	30,493,000	90

[a] The Upper Mississippi-north includes Pools 1–13, the Upper Mississippi-South includes Pools 14–26, and the Middle Mississippi includes the unimpounded reach from below Pool 26 to the confluence of the Ohio River. Collectively these three river segments comprise the Upper Mississippi River.

The river-continuum concept (Vannote et al. 1980) was developed from observations on unperturbed forested watersheds at northern-temperate latitudes. The concept postulates that physical and biological structure in these systems is determined from physical forces that change predictably from the headwaters to the mouth, resulting in a longitudinally oriented continuum of features. Energy for biological production is assumed to come from three sources: local organic inputs (allochthonous), primary production within the stream (autochthonous), and transport of organic material within the stream. The relative prominence of each of these energy sources is predicted to vary along the river continuum, with allochthonous inputs being prominent in low stream order reaches, autochthonous sources predominating in midstream order reaches, and downstream transport dominating in high stream order reaches. Similarly, secondary productivity (e.g., invertebrates) and life-history traits of dominant organisms will be predictable based on energy sources along the continuum, with shredders and collectors dominating in low stream order reaches, collectors and grazers dominating in midstream order reaches, and collectors dominating in high stream order reaches. Differences in the variation of hydrologic, temperature, and organic matter sources along the stream order continuum predict that medium-sized rivers should have the greatest biotic diversity.

The flood-pulse concept (Junk et al. 1989) incorporates a lateral dimension into river theory, stating that the most important hydrological feature of large rivers is the annual flood pulse. Under this theory, carbon that accumulates on the floodplain throughout an annual cycle is assimilated by biogeochemical processes during and following a flood pulse that inundates vast carbon reserves on the floodplain. Biotic communities are predicted to be in dynamic equilibrium with the dynamics of the flood pulse (e.g., timing, duration, and magnitude). This equilibrium is possible because of the large size of floodplain river systems and the attenuating and moderating effects of this size on the flood pulse, which results in some degree of annual flood predictability. Thus, flood pulses that are too short may not allow flood-dependent organisms time to complete reproductive cycles whereas those that are too long may not allow terrestrial vegetation to develop. Such flood pulses are predicted to enhance system productivity and to support and sustain biodiversity. Contrary to the river-continuum concept, the flood-pulse concept predicts organic matter from upstream origins is insignificant for river production relative to organic material produced and consumed locally on the floodplain. Thus, when the lateral dimensions of floodplain rivers are considered, biotic diversity may be highest in large rivers rather than medium-sized rivers as predicted by the river-continuum concept and lateral connectivity is viewed as critical to perpetuating ecological integrity (Junk 1999; Ward et al. 1999).

However, main stem impoundments have altered the natural hydrology of the UMR and corresponding floodplain inundation regimes (Sparks et al. 1998) and permanently inundated sizeable areas of former floodplain. Moreover, urban and agricultural developments have isolated sizeable portions of most of the Earth's floodplain systems, in effect making them functionally extinct (Tockner and Stanford 2002). Such developments serve to alter the dynamic equilibrium between connected and disconnected landscape features present in natural systems (Galat et al. 1998). Several recent studies have begun to document the ecological consequences of these alterations. Examples include decreased biotic diversity (Bornette et al. 1998; Matthews and Robison 1998; Tockner et al. 1999*b*; Ward et al. 1999; Stein 2001; Ward and Tockner 2001), and biotic production (Welcomme 1979; Bayley 1988; Mitsch and Gosselink 2000), and increased pollution (Van den Brick et al. 1996; Burkart and James 1999; David and Gentry 2000; Goolsby et al. 2000), and species invasion rates (Galat and Zweimueller 2001).

Upper Mississippi River Development and Effects on Lateral Connectivity

The Upper Mississippi River System (Figure 1) has undergone a long history of development that has greatly influenced lateral connectivity and the ecology of the river (Sparks 1995; Galat and Zweimueller 2001; Anfinson 2003). Human alterations in the past two centuries have isolated much of the floodplain and seriously degraded remaining floodplain habitats. Alterations have been progressive and largely center on making the river navigable for commercial shipping and on developing floodplains for agricultural production using flood-control measures. Physical, chemical, and ecological changes associated with these alterations are detailed in many studies (e.g., Simons et al. 1974; Belt 1975; Sparks 1992; Scientific Assessment and Strategy Team 1994; Wlosinski 1994; Yin and Nelson 1995).

Navigation-related modifications began in 1823 with snag removal and sandbar dredging (Figure 5), progressed to the construction of channel-training structures by 1873 (Figure 6), and culminated in the construction of 29 low head dams in the 1930s (Figure 1; Fremling and Claflin 1984; Anfinson 2003). These navigation improvements resulted in altered flow regimes (Johnson et al. 1995, see Figure 4 therein), which in turn affected hydraulic processes (Wlosinski 1994) and sediment transport dynamics (DeHaan 1998) critical for maintaining diverse physical habitats. Impoundment also resulted in the permanent inundation of vast expanses of former floodplain (Scientific Assessment and Strategy Team 1994).

In the same period, agriculture development on the floodplain was pronounced and had two major effects on UMR floodplains. Levees were constructed to incorporate rich alluvial floodplain soils into agricultural production (Figure 7), disconnecting floodplains from the main stem of the river. Increases in the scale of agriculture operations and tillage practices also resulted in large increases in the sediment load being

Figure 6. Two time-lapsed photographs of the same area on the Open River Reach of the Mississippi River, near Grand Tower, Illinois. These photographs from the 1930s (*top*) and the 1950s (*bottom*) demonstrate channel-training measures enacted to increase main channel velocities, minimizing the need for in-channel navigation maintenance. Geomorphic responses in non-bedrock river bottom zones include channel incision, which reduces the frequency of water elevations required for lateral connectivity in large areas of the Upper Mississippi River. For example, in regions of the Middle Mississippi River (St. Louis, Missouri, to Cairo, Illinois), many side channels "perch" above the main stem of the Mississippi River during periods of lower flows. (Photograph from N. Moore [1972].)

delivered to the UMR (DeHaan 1998). Additional alterations associated with floodplain isolation include railway and road embankments, bridges, and floodwalls in urban and residential settings.

The UMR floodplain environment exists now as a complex mosaic of private and public lands comprised principally of agriculture, urban, navigation, commercial, and natural resource interests. Complex ownership patterns and the multiuse nature of the UMR floodplain present substantial challenges to natural resource managers throughout the basin.

Floodplain Status and Management

River scientists have not yet developed reliable methods that can quantify connectivity of habitats and incorporate the variability in land and water elevation typical of large rivers. However, in the UMR, differences in land use, levee prominence, and impoundment characteristics can be used to develop a coarse classification of the degree where floodplains are connected to the main stem. This classification does not measure connectivity explicitly, but provides useful proxies for assessing large-scale patterns that presently exist in the floodplain (Laustrup and Lowenberg 1994).

General System Overview

On the basis of the connection to the main channel, present floodplain habitats of the UMR can be classified into three general categories. The first category is Isolated Floodplain. Isolated Floodplains where the historical floodplain has been completely sequestered behind levees (Figure 8) and are virtually never connected to the river. Often these areas have been converted to residential, urban, and agricultural use. Conversion of historically connected floodplain areas to isolated levied areas has been profound in many areas of the UMR (Figure 8). The amount and distribution of Isolated Floodplains varies considerably by geomorphic reach within the UMR (U.S. Geological Survey 1999; Table 1). The greatest isolation exists in the unimpounded Mississippi River (83% of floodplain sequestered behind levees), lower Illinois River (60%), and lower impounded Mississippi River (Pools 14–26; 50%). Comparatively, the upper impounded Mississippi River (Pools 1–13) is only lightly affected by levees (3%).

The second category is Continuously Inundated Floodplain. Continuously Inundated Floodplains have been permanently inundated as a result of impoundment (Figure 9) and, thus, are always connected to the main channel. They exist in the lower portions of

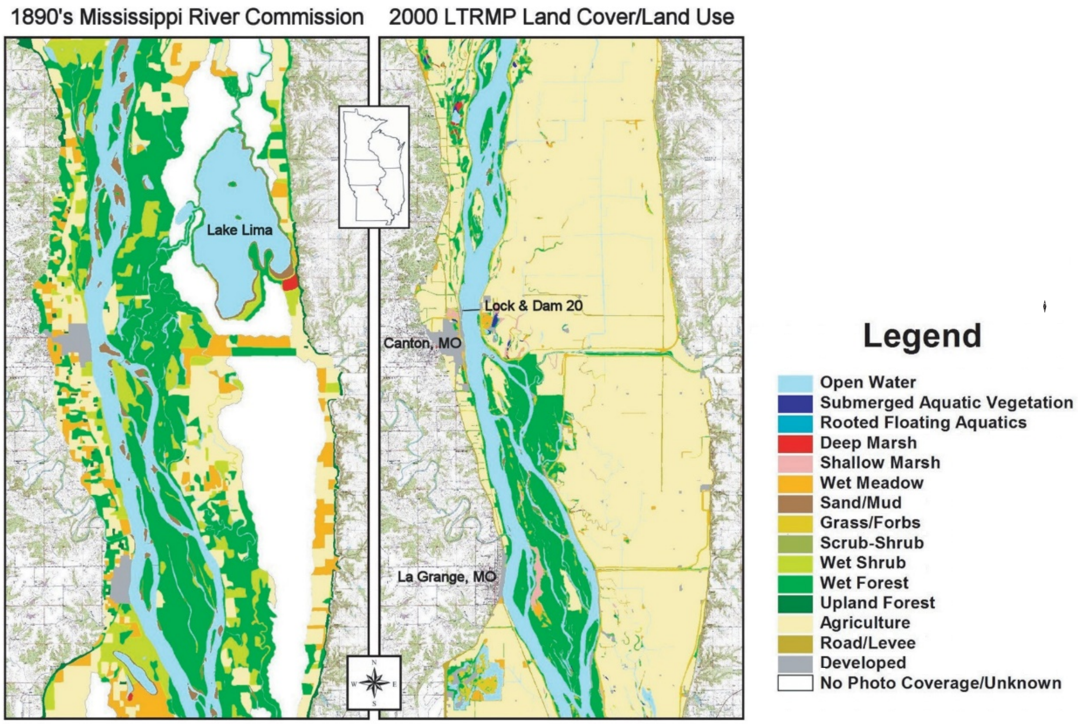

Figure 7. The effects of levee development and enrollment of floodplain lands into agriculture have been profound in many areas of the Upper Mississippi River System. This example from Pool 20 demonstrates changes in land cover over the past century. The image on the left was generated using Geographic Information System and floodplain data from a Mississippi River Commission survey conducted in 1890. The image on the right was compiled using Geographic Information System and land cover/land use data mapped from aerial photographs of the floodplain in 2002 (Larry Robinson, Upper Midwest Environmental Sciences Center, personal communication). Between the two periods, agriculture increased 275%, open water decreased 23%, wet forest decreased 54%, wet meadow decreased 58%, and wet shrub decreased 99%.

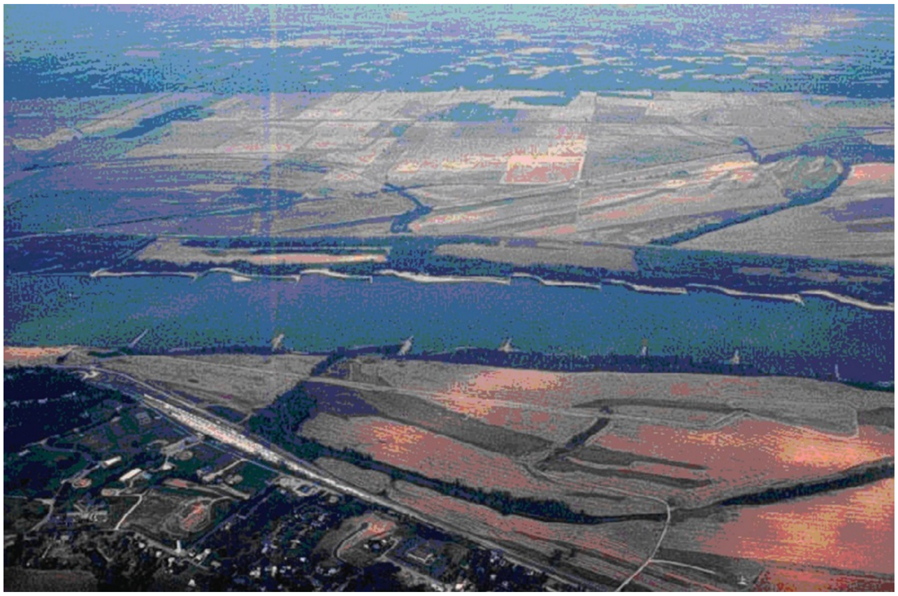

Figure 8. A typical example of isolated floodplain environments in the Middle Mississippi River region (St. Louis, Missouri, to Cairo, Illinois) near St. Genevieve, Missouri. This photograph demonstrates the wholesale conversion of Mississippi River floodplains to agricultural uses through a system of high levees.

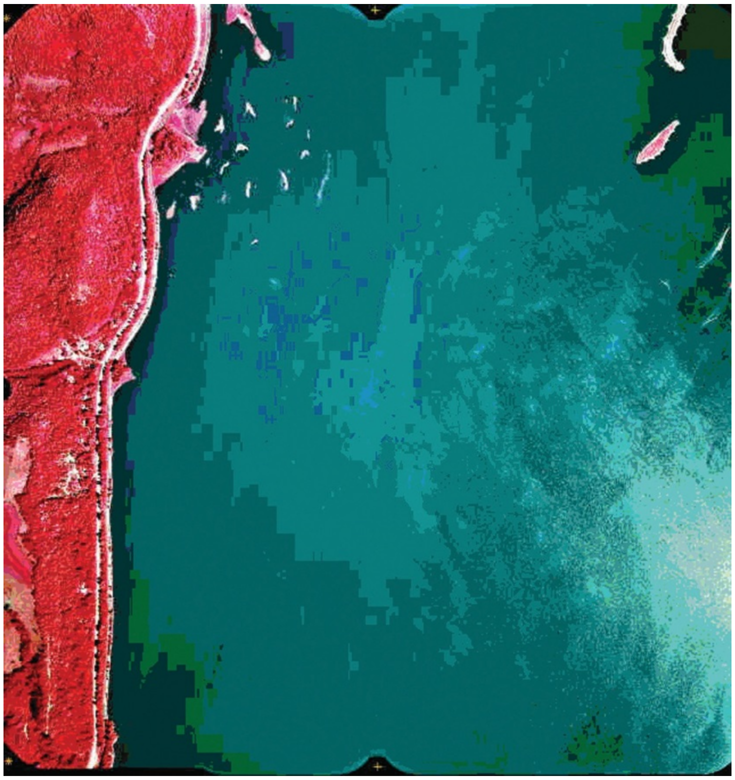

Figure 9. An example of a continuously inundated floodplain of the Upper Mississippi River in Pool 8 near Brownsville, Minnesota. These areas exist in the lower portions of river pools within the impounded reaches of the Upper Mississippi River and exist as a consequence of impoundment. Before impoundment, these areas consisted of a rich mix of side channel, island, and backwater environments that provided aquatic to terrestrial linkages that ebbed with varying hydrology. Today, water levels are held artificially high and stable. While fishes are free to move about in these environments, habitat quality issues may limit use.

river pools within the impounded reaches of the UMR. Their present habitat characteristics are the direct result of increased and stabilized water levels in impounded sections of the river following dam construction. The presence of artificially stable and high water levels throughout the year has led to wind-induced island erosion sediment deposition, loss of diversity in depths, loss of aquatic vegetation, and disruption of the seasonal cycle between aquatic and terrestrial habitats. While fish can physically access such areas any time, the quality of these areas as habitat may restrict use within the UMR.

The third category is Seasonally Inundated Floodplain. Seasonally Inundated Floodplains encompass a variety of seasonally inundated terrestrial areas as well as reconnected backwater habitats that are isolated from the main channel throughout much of the year (Figure 10). Low elevation areas may be connected to the river almost every year, whereas areas at higher elevation may be connected only during extreme flow events. Consequently, these areas retain some degree of floodplain function in the system, although the extent of the function is dependent on regional geomorphology, floodplain elevation, and altered hydrology.

Present Management of UMR Floodplains

Rasmussen et al. (1999) recognized two general categories of floodplain management in the UMR. The first of these is “controlled flooding.” Areas managed by controlled flooding are protected by levees, and water levels are actively managed using some combination of pumps, drains, and water control structures. Generally, these units are actively managed as moist soil units with some combination of the following three goals: (1) artificially simulate a spring flood pulse for fisheries production, (2) initiate a summer drawdown for moist-soil vegetation, or (3) simulate a fall flood pulse for waterfowl and shorebird use during migration (Fredrickson 1991; Heitmeyer et al. 1993). Reid et al. (1989) reported that moist-soil management is practiced on more than 80% of the National Fish and Wildlife Refuges in the United States.

The second category of floodplain management is “uncontrolled flooding” or passive management. This technique permits the portion of floodplain under management to be inundated at intervals dictated by the hydrograph and the surrounding landscape features. Consequently, the amount and degree of connection to the main channel can vary substantially, both seasonally and inter-annually. Often, limited “active” management is implemented on these passively managed areas to enhance habitat values within the unit. Examples include the installation of flow

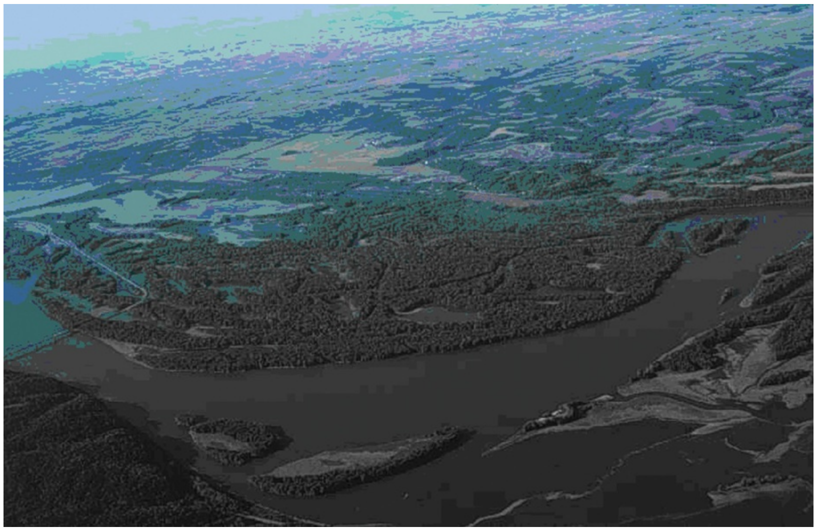

Figure 10. An example of a seasonally inundated floodplain of the Upper Mississippi River near Bellevue, Iowa. These areas exist variously and to lesser or greater extents throughout the Upper Mississippi River. In impounded sections, these areas typically are found in the upper two-thirds of the pool, while they are largely limited to main and side channel margins in the nonpooled sections of the system. They are comprised of a rich diversity of terrestrial and aquatic boundaries, including backwater lakeshores, main and side channel margins, point bars, and islands. Also, portions may be void of vegetation or have various forms of emergent vegetation or forests, the composition will be dependent on the frequency, duration, and magnitude of inundation.

deflecting devices to promote scour and channel formation, levee breaching, and removal of shoreline revetments.

Many U.S. Fish and Wildlife Service lands are subject to management constraints mainly because of land ownership restrictions and operation and maintenance costs. The most restrictive situation arises when the Service lands lie within a levee management district. The existence of other private landowners within the levee district requires consideration of the economic, social, and political consequences of ecologically beneficial management activities on Service lands. Consequently, biotic benefits on these lands tend to be limited to migratory waterfowl, passerines, and non-riverine fish and wildlife species, as high elevation levees may severely or entirely restrict lateral movements of fishes from channel environments.

When Service lands are not within a levee management district, there is much more flexibility in management. Under this scenario, managers can minimize threats of catastrophic breach and scour, permit more frequent spring flooding and fish passage opportunities, allow for moist-soil vegetation management, and allow fall flooding for migratory waterfowl use. However, the cost of initial infrastructure development and annual maintenance may limit some management options.

Lateral Connectivity—its Relevance to Fishes

We summarize the literature on associations between lateral connectivity and fish responses at several spatial scales and levels of ecological organization. Our presentation draws on recent findings in European systems as well as on findings from the UMR.

Riverine fish species have evolved migratory patterns and life-history characteristics to exploit seasonally predictable flood pulses and make use of resulting seasonal habitats and energy sources, particularly for reproduction, feeding, and refuge from intolerable conditions (Welcomme 1979; McKeown 1984; Petts 1989; Winemiller and Rose 1992; Scheimer 2000). Thus, seasonal use of floodplain habitats is common in river fishes worldwide (Welcomme 1979; Petts 1989; Winemiller and Rose 1992). As a consequence, large river fish communities exhibit high diversity, which has been attributed to the structural diversity and habitat richness of floodplain environments (Schiemer 2000).

Role in Reproduction

The timing and duration of the flood pulse are particularly critical to UMR fishes that require lateral access to floodplain environments for reproduction. Ideal conditions for reproduction of fish species that spawn on the floodplain exist in years when the flood pulse and water temperature rise are coupled (Figure 11; Junk et al. 1989). Bayley (1991) observed that a coupled rise in temperature and discharge results in increased fish yield, a measure of production, and termed this observation as the "Flood-Pulse Advantage." Levee development and enhancement on UMR floodplains reduce the likelihood of such an advantage because flood waters are conveyed by the main channel on the river side of the levees rather than by the floodplain. Thus, flood waters are less likely to interact with the floodplain to the advantage of fishes because of levee constriction (Wlosinski 1994; Wlosinski and Olsen 1994; Sparks 1995).

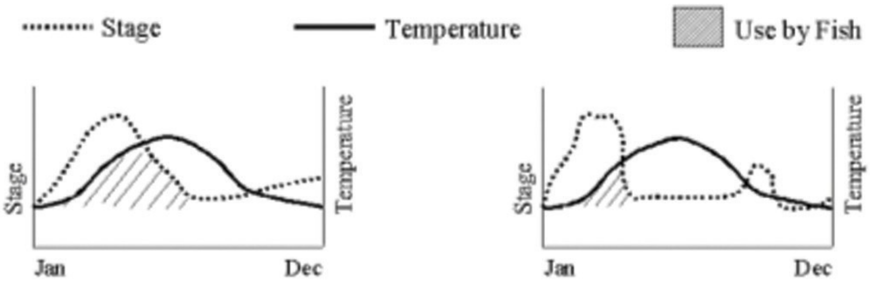

Figure 11. Ideal spawning conditions for floodplain spawning fishes occur when the floodpulse and temperature rise are coupled (*left*) and are least favorable when the floodpulse recedes ahead of the temperature rise (*right*). Bayley (1991) termed this the "Flood-Pulse Advantage."

Increases in the production of some fish species following flood years (i.e., following periods of increased floodplain connectivity) demonstrate the foregone production when fish are denied seasonal access to floodplain habitats. For example, Gutreuter et al. (1999) tested for differences in growth responses of several fish species using long-term monitoring data from the UMR, comparing growth following a 500-year flood event that breached many levees in the UMR with growth from non-flood years. Growth was used as a surrogate for production as it represents the rate where biomass is accrued by individuals in a population. Consistent with the flood-pulse concept (Junk et al. 1989), Gutreuter et al. (1999) provided evidence for increased growth of some UMR fishes in the Great Flood of 1993. Benefits in growth were restricted to fishes that exploited the moving littoral zone. Theiling et al. (1999) reported a greater than fourfold increase in the number of fish species using a backwater complex in lower Pool 26 following the Great Flood of 1993, suggesting increased use of floodplains when accessible. It remains uncertain whether these observations reflected local production because of floodplain connectivity or whether these observations represented use of the floodplain as a refuge from high flows. Thus, there is evidence that increased access to the floodplain during annual flood pulses can increase the production of some important UMR fish species and suggests the potential for targeted management.

The preceding discussion focused on large-scale fish responses to floods, but local responses can also be noteworthy. For example, fish production within refuge areas managed by controlled flooding can be substantial. Lake Chautauqua is a backwater lake on the Illinois River that has an upper section—480-ha Kikunessa Pool, managed for waterfowl and fish—and a lower section—970-ha Wasenza Pool, managed as a moist-soil unit by the U.S. Fish and Wildlife Service. Fish production in the Wasenza Pool in 1996 was estimated between 18 and 27 million larval/early juvenile fishes representing 34 taxa (Irons et al. 1997). Subsequent studies of larval fish emigration from Wasenza Pool revealed that larger numbers of fish were produced in relatively high water years when the levees were overtopped versus years when levees were not overtopped, suggesting that adult fish access to the pool for spawning may be limited during normal-water years.

Role in Survival

Whereas flood pulses are viewed as critical determinants of juvenile production, UMR fishes are generally long-lived (Galat and Zweimueller 2001). Thus, survival of fishes produced following a flood pulse depends on whether suitable habitat conditions are sufficiently present throughout the entire life of UMR fishes. Survival for many species depends on laterally connected, low-velocity habitats during nonflood pulse periods that provide foraging and overwintering habitats (Knights et al. 1995; Barko and Herzog 2003; Barko et al. 2004*a*,*b*). These habitats include a diverse array of side channel, slough, and backwater environments that provide refuge and foraging habitats for juvenile and adult fishes of many UMR species. The availability of these habitats to UMR fishes can have important effects on population dynamics. These are the types of habitats most likely to be affected by managing floodplain connectivity.

The fate of juvenile fishes produced within controlled areas, such as Wasenza Pool within Lake Chautauqua on the Illinois River, remains unknown. Recent analyses of LTRM fish data suggest that survival of juvenile fishes produced during the Great Flood of 1993, a high connectivity event, was species-specific (Barko et al. 2005; Chick et al. 2005). Within the Open River Reach of the Mississippi River, near Jackson, Missouri, strong year classes of bluegill (*Lepomis macrochirus*), black crappie (*Pomoxis nigromaculatus*), and common carp were produced in 1993 (Figure 12), presumably in controlled areas that became flooded. However, by 1995, bluegill and black crappie were nearly absent from the LTRM samples, suggesting high mortality. Conversely, common carp remained abundant, although abundance declined steadily through time, suggesting little subsequent recruitment (Figure 12). All three of these species require or benefit from floodplain habitats for reproduction, whereas only bluegill and black crappie exhibit a strong preference for low-velocity habitats as adults. This suggests that access to low-velocity foraging or winter habitats on the floodplain may be limiting the abundance of bluegill and black crappie in this reach of river. This example highlights the importance of lateral connectivity during periods other than reproduction.

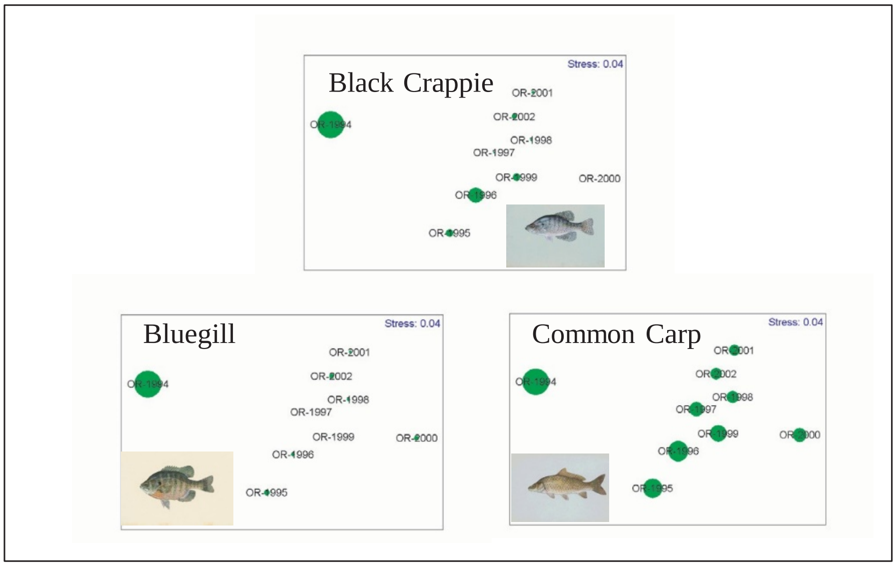

Figure 12. In the Open River Reach of the Upper Mississippi River System, reproductive success was high following the Great Flood of 1993 for many fish that require access to the floodplain for spawning (as indicated by the size of the green dot for the three species presented). However, in years after the flood (as labeled on each of the plots), only species that were habitat generalists, like common carp (*Cyprinus carpio*), persisted as adults (e.g., green dots are small or absent in following years for bluegill (*Lepomis macrochirus*) and black crappie (*Pomoxis nigromaculatus*), but persistent for common carp). Species like bluegill and black crappie requiring backwater habitats as adults experienced high mortality and were lost within 1 to 2 years. This response indicates that the adult life-history requirements for many species are not being met in the lower reaches of the Upper Mississippi River System (Barko et al. 2005; Chick et al. 2005).

Upper Mississippi River floodplains serve as critical overwintering and feeding habitats for some fish species. Backwaters provide lower current velocities and higher water temperatures in winter relative to the main channel, making them energetically favorable. However, many of these same backwaters experience low dissolved oxygen levels because of high biological oxygen demand and low current velocities (Johnson and Jennings 1998). Knights et al. (1995) reported that bluegill and black crappie in an UMR backwater preferred winter habitats characterized by water temperatures >1°C and undetectable current velocity. When dissolved oxygen levels fell below 2 mg/L, both species sought areas with higher dissolved oxygen but would avoid areas with water temperatures <1°C and current velocities >1 cm/s. Similar preferences for higher water temperatures, low current velocities, and adequate dissolved oxygen have been documented for largemouth bass (*Micropterus salmoides*) in the Upper Mississippi and Illinois Rivers (Gent et al. 1995; Raibley et al. 1997). These species are known to exist in channel habitats at other times of the year (LTRM, unpublished data); thus, restricted access to floodplain habitats before winter may lead to reduced survival, reproduction, and growth on the basis of habitat preferences.

In contrast, use of floodplain habitats by typical large river fishes such as paddlefish (*Polyodon spathula*) and lake sturgeon (*Acipenser fulvescens*) is poorly understood. Recent telemetry studies have shown that both species use floodplain habitats as feeding areas (Knights et al. 2002*a*; Zigler et al. 2003). Although use of floodplain habitats by paddlefish and lake sturgeon has been documented, the benefits gained from the use of these habitats remain unknown. In Pool 8 of the UMR, adult paddlefish preferred off-channel habitats with current velocities <5 cm/s and depths >4 m (Zigler et al. 2003). It remains unclear whether paddlefish used these habitats to avoid high flows for feeding or for some other purpose. Adult lake sturgeon also used floodplain habitats, but unlike paddlefish, was in a wide range of current velocities (Knights et al. 2002*a*). This suggests that adult lake sturgeon may benefit from access to floodplain habitats for feeding. These studies suggest that paddlefish and lake sturgeon are wide ranging and use a broad array of habitat types, including floodplain habitats, during their lifetime. The status of paddlefish and lake sturgeon as U.S. Fish and Wildlife Service trust species increases the importance of management actions that benefit these species. Therefore, to enhance populations of these large-bodied fishes, more research should be directed at understanding what constitutes good floodplain habitat for these fishes and how to best connect floodplain habitat with the main stem river.

The role of floodplain habitats for reproduction and survival suggests that alternatives for managing UMR floodplains for fisheries benefits will require an integrated approach. Effective management needs to know which species use these habitats, the temporal nature of fish use, and the life-history requirements that are met to determine the potential benefits of increased access to floodplain habitats and to plan and design effective passage alternatives. Potential goals of enhanced lateral fish passage are many, but should be founded in an integrated approach to floodplain management.

Life-History Considerations

The ichthyofauna of the UMR is incredibly rich and diverse. Of the nearly 600 fish species documented within North America, 144 (nearly one quarter) have been collected in the UMR by the LTRM. The Mississippi River Basin as a whole exhibits the highest diversity of freshwater fishes for any region of the world at comparable latitudes (Robison 1986, cited in Scientific Assessment and Strategy Team 1994). Many of these species use floodplain environments to fulfill essential life needs (e.g., reproduction, feeding, and refuge from intolerable conditions; Galat and Zweimueller 2001). Understanding how floodplain isolation affects fish populations and communities requires a detailed understanding of the life history of each of these species.

Life-history traits can be defined as a suite of characteristics particular to a species that describe its association to the environment where it evolved or presently exists. These characteristics can be conceptualized as particular to the physiology, behavior, and general ecology of the species. Examples of general life-history trait categories include reproductive strategies, habitat associations, feeding affinities, phylogenetic associations, and physiological tolerances. Generally, species demonstrate physiological affinities and behavioral associations such that some combination of life-history traits define a concept of niche or a suite of conditions that meet critical life-history needs and defines the general association of a species to its environment.

Knowledge of life-history strategies is critical in planning effective habitat restoration of freshwater communities (Regier 1974; Power et al. 1988; Mobrand et al. 1997; Schmutz and Jungwirth 1999; Naiman and Turner 2000; Zalewski et al. 2001; Schiemer et al. 2002). For example, fish life-history information has been used to create indices of biological integrity that function to detect habitat degradation or to evaluate habitat restoration (Oberdorff and Hughes 1992; Lyons et al. 2001). Also, life-history information has been essential to manage species of special interest such as exploited sport and commercial species, threatened or endangered species, and undesirable exotic species (Fogarty et al. 1991; Casselman and Lewis 1996; Lappalainen and Kjellman 1998; Nislow 1998; Schrank and Guy 2002).

Given the diversity of the UMR fish fauna and the variety of floodplain units managed by the U.S. Fish and Wildlife Service, we cannot provide a detailed account of which management practices would benefit which species in each area. We do, however, provide information that should be considered in the context of actively and passively managed floodplains.

Considerations for Actively Managed UMR Floodplains

Actively managed floodplain units present unique physiological and behavioral challenges to fishes. Water exchange between the managed unit and the channel is commonly achieved using a series of pumps and gates. With gated control structures, a head differential exists across the gate because of differences in water elevation between the managed unit and the connecting channel. High-head differentials can result in current velocities that exceed the swimming performance of most UMR fish species. We were unable to find information on common head differentials for actively managed floodplain units in our literature review, but generally, as head increases, water velocity through a control structure increases with a constant gate opening size.

Directionality of flow across the control structure also probably affects lateral passage opportunities in actively managed floodplain units. Fish have highly evolved sensory systems for detecting and responding to flow, however, these sensory systems require fish to orient into flowing water for information exchange between the sensory system and the environment (Jobling 1995). This is the basis for the concept of “attractant flow” commonly used in longitudinal passage settings (Barry and Kynard 1986; Barekyan et al. 1988; Bunt et al. 1999). Attractant flow is an area at the base of a water control structure where flow is modified to attract target fishes and direct them through a control structure. However, in actively managed lateral passage settings, this concept may be reversed. For lateral passage, fish must move with the flow to enter areas as they fill and leave those areas as they drain. Thus, attractant flows may cause fish to move in the wrong direction and actually reduce lateral fish passage.

The physical characteristics of gates used to exchange water may also limit lateral fish passage into managed units. The size of the gate may preclude some large-bodied species from passing. Because water levels in managed units are controlled by incrementally lifting horizontally placed “logs” from the top of the gate (e.g., stop-log gate water control structures), some benthic species may be precluded from passing over these structures. Finally, the actual composition of the gate itself may preclude certain species. For example, paddlefish, which use their rostrum to detect the electrical impulses of their zooplankton prey, demonstrate aversions to weak electrical fields generated by metallic objects in the absence of visual cues (Wilkens et al. 1997; Gurgens et al. 2000). Thus, paddlefish may avoid water control and fish passage structures that typically include metal in their construction. Little is known about how these factors affect lateral fish passage. More research is needed to develop water control structures that can effectively pass large and small fishes in both directions.

Considerations for Passively Managed UMR Floodplains

Passively managed units do not present nearly the range of physiological and behavioral challenges that actively managed units do. However, their availability to fishes varies considerably over time and space as a function of annual hydrology and floodplain and levee elevation.

Summer drawdown is a technique that lowers water levels in summer to promote growth of aquatic macrophytes and to consolidate sediments (Lubinski et al. 1991). This technique has proven successful at small and poolwide scales and is gaining popularity. When applied at the poolwide scale, the reduction in water levels is greater in the lower reaches of the pool than in the upper reaches; thus, drawdowns have their greatest effect in the lower impounded areas. A potential biological cost of this management technique is loss of fish nursery habitat as shallow areas are dewatered (Theiling 1995), although the long-term consequences on fish populations remain unclear. For example, larval and juvenile fishes may experience increased mortality if connections to traditional nursery areas are lost or these areas are dewatered. However, new nursery areas may develop in other locations that were previously too deep. We may be able to predict the location and availability of new nursery areas and other critical habitats based on models of floodplain elevation flow characteristics and corresponding vegetation responses. In addition, many fish species may benefit in the future if the drawdown increases emergent vegetation that provides food, cover, and spawning habitat during subsequent increases in water levels. Wlosinski et al. (2000) found little difference in fish abundance or diversity following three consecutive years of drawdowns on Pools 24–26. However, little information is available on long-term and species-specific effects of large-scale (i.e., poolwide) drawdowns on UMR fish populations.

Significant questions remain about water-level management and its effects on UMR fishes. For example, studies have suggested that increases in water levels in winter may increase overwinter survival of some fishes by introducing oxygen rich water into backwaters subject to high biological oxygen demand (Gent et al. 1995; Johnson and Jennings 1998). However, reduction of water levels in winter may result in high mortality because of anoxia, as fish become stranded in backwaters (Raibley et al. 1997). Water control structures may help in maintaining relatively warmwater temperatures, low current velocities, and dissolved oxygen levels >2 mg/L in backwaters in winter. Thus, actively managed refuge lands have the potential to provide such critical habitat needs in reaches where overwintering areas for fish are otherwise limited (Gutreuter 2004).

Progressive techniques for managing "uncontrolled" UMR floodplains may affect the future roles of "controlled" floodplains. Poolwide water-level manipulations designed to elicit particular physical, chemical, and biological responses have the potential to affect vast portions of the floodplain. By mimicking the natural flood pulse, these manipulations may provide large-scale enhancement of wildlife habitat throughout the UMR. If poolwide water-level management can duplicate the habitat conditions created by moist-soil management within controlled areas, existing controlled areas can be used to provide habitat for other wildlife concerns.

Each area of the floodplain and U.S. Fish and Wildlife Service refuge holdings is distinct, with a unique set of challenges to provide enhanced lateral fish passage. Some areas are passively managed while others are actively managed as moist-soil units. Approaches and goals will differ among sites and can provide the foundation for an integrated management program to benefit a range of management goals from species of concern to regional biodiversity. Management experiments should play a key role in developing and evaluating management alternatives, filling information gaps, and finding common principles that apply across different areas. Given the incredible faunal diversity of UMR fish assemblages, the variety of sizes and types of floodplain environments throughout the UMR, and a host of different management goals, we cannot possibly identify every need at every scale. Rather, we conclude that a few key pieces of information and research could lay the foundation for an integrated management and science approach to lateral connectivity issues in the basin. Below, we identify and elaborate on these broad informational and research needs.

Information Needs and Conclusions

The goal of this report is to identify information and research needs required to enhance management of fisheries resources on National Fish and Wildlife Refuges on the Upper Mississippi River. Although the scope of this effort precludes us from identifying needs at specific management units, our literature review consistently revealed particular broad themes concerning information gaps.

Dam and levee construction have altered the riverine landscape and isolated a large portion of floodplain habitat. The disruption of natural fluvial processes has had a homogenizing effect on riverine habitats, wherein habitats lose diversity and complexity and become more similar and homogenous. Refuge lands, whether leveed or unleveed, suffer from habitat homogenization. Habitat diversity is presently being restored to some unleveed refuge lands through various forms of habitat rehabilitation and experimental water-level manipulations. However, opportunities for increasing habitat diversity on leveed refuge lands are much more limited, spatially and physically. While the physical characteristics of floodplain refuge lands vary notably and management goals and methods are quite different between these types of lands, we suggest that a few broad, yet key informational sources could lay the foundation for enhanced management and research on these lands.

The first information need for predicting where and how management of refuge lands can affect fish resources is to compile a geospatial inventory of floodplain habitats along the UMR. Such a database would contain information on spatial extent (size, distance to the main channel, depth), land use (categorical representation of land use at several scales, proximity to contiguous channels, management practices), water control structures (levee type, presence or absence of a spillway, levee height, pumps, stop-log gates, and composition), and ownership. These data would provide many management and scientific benefits.

For the manager, the availability of floodplain habitats within a given pool or reach could identify areas in need of enhanced floodplain connectivity to determine how to best manage specific parcels of land to enhance reachwide benefits to fish. Inclusion of historical floodplain extent would more accurately assess the magnitude of floodplain loss within a pool or reach. For the research scientist, such data would provide a framework for determining how the effects of manipulations (natural or experimental can be assessed within the refuge framework.

Fortunately, abundant data on UMR floodplains are available in survey maps and remotely sensed information. Many of these data are accessible through the Upper Midwest Environmental Sciences Center's Web site (*http://www.umesc.usgs.gov/*, accessed May 2004), and various state agency offices. Additionally, many systemic survey sets not available through the Upper Midwest Environmental Sciences Center's Web site are presently being compiled by a team of university researchers at Southern Illinois University under a National Science Foundation grant (Table 2). The Southern Illinois University data sources are particularly relevant for lateral connectivity issues because they represent a relatively long time series of floodplain changes permitting quantification of engineering changes and floodplain responses over the past century. Because many of these data sources have only recently been digitally registered and rectified, little work has been done to quantify these changes to date.

A second information need relates to the elevation of lands within the floodplain and their frequency of connection to the main channel. Data on elevations of floodplains and levees would enable managers to model the seasonal extent of inundation of floodplains, as well as frequency and degree of connection of floodplain habitats to the main channel. Available elevation data vary in their accuracy, resolution, and availability. Coarse data are derivable from various river survey maps (Table 2), and 30-m resolution digital elevation models are

Table 2. Survey map sets by major river reach and publication year compiled by researchers at Southern Illinois University under a National Science Foundation grant. Each set has been digitally registered and rectified. For additional information, contact Dr. Nicholas Pinter, Department of Geology, Southern Illinois University.

River reach	Map set name	Year of publication
Lower Mississippi River	Preliminary map of the Lower Mississippi River	1881
	Survey of the Mississippi River	1890
	Survey of the Mississippi River	1911–1915
	Flood control and navigation map of the Mississippi River	1933
	Mississippi River and Levee Charts: Cairo, Illinois, to Rosedale, Mississippi	1937
	Flood control and navigation map of the Mississippi River	1948
	Mississippi River hydrographic survey: USACE[a], MUMRRhis Engineering District	1951
	Mississippi River hydrographic survey: USACE New Orleans Engineering District	1952
	Mississippi River hydrographic survey: USACE Vicksburg Engineering District	1952
	Flood control and navigation map of the Mississippi River	1957
	Mississippi hydrographic survey: USACE MUMRRhis District	1962–1964
	Flood control and navigation map of the Mississippi River	1968
	Flood control and navigation map of the Mississippi River	1977
	Flood control and navigation map of the Mississippi River	1983
	Flood control and navigation map of the Mississippi River	1998
Middle Mississippi River	Survey of the Upper Mississippi River	1880–1881
	Mississippi River: Saint Louis, Missouri, to Cario, Illinois	1908
	Hydrographic survey maps of the Mississippi River: mouth of Ohio River Miles 0 to 300	Compilation of various surveys 1939, 1947, 1956, and 1961
	Program of improvements	1940
	Mississippi River between mouths of Ohio and Missouri Rivers	1948
	Hydrographic survey of the Mississippi River: River Miles 0 to 300	1972
	Hydrographic survey of the Mississippi River: River Miles 0 to 202	1983
	Upper Mississippi River navigation charts: Maps 94 through 118 only	2001
Upper Mississippi River	Map of the Mississippi River from Falls of Saint Anthony to junction of Illinois River	1878
	Upper Mississippi River: Minneapolis to mouth of Missouri River	1895
	Map of the Mississippi River from Falls of Saint Anthony to junction of Illinois River	1915
	Upper Mississippi River: Hasting, Minnesota, to Grafton, Illinois	1930
	Map of the Mississippi River from Falls of Saint Anthony to junction of Illinois River	1905
Upper and Middle Mississippi River	Survey of the Upper Mississippi River	1895
Minnesota and Mississippi Rivers	Minnesota and Mississippi Rivers as far south as Arkansas	1869
Illinois River	Illinois Waterway navigation charts	1999
Missouri River	Missouri River, Missouri, Kansas, Nebraska, hydrographic survey	1987
Lower Missouri River	Missouri River, Rulo, Nebraska to mouth	1940
	Missouri River hydrographic survey: Rulo, Nebraska, to mouth	1994
Upper Missouri River	Missouri River hydrographic survey: Ponca State Park to Rulo, Nebraska	1994
	Missouri River, Kansas to Sioux City	1929

[a] USACE = U.S. Army Corps of Engineers

available through the U.S. Geological Survey (*http://seamless.usgs.gov/*, accessed May 2005). However, even the digital elevation models may be too coarse for many research and management needs. Such sources are regarded as too coarse because UMR floodplain environments are extremely low gradient landscapes, requiring highly precise elevation data for floodplain inundation and lateral connectivity modeling. Ideally, high-resolution elevation data, as could be provided with Light Detection and Ranging (LIDAR) technology, would provide the greatest utility. However, LIDAR data are only available for small areas within the UMR (e.g., St. Louis area, Mississippi River). Information on the frequency of water elevations is also necessary for assessing lateral connectivity events. Empirically derived estimates of water elevation frequencies based on long-term hydrologic data have been determined by river mile for the Mississippi River (*http://www.umesc.usgs.gov/data_library/water_elevation/flood_potential.html*, accessed May 2005). However, such estimates presently do not exist for the Illinois River.

In addition to mapping floodplain availability for fishes, floodplain elevation data will allow modeling of the type and quality of floodplain habitats available to fishes at various water-level elevations. Habitat quality is a poorly understood characteristic in UMR floodplain ecosystems (but see Knights et al. 1995; Johnson and Jennings 1998). Floodplain habitats encompass a number of aquatic area types described for the UMR including contiguous and isolated floodplain lakes, contiguous and isolated shallow aquatic areas, and impounded areas and the various secondary and tertiary channels which connect them to the main stem (Wilcox 1993). However, each of these aquatic area types is characterized by a range of physical variables (depth, current velocity, temperature, substrate, vegetative cover, etc.) that vary both spatially and temporally. Different combinations of these variables determine the suitability of these areas for various fishes. Many of these physical characteristics have been negatively affected by high siltation rates and disruption of natural fluvial processes. Access to high-resolution elevation data would allow managers and researchers to model the effects of manipulating water levels or breeching levees and to more effectively characterize issues related to habitat quality.

A third primary information need is detailed life-history data for the large number of species that comprise the UMR fish community. Effective fisheries management strategies for the UMR must be based on an understanding of the life-history characteristics of the large number of species that comprise the fish community. To determine the potential benefits of increased access to floodplain habitats, we need to know which species use these habitats, the temporal nature of fish use, and the life-history requirements that are met. A thorough compilation of life-history data is necessary to determine potential effects of management actions on particular fish species (e.g., U.S. Fish and Wildlife Service trust species), as well as particular ecological guilds and community-based indicators. Such a database is presently being compiled by the LTRM (O'Hara et al., in review).

Second order needs would include developing a classification of floodplain habitats based on physical and chemical features, then developing models and decision support systems that combine this information to help predict the effects of different management actions and identify research and experiments to fill information gaps.

Not all fishes should benefit from increased access to floodplain habitats. Several nonnative fish species, particularly Bigheaded carps (*Hypopthalmichthys* spp.), have invaded the UMR in the last few years and the trend is likely to continue (Irons et al., in review). Because these are recent introductions, little is known about how these species exploit UMR habitats. Methods for preventing the spread of these species have been largely ineffective. In our review of the literature, we found few examples of effective exclusion structures. The few examples we found were highly engineered solutions, requiring continual maintenance and labor expenditures, with only marginal benefits and, in our opinion, with limited potential for application on the UMR (Royal Botanical Gardens 1998; *http://www.rbg.ca/pdf/FISHWAY.*

pdf, accessed May 2005). Thus, more research is needed to develop methods or devices that would allow cost effective and selective passage of fish species through water control structures or other constriction points.

Sequestering floodplain habitats through levee construction has imposed structural limitations on fish use of refuge lands. The type of water control structure, its dimensions, and possibly even its material composition can affect fish access to these areas. Construction, maintenance, and operating costs can limit the effectiveness of water control structures for passing fish. Passive water control structures, such as levee notches or spillways, only permit fish passage once the minimum water level has been attained. The dimensions of the water control device may also limit fish use, especially by large-bodied fishes. Even the material from which control devices are constructed may affect fish use of passage structures. Additionally, present water control structures may not provide the necessary environmental cues (e.g., attractant flows) to promote fish movement between the floodplain and main channel. Research on the development and testing of water control structures that effectively pass target species and life stages is required to enhance biological connectivity to these actively managed areas.

Although the floodplain can be viewed as a continuum across space and time, similarities in spatial, physical, and chemical properties exist among different segments of UMR floodplain environments that would permit classification of similar habitat types. Such a classification would be based on key habitat attributes (e.g., morphoedaphic and chemical characteristics) and could lead to the development of management alternatives tailored to particular classes of floodplain habitats. When biotic data are available or can be collected, such a classification permits investigation of hypothesized species occurrence or use on the basis of life-history traits. This approach could provide insight into potential bottlenecks in the life-history needs of UMR fishes and help evaluate whether any given class or specific floodplain unit could be managed to help alleviate such bottlenecks.

In conclusion, our review of the literature revealed conceptual advances in connectivity and identified alternative theoretical constructs for managing and understanding the role lateral connectivity plays in overall river system function. However, specific information concerning fisheries management in laterally altered environments was less available. We identified information and data gaps on the principle that effective management and restoration of UMR fishery resources should be based on a mechanistic understanding of how physical and biological systems interact and how human activities influence these interactions.

We identified three first order and three second order information needs required to construct such a mechanistic understanding. First order information needs are (1) a geospatial inventory of floodplain habitats along the UMR, (2) high-resolution floodplain elevation data, and (3) a detailed life-history database for UMR fishes. Second order information needs are (1) development of nonnative fish species exclusion methods, (2) an understanding of fish behavior responses to water control structures, and (3) the classification of floodplain habitats based on physiologically relevant fish habitat variables.

Finally, we suggest that filling these information gaps should proceed by compiling and centralizing readily available data sources, supplemented by new data sources as they become available. However, readily available data will not meet all of the needs in each of these areas. In such instances, directed research will probably prove the most efficient method for filling information gaps. We suggest that experimental approaches conducted in an adaptive management framework hold the best promise. For example, public landscapes within the UMR floodplain, such as U.S. Fish and Wildlife Service refuge holdings, can be viewed as replicate units for study (e.g., fish behavior studies around water control structures). Similar units can be divided randomly into test and control sites. We recognize that multiple uses of many refuge lands may preclude such experimental treatment. However, when possible, such experiments hold great promise for effective and efficient learning to greatly increase management capabilities.

References

Amoros, C., and G. Bornette. 2002. Connectivity and biocomplexity in waterbodies of riverine floodplains. Freshwater Biology 47(4):761–776.

Anfinson, J. O. 2003. The river we have wrought: a history of the upper Mississippi. University of Minnesota Press, Minneapolis, Minnesota. 365 pp.

Barekyan, A. S., B. S. Malevanchik, and M.A Skorobogatov. 1988. Promising designs of fishways. Hydrotechnical Construction 22(7):384–388.

Barko, V., and D. Herzog. 2003. Relationship among side channels, fish assemblages, and environmental gradients in the unimpounded Upper Mississippi River. Journal of Freshwater Ecology 18(3):377–382.

Barko, V. A., D. P. Herzog, R A. Hrabik, and J. S. Scheibe. 2004*a*. Relationships among fish assemblages and main channel border physical habitats in the unimpounded Upper Mississippi River. Transactions of the American Fisheries Society 133:370–383.

Barko, V. A., M. W. Palmer, D. P. Herzog, and B. Ickes. 2004*b*. Influential environmental gradients and spatiotemporal patterns of fish assemblages in the unimpounded Upper Mississippi River. American Midland Naturalist 152(2):369–385.

Barko, V. A., B. S. Ickes, D. P. Herzog, R. A. Hrabik, J. H. Chick, and M. A. Pegg. 2005. Spatial, temporal, and environmental trends of fish assemblages within six reaches of the Upper Mississippi River System. U.S. Geological Survey, Upper Midwest Environmental Sciences Center, La Crosse, Wisconsin, February 2005. Technical Report LTRM 2005-T002. 27 pp.

Barry, T., and B. Kynard. 1986. Attraction of adult American shad to fish lifts at Holyoke Dam, Connecticut River. North American Journal of Fisheries Management 6:233–241.

Bayley, P. B. 1988. Factors affecting growth rates of young tropical floodplain fishes: Seasonality and density-dependence. Environmental Biology of Fishes 21(2):127–142.

Bayley, P. B. 1991. The flood pulse advantage and the restoration of river-floodplain systems. Regulated Rivers: Research & Management 6(2):75–86.

Belt, C. B. 1975. The 1973 flood and man's constriction of the Mississippi River. Science 189:681–684.

Benda, L., and 6 authors. 2004. The Network Dynamics Hypothesis: How channel networks structure riverine habitats. Bioscience 54(5):413–427.

Bornette, G., C. Amoros, and N. Lamouroux. 1998. Aquatic plant diversity in riverine wetlands: The role of connectivity. Freshwater Biology 39(2):267–283.

Bunt, C. M., C. Katopodis, and R. S. McKinley. 1999. Attraction and passage efficiency of white suckers and smallmouth bass by two Denil fishways. North American Journal of Fisheries Management 19(3):793–803.

Burkart, M. R., and D. E. James. 1999. Agricultural-nitrogen contributions to hypoxia in the Gulf of Mexico. Journal of Environmental Quality 28(3):850–859.

Casselman, J. M., and C. A. Lewis. 1996. Habitat requirements of northern pike (*Esox lucius*). Canadian Journal of Fisheries and Aquatic Sciences 53(1):161–174.

Chick, J. H., B. S. Ickes, M. A. Pegg, V. A. Barko, R. A. Hrabik, and D. P. Herzog. 2005. Spatial structure and temporal variation of fish communities in the Upper Mississippi River. U.S. Geological Survey, Upper Midwest Environmental Sciences Center, La Crosse, Wisconsin, April 2005. LTRM Technical Report 2005-T004. 15 pp.

Church, M. 2002. Geomorphic thresholds in riverine landscapes. Freshwater Biology 47(4):541–557.

Connell, J. H. 1978. Diversity in tropical rainforests and coral reefs. Science 199:1302–1310.

David, M. B., and L. E. Gentry. 2000. Anthropogenic inputs of nitrogen and phosphorus and riverine export for Illinois, USA. Journal of Environmental Quality 29(2):494–508.

DeHaan, H. C. 1998. Large river sediment transport and deposition: An annotated bibliography. U.S. Geological Survey, Environmental Management Technical Center, Onalaska, Wisconsin, April 1998. LTRM 98-T002. 85 pp.

Elwood, J. W., J. D. Newbold, R. V. O'Neill, and W. Van Winkle. 1983. Resource spiraling: an operational paradigm for analyzing lotic ecosystems. Pages 3–27 *in* T. D. Fontaine, and S. M. Bartell, editors. Dynamics of lotic ecosystems. Ann Arbor Science, Michigan.

Fogarty, M. J., M. P. Sissenwine, and E. B. Cohen. 1991. Recruitment variability and the dynamics of exploited marine populations. Trends in Ecology & Evolution 6:241–246.

Fredrickson, L. H. 1991. Strategies for water level manipulations in moist-soil systems. Waterfowl Management Handbook, Fish and Wildlife Leaflet 13.4.6. 8 pp.

Fremling, C. R., and T. O. Claflin. 1984. Ecological history of the Upper Mississippi River. Contaminants in the Upper Mississippi River: Proceedings of the 15th Annual Meeting of the Mississippi River Research Consortium, La Crosse, Wisconsin.

Galat, D. L., and 13 co-authors. 1998. Flooding to restore connectivity of regulated, large-river wetlands. Bioscience 48(9):721–733.

Galat, D. L., and I. Zweimueller. 2001. Conserving large-river fishes: is the highway analogy an appropriate paradigm? Journal of the North American Benthological Society 20(2):266–279.

Gent, R., J. Pitlo, Jr., and T. Boland. 1995. Largemouth bass response to habitat and water quality rehabilitation in a backwater of the upper Mississippi River. North American Journal of Fisheries Management 15(4):784–793.

Goolsby, D. A., W. A. Battaglin, B. T. Aulenbach, and R. P. Hooper. 2000. Nitrogen flux and sources in the Mississippi River Basin. Science of the Total Environment 248(2-3):75–86.

Gurgens, C., D. F. Russell, and L. A. Wilkens. 2000. Electrosensory avoidance of metal obstacles by the paddlefish. Journal of Fish Biology 57(2):277–290.

Gutreuter, S. 2004, Challenging the assumption of habitat limitation: an example from centrarchid fishes over an intermediate spatial scale: River Research and Applications 20:413–425.

Gutreuter, S., A. D. Bartels, K. Irons, and M. B. Sandheinrich. 1999. Evaluation of the flood-pulse concept based on statistical models of growth of selected fishes of the Upper Mississippi River System. Canadian Journal of Fisheries and Aquatic Sciences 56(12):2282–2291.

Heitmeyer, M. E., J. W. Nelson, B. D. J. Batt, and P. J. Caldwell. 1993. Waterfowl conservation and biodiversity. Presented at the 55th Midwest Fish and Wildlife Conference, St. Louis, Missouri. 13 pp.

Ickes, B. S., J. H. Wlosinski, B. C. Knights, and S. J. Zigler. 2001. Fish passage through dams in large temperate floodplain rivers: an annotated bibliography. U.S. Geological Survey, Upper Midwest Environmental Sciences Center, La Crosse, Wisconsin. An LTRM Web-based report available online at http://www.umesc.usgs.gov/LTRM_fish/fish_ passage_biblio.html. (Accessed June 2001.)

Irons, K., B. S. Ickes, S. DeLain, E. Gittinger, C. Kohler, D. Ostendorf, and E. Ratcliff. In review. Non-native fishes of the Upper Mississippi River System. U.S. Geological Survey, Upper Midwest Environmental Sciences Center, La Crosse, Wisconsin.

Irons, K. S., P. T. Raibley, K. D. Blodgett, and R. E. Sparks. 1997. Progress Report: Lake Chautauqua Fish Production Study, 1996. Illinois Natural History Survey, Aquatic Ecology Technical Report 97/13. 59 pp.

Jobling, M. 1995. Environmental biology of fishes. Chapman and Hall, New York. 455 pp.

Johnson, B. L., and C. A. Jennings. 1998. Habitat associations of small fishes around islands in the upper Mississippi River. North American Journal of Fisheries Management 18(2):327–336.

Johnson, B. L., W. B. Richardson, and T. J. Naimo. 1995. Past, present, and future concepts in large river ecology. Bioscience 45(3):134–141.

Junk, W. J. 1999. The flood pulse concept of large rivers: Learning from the tropics. River Ecosystem Concepts 115(3):261–280.

Junk, W. J., P. B. Bayley, and R. Sparks. 1989. The flood pulse concept in river-floodplain systems. Canadian Special Publication of Fisheries and Aquatic Resources 106:110–127.

Knights, B. C., B. L. Johnson, and M. Sandheinrich. 1995. Responses of bluegills and black crappies to dissolved oxygen, temperature, and current in backwater lakes of the Upper Mississippi River during winter. North American Journal of Fisheries Management 15(2):390–399.

Knights, B. C., J. M. Vallazza, S. J. Zigler, and M. R. Dewey. 2002*a*. Habitat and movement of lake sturgeon in the Upper Mississippi River System, USA. Transactions of the American Fisheries Society 131:507–522.

Knights, B. C., J. H. Wlosinski, J. A. Kalas, and S. W. Bailey. 2002*b*. Estimating upstream fish passage opportunities at Ohio River mainstem dams. Draft final report to the U.S. Army Corps of Engineers, Nashville District, Nashville, Tennessee. 125 pp.

Lappalainen, J., and J. Kjellman. 1998. Ecological and life history characteristics of ruffe (*Gymnocephalus cernuus*) in relation to other freshwater fish species. Journal of Great Lakes Research 24(2):228–234.

Laustrup, M. S., and C. D. Lowenberg. 1994. Development of a systemic land cover/land use database for the Upper Mississippi River System derived from Landsat Thematic Mapper satellite data. National Biological Survey, Environmental Management Technical Center, Onalaska, Wisconsin, May 1994. LTRM 94-T001. 103 pp.

Lubinski, K. S., G. Carmody, D. Wilcox, and B. Drazkowski. 1991. Development of water level regulation strategies for fish and wildlife, Upper Mississippi River System. Regulated Rivers: Research & Management 6(2):117–124.

Lyons, J., R. R. Piette, and K. W. Niermeyer. 2001. Development, validation, and application of a fish-based index of biotic integrity for Wisconsin’s large warmwater rivers. Transactions of the American Fisheries Society 130(6):1077–1094.

Matthews, W. J., and H. W. Robison. 1998. Influence of drainage connectivity, drainage area and regional species richness on fishes of the interior highlands in Arkansas. American Midland Naturalist 139(1):1–19.

McKeown, B. A. 1984. Fish migration. Croom Helm, London. 224 pp.

Mitsch, W. J., and J. G. Gosselink. 2000. Wetlands. John Wiley and Sons. New York.

Mobrand, L. E., J. A. Lichatowich, L. C. Lestelle, and T. S. Vogel. 1997. An approach to describing ecosystem performance `through the eyes of salmon.’ Canadian Journal of Fisheries and Aquatic Sciences 54(12):2954–2973.

Moore, N. R. 1972. Improvement of the lower Mississippi River and tributaries, 1931–1972. Mississipppi River Commission, Vicksbury, Mississippi.

Naiman, R. J., and M. G. Turner. 2000. A future perspective on North America’s freshwater ecosystems. Ecological Applications 10(4):958–970.

Nislow, K. 1998. The relationship between habitat and performance of age-0 Atlantic salmon. Ph.D Dissertation. Dissertation Abstracts International Part B: Science and Engineering 58(8):4021.

Oberdorff, T., and R. M. Hughes. 1992. Modification of an index of biotic integrity based on fish assemblages to characterize rivers of the Seine Basin, France. Hydrobiologia 228(2):117–130.

O'Hara, M., B. S. Ickes, E. Gittinger, S. DeLain, T. Dukerschein, M. Pegg, and J. Kalas. In review. Development of a life-history database for Upper Mississippi River fishes. U.S. Geological Survey, Upper Midwest Environmental Sciences Center, La Crosse, Wisconsin.

Petts, G. E. 1989. Perspectives for ecological management of regulated rivers. Pages 3–24 *in* J. A. Gore and G. E. Petts, editors. Alternatives in Regulated River Management. CRC Press, Inc., Boca Raton, Florida,

Power, M. E., and 8 co-authors. 1988. Biotic and abiotic controls in river and stream communities. Journal of the North American Benthological Society 7(4):456–479.

Power, M. E., A. Sun, G. Parker, W. E. Dietrich, and J. T. Wootton. 1995. Hydraulic food-chain models. Bioscience 45(3):159–167.

Pringle, C. 2003. The need for a more predictive understanding of hydrologic connectivity. Aquatic Conservation: Marine and Freshwater Ecosystems 13:467–471.

Raibley, P. T., K. S. Irons, T. M. O'Hara, K. D. Blodgett, and R. Sparks. 1997. Winter habitats used by largemouth bass in the Illinois River, a large river-floodplain ecosystem. North American Journal of Fisheries Management 7(2):401–412.

Rasmussen, J., and 9 co-authors. 1999. Floodplain land management practices of the U.S. Fish and Wildlife Service on Upper Mississippi River System National Wildlife Refuges. Upper Mississippi River Ecosystem Levee Committee Final Report, June 24, 1999. 6 pp.

Regier, H. A. 1974. Application of ecological theory to the conservation of fishery resources. Food and Agriculture Organization of the United Nations, Rome, Italy.

Reid, F. A., J. R. Kelley, Jr., T. S. Taylor, and L. H. Fredrickson. 1989. Upper Mississippi Valley wetlands—refuges and moist-soil impoundments. Pages 181–202 *in* L. M. Smith, R. L. Pederson, and R. M. Kaminski, editors. Habitat management for migrating and wintering waterfowl in North America. Texas Technical University Press, Lubbock, Texas.

Robison, H. W. 1986. The geographic importance of the Mississippi River basin. Pages 267–286 *in* C. H. Hocutt and E. O. Wiley, editors. The geography of North American freshwater fishes. John Wiley and Sons. New York.

Royal Botanical Gardens. 1998. The Cootes Paradise fishway: Carp control techniques at Royal Botanical Gardens, Hamilton, Ontario, Canada. Royal Botanical Gardens Fishway FactSheet. 12 pp. Available online at *http://www.rbg.ca/pdf/FISHWAY.pdf*. (Accessed May 2005.)

Schiemer, F. 2000. Fish as indicators for the assessment of ecological integrity of large rivers. Hydrobiologia 422/423:271–278.

Schiemer, F., H. Keckeis, and E. Kamler. 2002. The early life history stages of riverine fish: ecophysiological and environmental bottlenecks. Comparative Biochemistry and Physiology A: Molecular and Integrative Physiology 133(3):439–449.

Schmutz, S., and M. Jungwirth 1999. Fish as indicators of large river connectivity: The Danube and its tributaries. Large Rivers 115(3):329–348.

Schrank, S. J., and C. S. Guy. 2002. Age, growth, and gonadal characteristics of adult bighead carp, *Hypophthalmichthys nobilis*, in the lower Missouri River. Environmental Biology of Fishes 64(4):443–450.

Scientific Assessment and Strategy Team. 1994. Science for floodplain management into the 21st century. Part 5 of the Report of the Interagency Floodplain Management Review Committee to the Administration Floodplain Management Task Force. Washington, D.C. 272 pp.

Simons, D. B., S. A. Schumm, and M. A. Stevens. 1974. Geomorphology of the Middle Mississippi River. Engineering Research Center, Colorado State University, Fort Collins, Colorado. Completion Contract Report to the U.S. Army Corps of Engineers, Waterways Experiment Station, Vicksburg, Mississippi.

Sparks, R. E. 1992. Risks of altering the hydrologic regime of large rivers. Pages 119–152 *in* J. Cairns, Jr., B. R. Niederlehner, and D. R. Orvos, editors. Predicting ecosystem risk, advances in modern environmental toxicology. Volume XX. Princeton Scientific Publishing Co., New Jersey.

Sparks, R. E. 1995. Need for ecosystem management of large rivers and their floodplains. BioScience 45:168–182.

Sparks, R. E., J. C. Nelson, and Y. Yin. 1998. Naturalization of the flood regime in regulated rivers. Bioscience 48(9):706–720.

Stein, B. A. 2001. A fragile cornucopia assessing the status of US biodiversity. Environment 43:11–22.

Theiling, C. H. 1995. Habitat rehabilitation on the Upper Mississippi River. Regulated Rivers: Research & Management 11(2):227–238.

Theiling, C. H., J. K. Tucker, and F. A. Cronin. 1999. Flooding and fish diversity in a reclaimed river-wetland. Journal of Freshwater Ecology 14(4):469–475.

Tockner, K., D. Pennetzdorfer, N. Reiner, F. Scheimer, and J. V. Ward. 1999*a*. Hydrological connectivity and the exchange of organic matter and nutrients in a dynamic river-floodplain system (Danube, Austria). Freshwater Biology 41(3):521–535.

Tockner, K., F. Schiemer, C. Baumgartner, G. Kum, E. Weigand, I. Zweimueller, and J. V. Ward. 1999*b*. The Danube Restoration Project: Species diversity patterns across connectivity gradients in the floodplain system. Regulated Rivers: Research & Management 15:1–3.

Tockner, K., F. Schiemer, and J. V. Ward. 1998. Conservation by restoration: The management concept for a river-floodplain system on the Danube River in Austria. Aquatic Conservation: Marine and Freshwater Ecosystems 8(1):71–86.

Tockner, K., and J. A. Standford. 2002. Riverine flood plains: present state and future trends. Environmental Conservation 29:308–330.

U.S. Geological Survey. 1999. Ecological status and trends of the Upper Mississippi River System 1998: A report of the Long Term Resource Monitoring Program. U.S. Geological Survey, Upper Midwest Environmental Sciences Center, La Crosse, Wisconsin, April 1999. LTRM 99-T001. 236 pp.

Van den Brick, F. W. B., G. Van der Velde, A. D. Buijse, and A. G. Klink. 1996. Biodiversity in the lower Rhine and Meuse River- floodplains: Its significance for ecological river management. Netherlands Journal of Aquatic Ecology 30(2-3):129–149.

Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell, and C. E. Cushing. 1980. The river continuum concept. Canadian Journal of Fisheries and Aquatic Science 37:130–137.

Ward, J. V. 1989. The four-dimensional nature of lotic ecosystems. Journal of the North American Benthological Society 8(1):2–8.

Ward, J. V., and J. A. Stanford. 1983. The serial discontinuity concept of lotic ecosystems. Pages 29–42 *in* T. D. Fontaine and S. M. Bartell, editors. Dynamics of lotic ecosystems, Ann Arbor Science, Michigan.

Ward, J. V., and K. Tockner. 2001. Biodiversity: towards a unifying theme for river ecology. Freshwater Biology 46(6):807–819.

Ward, J. V., K. Tockner, and F. Scheimer. 1999. Biodiversity of floodplain river ecosystems: ecotones and connectivity. Regulated Rivers: Research & Management 15(1-3):125–139.

Wellborn, G. A., D. K. Skelly, and E. E. Werner. 1996. Mechanisms creating community structure across a freshwater habitat gradient. Annual Review of Ecology and Systematics 27:337–363.

Welcomme, R. L. 1979. Fishery management in large rivers. Food and Agriculture Organization of the United Nations, Rome, Italy. Food and Agriculture Organization Fisheries Technical Paper 194. 60 pp.

Wilcox, D. B. 1993. An aquatic habitat classification system for the Upper Mississippi River System. U.S. Fish and Wildlife Service, Environmental Management Technical Center, Onalaska, Wisconsin. EMTC 93-T003. 9 pp. + Appendix A.

Wilkens, L. A., D. F. Russell, X. Pei, and C. Gurgens. 1997. The paddlefish rostrum functions as an electrosensory antenna in plankton feeding. Proceedings of the Royal Society of London, Series B: Biological Sciences 264(1389):1723–1729.

Winemiller, K. O., and K. A. Rose. 1992. Patterns of life-history diversification in North American fishes: Implications for population regulation. Canadian Journal of Fisheries and Aquatic Sciences 49(10):2196–2218.

Wlosinski, J. H. 1994. The relationship between discharge and water levels on the open-river portion of the Upper Mississippi River. National Biological Survey, Environmental Management Technical Center, Onalaska,Wisconsin. Report to the Scientific Assessment and Strategy Team.

Wlosinski, J. H., and E. R. Olson. 1994. Analysis of water level elevations and discharge on the Lower Missouri River. National Biological Survey, Environmental Management Technical Center, Onalaska, Wisconsin. LTRM 94- T004. 74 pp.

Wlosinski J. H., J. T. Rogala, T. W. Owens, K. L. Dalrymple, D. Busse, C. N. Strauser, and E. Atwood. 2000. Response of vegetation and fish during an experimental drawdown in three pools, Upper Mississippi River. U.S. Geological Survey, Upper Midwest Environmental Sciences Center, La Crosse, Wisconsin. LTRM 2000-T001. 18 pp. + Appendixes A–B.

Wootton, J. T. 1998. Effects of disturbance on species diversity: a multitrophic perspective. American Naturalist 152:803–825.

Wootton, J. T., M. S. Parker, and M. E. Power. 1996. Effects of disturbance on river food webs. Science 273(5281):1558–1561.

Yin, Y., and J. C. Nelson. 1995. Modifications to the Upper Mississippi River and their effects on floodplain forests. National Biological Service, Environmental Management Technical Center, Onalaska, Wisconsin, February 1995. LTRM 95-T003. 17 pp.

Zalewski, M., B. Bis, P. Frankiewicz, M.
Lapinska, and W. Puchalski. 2001. Riparian ecotone as a key factor for stream restoration. International Journal of Ecohydrology & Hydrobiology 1(1–2):245–251.

Zigler, S., M. Dewey, B. Knights, A. Runstrom, and M. Steingraeber. 2003. Movement and habitats of radio-tagged paddlefish in the Upper Mississippi River and tributaries. North American Journal of Fisheries Management
23(1):189–205.