A research framework for aquatic over-wintering issues in the Upper Mississippi River Basin

Outline of research program

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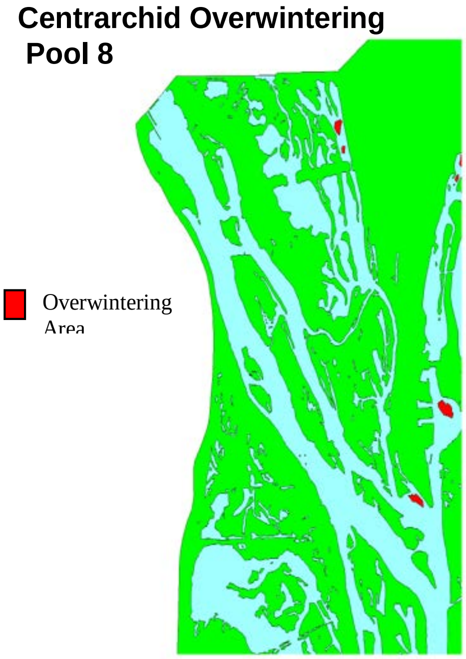

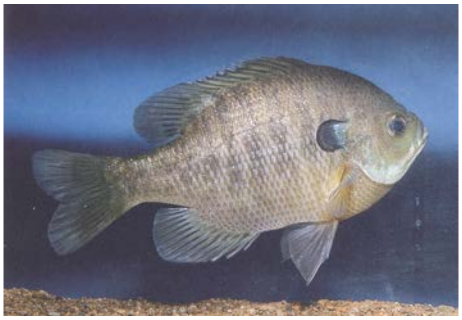

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1. Executive summary

This document details a framework for research into an over-arching hypothesis of winter habitat limitation on the production of limnophilic 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 Program (LTRMP).

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 Environmental Management Program (EMP), 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**. Initially, study subject focus will be on an assemblage of limnophilic fish species which are widely perceived to be limited by the quantity and quality of over-wintering habitats in the UMRS. Limnophils are those fish species common to lakes and backwaters, typified by their association with aquatic vegetation, low current velocities, poor swimming performance, and opportunistic feeding preferences. Many limnophilic species play key roles in the ecology of the UMRS, are highly valued by society for consumptive and non-consumptive uses, and thus are the focus of many habitat rehabilitation efforts within the basin.

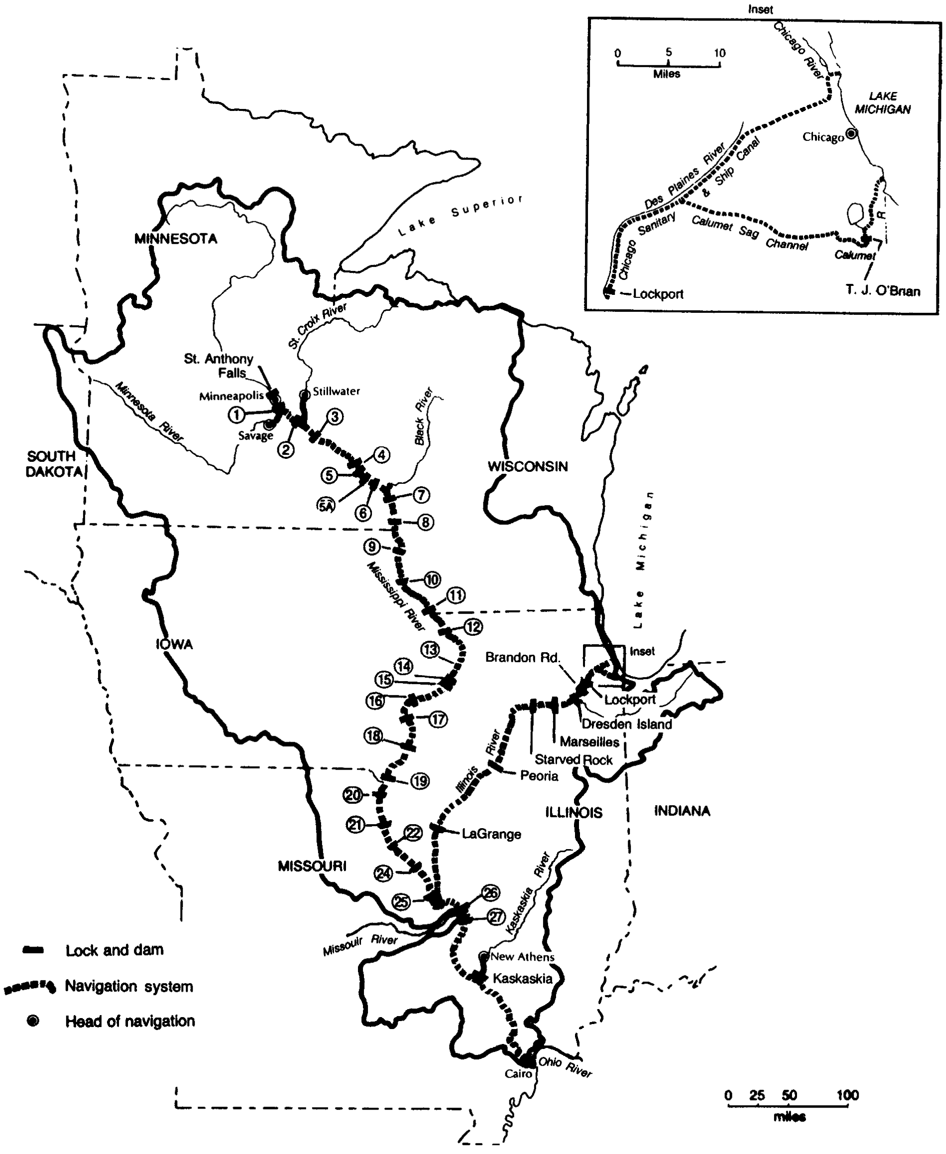

Figure 1. The Upper Mississippi River System.

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 has fundamentally altered river morphology and key fluvial processes that maintained diverse river environments in the 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 a cause 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).

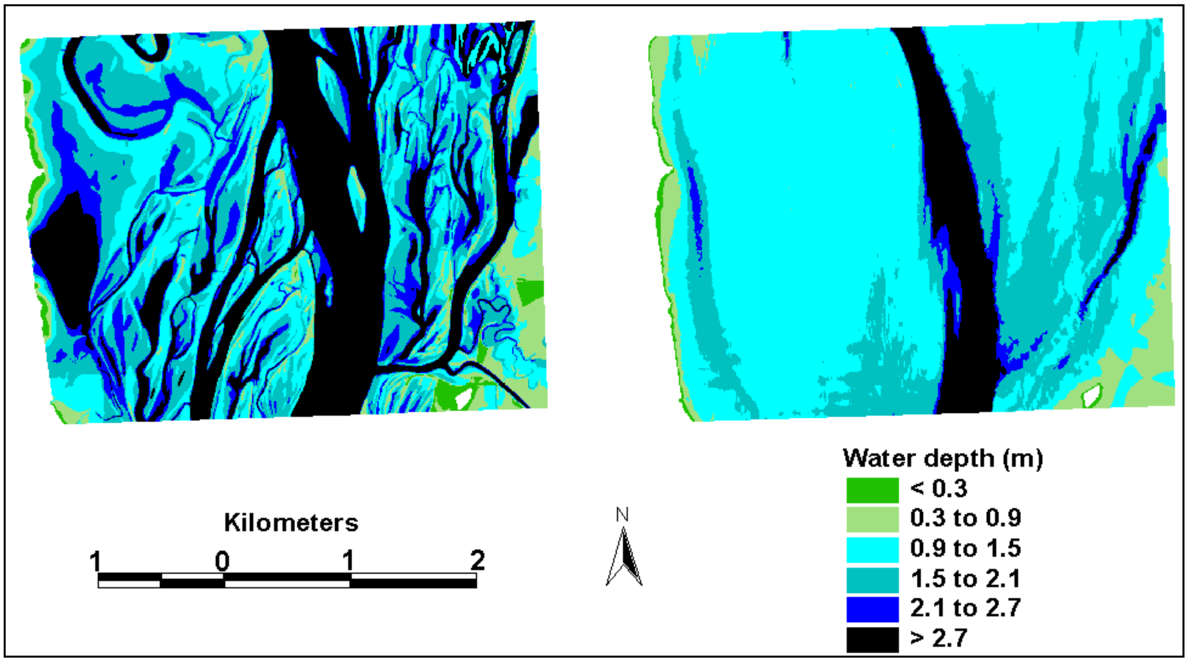

Figure 2. Changes in bathymetry of a portion of the impounded area in Pool 13, Upper Mississippi River, from 1940 (left) to 1990 (right).

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 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 centrarchid 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 Long Term Resources Monitoring Program [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 pools (Figure 3). Additionally, many HREPs are designed to improve over-winter conditions in backwaters, thus providing opportunities to test a hypothesis of over-winter habitat limitation.

Attention now shifts to which biotic responses (e.g., species) would be expected to demonstrate the effects of winter habitat limitation. Ideally, biotic responses should have life cycles closely coupled to backwater environments, be relatively simple to measure, and should respond to differences in (observational), or changes to (experimental), habitat.

The first criteria is met by considering backwater obligate fishes such as Centrarchids, Ictalurids, Clupeids, and Esocids (Appendix A). These limnophilic fishes are common to lakes and backwaters, and are typified by their association with aquatic vegetation, low current velocities, poor swimming performance, and opportunistic feeding preferences (West Consultants, Inc. 2000). All key life stages of these species are completed in backwaters. Methods for sampling these fishes are well-developed and responses are simple to measure. Many limnophilic species play key roles in the ecology of the UMRS and are highly valued for recreational uses. Accordingly, much of the public perceives river health based on the abundance and availability of these species. Many limnophilic species are targets of backwater rehabilitation efforts, and are thus expected to respond to changes in over-winter habitat. Also, many additional species that require backwater environments to fulfill parts of their life cycles (Kirby and Ickes *in press*; Ickes et al. 2005) may benefit from these rehabilitation efforts.

This proposal suggests a framework to explore a hypothesis of over-winter habitat limitation on production of limnolphilic fishes. 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.

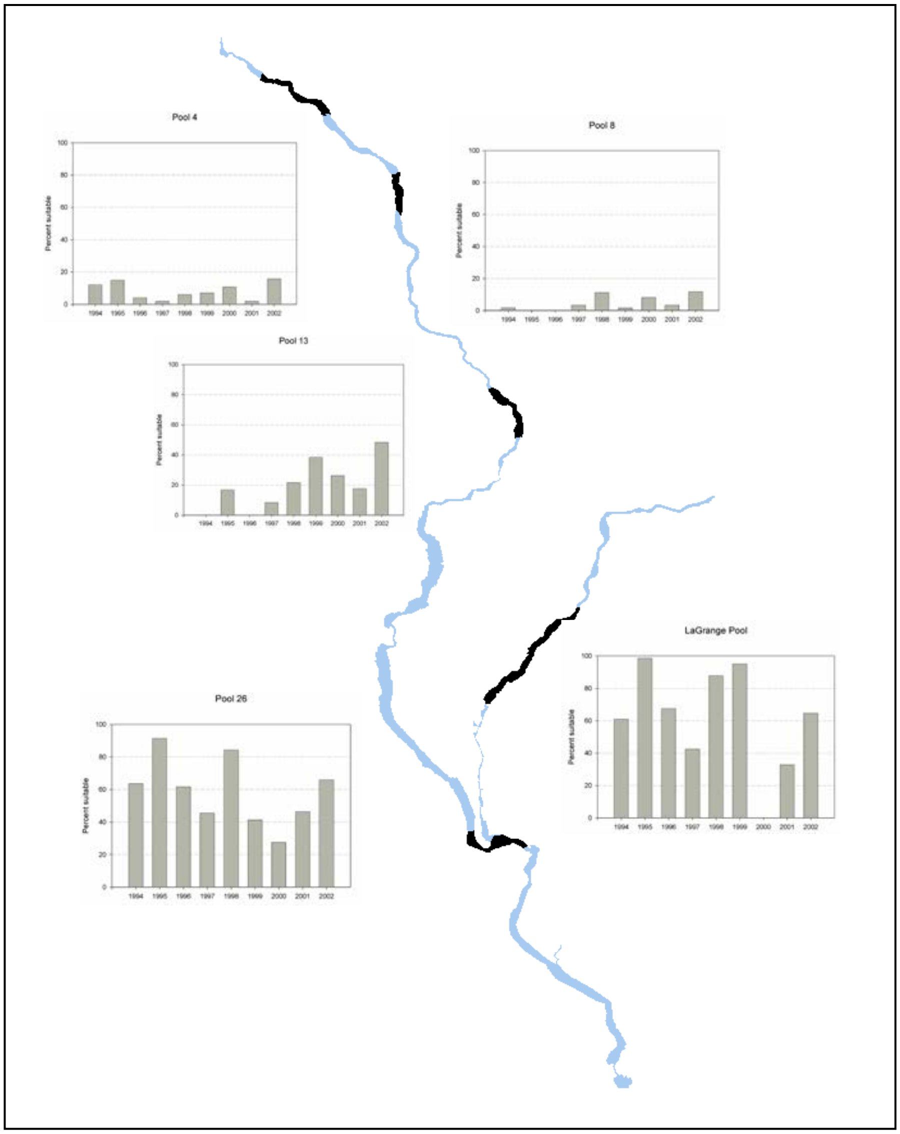

Figure 3. Percent of backwater area presumed suitable for limnophilic fishes during winter periods from 1994 to 2002. Suitability was assessed based on published physiologic tolerance thresholds during winter for several Centrarchidae species (Sheehan et al. 1990) and the spatial distribution of suitable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

1.3 Responses to measure and potential confounding factors

The most appropriate ecological unit for gauging limnophilic fish responses to habitat limitations is the population. Thus, production respones 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 limnophilic 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 limnophil 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 limnophils 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 stastistically 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 LTRMP 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 LTRMP fish counts and length-weight data to estimate biomass. LTRMP 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 factor. 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 into an 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 experiements. For example, we 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, we 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 statisticials 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 limnophilic 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 experiments al 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 LTRMP 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. We 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 limnophilic 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 limnophilic fishes in the UMRS 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 limnophilic 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 the conceptual model. 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 are gaining 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 conaminants, 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 limnophilic 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 usefullness 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 limnophils 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 dynamics, 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 limnophilic 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 limnophilic 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 limnophils – 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 infeasible to mark and recapture enough individuals to provide reliable estimates of such population parameters, at least at spatial scales approaching a pool. 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 limnophils 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 limnophils 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 limnophilic 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 limnophils 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 limnophils 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 limnophilic 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 pools)?
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 limnophilic 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 B 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. LTRMP 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 limnophilic production is expected in UMRS pools?
Elaboration: Establish a (crude?) theoretical benchmark for limnophilic production potential in UMRS pools.
Approach: Numerical models (Section 2.3.2).
Methodology: Application of existing or modified morphoedaphic and yield models (see Appendix B). Morphoedaphic features can be derived from existing GIS coverages and LTRMP data sources.

Potential confounding Factors: Model biases and inherent assumptions (e.g., pools 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 pools 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 limnophilic 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 pools 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 limnophilic fish abundance/biomass correlated with inter-annual differences in winter habitat suitability?
Elaboration: Covariation in summer abundance/biomass, as measured by the LTRMP, 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 limnophilic 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 the study subjects 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 limnophilic fish populations must address each of these mortality components because nearly all limnophils 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 limnophilic fish populations, does it vary among UMRS pools, 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 LTRMP 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 pool 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 limnophilic 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 LTRMP 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 pool 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 limnophilic 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 limnophils 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 limnophilic 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 limnophilic 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.

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Appendices

Appendix A. Characteristic limnophilic fishes in the UMRS and key life history attributes.

Phylogeny				**Reproduction**			**Feeding**	
Order	**Family**	**Species**	**Common name**	**Care**	**Dispersal**	**Substrate**	**Trophic level**	**Foraging mode**
Clupeiformes	Clupeidae	*Dorosoma cepedainum*	Gizzard shad	Non-guarder	Open substratum spawner	Lithopelagophil	Herbivore	Filter feeder
		Dorosoma petenense	Threadfin shad	Non-guarder	Open substratum spawner	Phytophil	Planktivore	Filter feeder
Siluriformes	Ictaluridae	*Ameiurus melas*	Black bullhead	Guarder	Nest spawner	Speleophil	Invertivore/carnivore	Benthic/whole body
		Ameiurus natalis	Yellow bullhead	Guarder	Nest spawner	Speleophil	Invertivore/carnivore	Benthic/whole body
		Noturus gyrinus	Tadpole madtom	Guarder	Nest spawner	Speleophil	Invertivore/planktivore	Benthic/particulate
Salmoniformes	Esocidae	*Esox lucius*	Northern pike	Non-guarder	Open substratum spawner	Phytophil	Carnivore	Whole body
Perciformes	Centrarchidae	*Lepomis cyanellus*	Green sunfish	Guarder	Nest spawner	Polyphil	Invertivore/carnivore	Drift/Whole body
		Lepomis gulosus	Warmouth	Guarder	Nest spawner	Lithophil	Invertivore/carnivore	Drift/Whole body
		Lepomis humilis	Orangespotted sunfish	Guarder	Nest spawner	Lithophil	Invertivore	Drift
		Lepomis macrochirus	Bluegill	Guarder	Nest spawner	Polyphil	Invertivore	Drift
		Micropterus salmoides	Largemouth bass	Guarder	Nest spawner	Polyphil	Invertivore/carnivore	Whole body
		Pomoxis annularis	White crappie	Guarder	Nest spawner	Phytophil	Invertivore/carnivore	Whole body
		Pomoxis nigromaculatus	Black crappie	Guarder	Nest spawner	Phytophil	Invertivore/carnivore	Whole body

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