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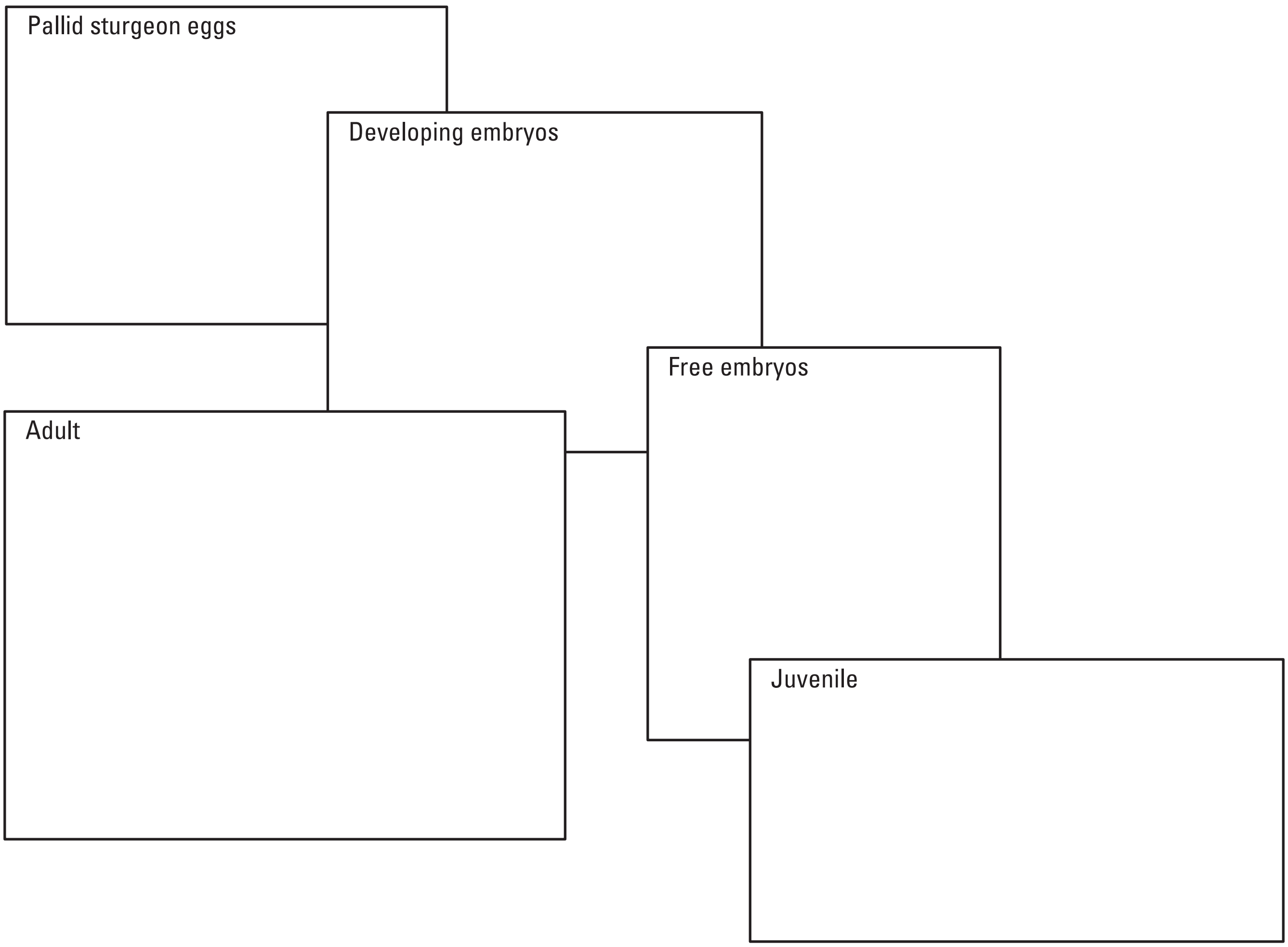
Missouri River *Scaphirhynchus albus* (Pallid Sturgeon) Effects Analysis—Integrative Report 2016

Scientific Investigations Report 2016–5064

U.S. Department of the Interior
U.S. Geological Survey

Cover photograph index:



Background image: shaded relief map of the Missouri River drainage basin, U.S. Geological Survey.

Photographs by U.S. Geological Survey personnel.

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U.S. Department of the Interior
U.S. Geological Survey

U.S. Department of the Interior
SALLY JEWELL, Secretary

U.S. Geological Survey
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U.S. Geological Survey, Reston, Virginia: 2016

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Conversion Factors

U.S. customary units to International System of Units

Multiply	By	To obtain
	Length	
foot (ft)	0.3048	meter (m)
mile (mi)	1.609	kilometer (km)
	Area	
acre	4,047	square meter (m^2)
acre	0.4047	hectare (ha)
acre	0.4047	square hectometer (hm^2)
acre	0.004047	square kilometer (km^2)
	Flow rate	
foot per second (ft/s)	0.3048	meter per second (m/s)
cubic foot per second (ft^3/s)	0.02832	cubic meter per second (m^3/s)
acre per mile (acre/mi)	2,514.6	square meter per kilometer (m^2/km)
mile per hour (mi/h)	1.609	kilometer per hour (km/h)
	Mass	
ounce, avoirdupois (oz)	28.35	gram (g)
pound, avoirdupois (lb)	0.4536	kilogram (kg)
ton, short (2,000 lb)	0.9072	metric ton (t)
ton, long (2,240 lb)	1.016	metric ton (t)

U.S. customary units to International System of Units

Multiply	By	To obtain
	Length	
millimeter (mm)	0.03937	inch (in.)
meter (m)	3.281	foot (ft)
kilometer (km)	0.6214	mile (mi)
kilometer (km)	0.5400	mile, nautical (nmi)
meter (m)	1.094	yard (yd)
	Area	
square kilometer (km^2)	247.1	acre
square kilometer (km^2)	0.3861	square mile (mi^2)
	Volume	
cubic kilometer (km^3)	0.2399	cubic mile (mi^3)
	Flow rate	
meter per second (m/s)	3.281	foot per second (ft/s)
metric ton per year (t/yr)	1.102	ton, short [2,000 lb] per year (ton/yr)
	Mass	
kilogram (kg)	2.205	pound avoirdupois (lb)

Temperature in degrees Celsius (°C) may be converted to degrees Fahrenheit (°F) as follows:

$$°F = (1.8 \times °C) + 32.$$

The standard measure of distance and location along the Missouri River is given in river miles (RM) upstream from the Mississippi River confluence. River miles are the standard units used by managers, engineers, and stakeholders.

Datums

Vertical coordinate information is referenced to the North American Vertical Datum of 1988 (NAVD 88).

Horizontal coordinate information is referenced to the World Geodetic System of 1984 (WGS 84).

Abbreviations

1D	one dimensional
2D	two dimensional
AM	adaptive management
CEM	conceptual ecological model
CPUE	catch per unit effort
dph	days post-hatch
DRM	Daily Routing Model
EA	effects analysis
HAMP	Habitat Assessment and Monitoring Program
HEC–EFM	Hydrologic Engineering Center Ecosystems Functions Model
HEC–RAS	Hydrologic Engineering Center River Analysis System
HEC–ResSim	Hydrologic Engineering Center Reservoir Simulation Model
IRC	interception-rearing complex
ISAP	Independent Science Advisory Panel
MRRMP	Missouri River Recovery Management Plan
MRRP	Missouri River Recovery Program
MU	management unit
PSPAP	Pallid Sturgeon Population Assessment Project
SWH	shallow-water habitat
USACE	U.S. Army Corps of Engineers
USFWS	U.S. Fish and Wildlife Service
USGS	U.S. Geological Survey
WRDA 2007	Water Resources Development Act of 2007
YOY	young-of-year

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The authors gratefully acknowledge engaged and useful technical reviews by the Missouri River Recovery Implementation Committee's Independent Science Advisory Panel (Dr. Steve Bartell, Dr. Martin Doyle, Dr. Adrian Farmer, Dr. Christopher Guy, Dr. Gary Lamberti, Dr. Dennis Murphy, and Dr. Robb Turner), Dr. Brian Graeb (South Dakota State University, Dr. Martin Hamel (University of Nebraska), Dave Fuller (Montana Fish, Wildlife, and Parks), Neil Bass (U.S. Army Corps of Engineers), and Dave Herzog (Missouri Department of Conservation). We are especially indebted to Dr. Edward Heist, Southern Illinois University-Carbondale, for help with writing sections on genetics and effective population size. We gratefully acknowledge the Missouri River Relief and the Missouri Resources Assessment Partnership for access to the trash dataset used in appendix 2.

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Missouri River *Scaphirhynchus albus* (Pallid Sturgeon) Effects Analysis—Integrative Report 2016

By Robert B. Jacobson,[1] Mandy L. Annis,[1] Michael E. Colvin,[2] Daniel A. James,[3] Timothy L. Welker,[4] and Michael J. Parsley[5]

Abstract

The Missouri River Pallid Sturgeon Effects Analysis was designed to carry out three components of an assessment of how Missouri River management has affected, and will affect, population dynamics of endangered *Scaphirhynchus albus (*pallid sturgeon): (1) collection of reliable scientific information, (2) critical assessment and synthesis of available data and analyses, and (3) analysis of the effects of actions on listed species and their habitats. This report is a synthesis of the three components emphasizing development of lines of evidence relating potential future management actions to pallid sturgeon population dynamics. We address 21 working management hypotheses that emerged from an expert opinion-based filtering process.

The ability to quantify linkages from abiotic changes to pallid sturgeon population dynamics is compromised by fundamental information gaps. Although a substantial foundation of pallid sturgeon science has been developed during the past 20 years, our efforts attempt to push beyond that understanding to provide predictions of how future management actions may affect pallid sturgeon responses. For some of the 21 hypotheses, lines of evidence are limited to theoretical deduction, inference from sparse empirical datasets, or expert opinion. Useful simulation models have been developed to predict the effects of management actions on survival of drifting pallid sturgeon free embryos in the Yellowstone and Upper Missouri River complex (hereafter referred to as the “upper river”), and to assess the effects of flow and channel reconfigurations on habitat availability in the Lower Missouri River, tributaries, and Mississippi River downstream of Gavins Point Dam (hereafter referred to as the “lower river”). A population model also has been developed that can be used to assess sensitivity of the population to survival of specific life stages, assess some hypotheses related to stocking decisions, and explore a limited number of management scenarios.

Consideration of lines of evidence for each of the 21 hypotheses includes a discussion of how the degree of uncertainty and risk associated with each hypothesis may guide science and implementation strategies. Implementation strategies include full implementation in the field, limited implementations as field-scale experiments, or (in the case of greatest uncertainty) implementation as learning actions, including research and opportunistic experiments or field-based gradient studies. Given the substantive uncertainties associated with pallid sturgeon population dynamics and the need to continually assimilate and assess new information, we proposed that an Effects Analysis-like process should be considered an integral part of ongoing Missouri River adaptive management.

Introduction

The need for a broadly defined effects analysis was recognized by the Missouri River Independent Science Advisory Panel (ISAP) (Doyle and others, 2011). The Missouri River ISAP wrote (Doyle and others, 2011, p. 4), “The development of an adaptive management plan should be preceded by and based upon an effects analysis that incorporates new knowledge that has accrued since the 2003 Biological Opinion,” referring to the U.S. Fish and Wildlife Service’s (USFWS) amended biological opinion for operation of the Missouri River main stem reservoir system, maintenance of the Missouri River Bank Stabilization and Navigation Project, and operation of the Kansas River reservoir system (U.S. Fish and Wildlife Service, 2003). The concept of an effects analysis (EA) is explained by Murphy and Weiland (2011) as a systematic evaluation of how Federal agency actions may harm a listed species. The three essential components of an EA are the following:

- Collection of reliable scientific information,
- Critical assessment and synthesis of available data and analyses, and

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[2]Oregon State University and Mississippi State University.

[3]U.S. Fish and Wildlife Service.

[4]U.S. Army Corps of Engineers.

[5]U.S. Geological Survey (retired).

- Analysis of the effects of actions on listed species and their habitats.

The last EA component ideally consists of predictive, quantitative models that can be used to forecast expected ecological costs and benefits of a management action and evaluate tradeoffs with socioeconomic costs and benefits. The output of an EA also should provide a useful framework for ongoing assimilation of data from hypothesis-driven monitoring and research. If EA models are sufficiently quantitative, the EA can be used to evaluate alternative management actions in structured decision making (Murphy and Weiland, 2014). In the ideal situation, an EA includes quantitative population dynamics or population viability models that can be used to forecast population effects of management actions (Murphy and Weiland, 2011, 2014).

The motivation for an EA arose not only from the recommendations of the Missouri River ISAP but also from the information needs of the U.S. Army Corps of Engineers (USACE) Missouri River Recovery Management Plan (MRRMP), which evolved at the same time. The MRRMP is a multiyear structured decision process intended to assess past performance of the Missouri River Recovery Program (MRRP) and evaluate alternatives for future implementation (U.S. Army Corps of Engineers, 2014). Scientific analyses and models completed by the EA are expected to help frame design and modeling of alternatives for the MRRMP.

The Missouri River EA began in fall 2013 in collaboration with the MRRMP; the EA consists of three interactive efforts:

- *Hydrology, Hydraulics, and Geomorphology Team.*—Dr. Craig Fischenich, USACE, Lead.

- *Pallid Sturgeon Team.*—Dr. Robert Jacobson, U.S. Geological Survey (USGS), Lead.

- *Interior Least Terns and Piping Plovers Team.*—Dr. Kate Buenau, Pacific Northwest National Laboratories, Lead.

The three interactive teams have worked together closely in developing models linking management actions to habitat and species responses. The efforts reported here are for the *Scaphirhynchus albus* (pallid sturgeon) analysis.

Foundational information for this report is documented in three precursor USGS open-file reports (fig. 1):

1. *Jacobson, Annis, and others (2015).*—This report compiles and provides an assessment of available information and modeling resources that can be used to understand historical and future changes of pallid sturgeon populations. This report focuses on cataloging information available for evaluating past, present, and future stressor-response relations in pallid sturgeon population dynamics.

2. *Jacobson, Parsley, and others (2015).*—This report describes conceptual ecological models (CEMs) intended to document and illustrate driver-stressor-response ecological relations for Missouri River pallid sturgeon. The CEMs were collaboratively developed through a workshop process that began shortly before the EA began in summer 2013. The EA report refined, documented, and organized the CEMs.

3. *Jacobson and others (2016).*—This reports the process of developing a hierarchy of hypotheses to depict relations in the CEMs. The process of hypothesis formulation and filtering was achieved through a series of expert-opinion surveys, starting with hundreds of “global” hypotheses emanating from the CEMs and ending with 21 working management hypotheses.

The present report integrates the previous three to present a lines-of-evidence analysis of the 21 hypotheses. The analysis includes best-available combinations of qualitative and quantitative models, theoretical and empirical data, and expert opinion. The analysis also includes discussion of how the EA fits within the evolving adaptive management (AM) structure of the Missouri River.

Scope and Objectives

The Missouri River Pallid Sturgeon EA is structured to provide information to address the fundamental species objective developed by the USFWS: “Avoid jeopardizing the continued existence of the pallid sturgeon from U.S. Army Corps of Engineers actions on the Missouri River.” (U.S. Fish and Wildlife Service, written commun., September 12, 2013 [Draft Species Objectives, p. 1]). The USFWS notes that this objective is consistent with species recovery goals (U.S. Fish and Wildlife Service, 2014) but specific to Missouri River management actions. The fundamental species objective is accompanied by subobjectives that are measurable and relevant:

- *Subobjective 1.*—Increase pallid sturgeon recruitment to age 1.

- *Subobjective 2.*—Maintain or increase numbers of pallid sturgeon as an interim measure until sufficient and sustained natural recruitment happens.

The emphasis on recruitment reflects the fact that wild-spawned young-of-year (YOY) or juvenile pallid sturgeon have not been captured in the Upper Missouri River (Missouri River upstream from the headwaters of Lake Sakakawea) and have been captured only rarely in the Lower Missouri River (Missouri River downstream from Gavins Point Dam) (fig. 2). Until 2015, there had been no documented captures of genetically identified, wild-spawned pallid sturgeon free embryos, larvae, or YOY in the lower river (U.S. Fish and Wildlife Service, 2014). Within the last few years, however, as genetic identifications to discriminate *Scaphirhynchus platorynchus* (shovelnose sturgeon) from pallid sturgeon and wild-spawned from hatchery-spawned pallid sturgeon have become more reliable, analyses have confirmed captures of a small number of wild-spawned free-embryo and larval pallid sturgeon during intensive directed sampling (DeLonay, Chojnacki, Jacobson, Braaten, and others, 2016; Dr. Edward Heist, written commun., 2015). In addition, small numbers of probable wild juvenile pallid sturgeon have been collected in standard monitoring efforts (Kirk Steffensen, Nebraska Game and Parks Commission, written commun., 2016). These catches indicate that limited recruitment is happening in the Lower Missouri River, but the number of pallid sturgeon is not considered sufficient to maintain the population (U.S. Fish and Wildlife Service, 2014).

Geographic Scope

The geographic scope of the EA is the Upper Missouri River main stem from Fort Peck Dam to the headwaters of Lake Sakakawea, the Yellowstone River upstream from the confluence with the Upper Missouri River for an unspecified distance, the Lower Missouri River main stem from Gavins Point Dam to the confluence with the Mississippi River at St. Louis, an unspecified distance downstream in the Mississippi River, and various tributaries to these river segments that might be occupied by pallid sturgeon (fig. 2). The distances on the Yellowstone and Mississippi Rivers remain unspecified at this time because of uncertainties in the geographic ranges occupied by subpopulations. Emerging data from microchemistry analyses indicate that age-0 *Scaphirhynchus* can disperse from the Missouri River to the Mississippi River, but it remains unclear how many immigrate to the Mississippi River and how far they disperse. The geographic scope is constrained in part by the decision-making authority of the USACE and in part by the present (2016) understanding of the geographic distribution of pallid sturgeon. The reservoirs and inter-reservoir reaches (from Lake Sakakawea to Lewis and Clark Lake) are excluded from the analysis based on the assumption that these habitats are unlikely to support reproductive populations of pallid sturgeon; this assumption may be relaxed if future information contradicts it.

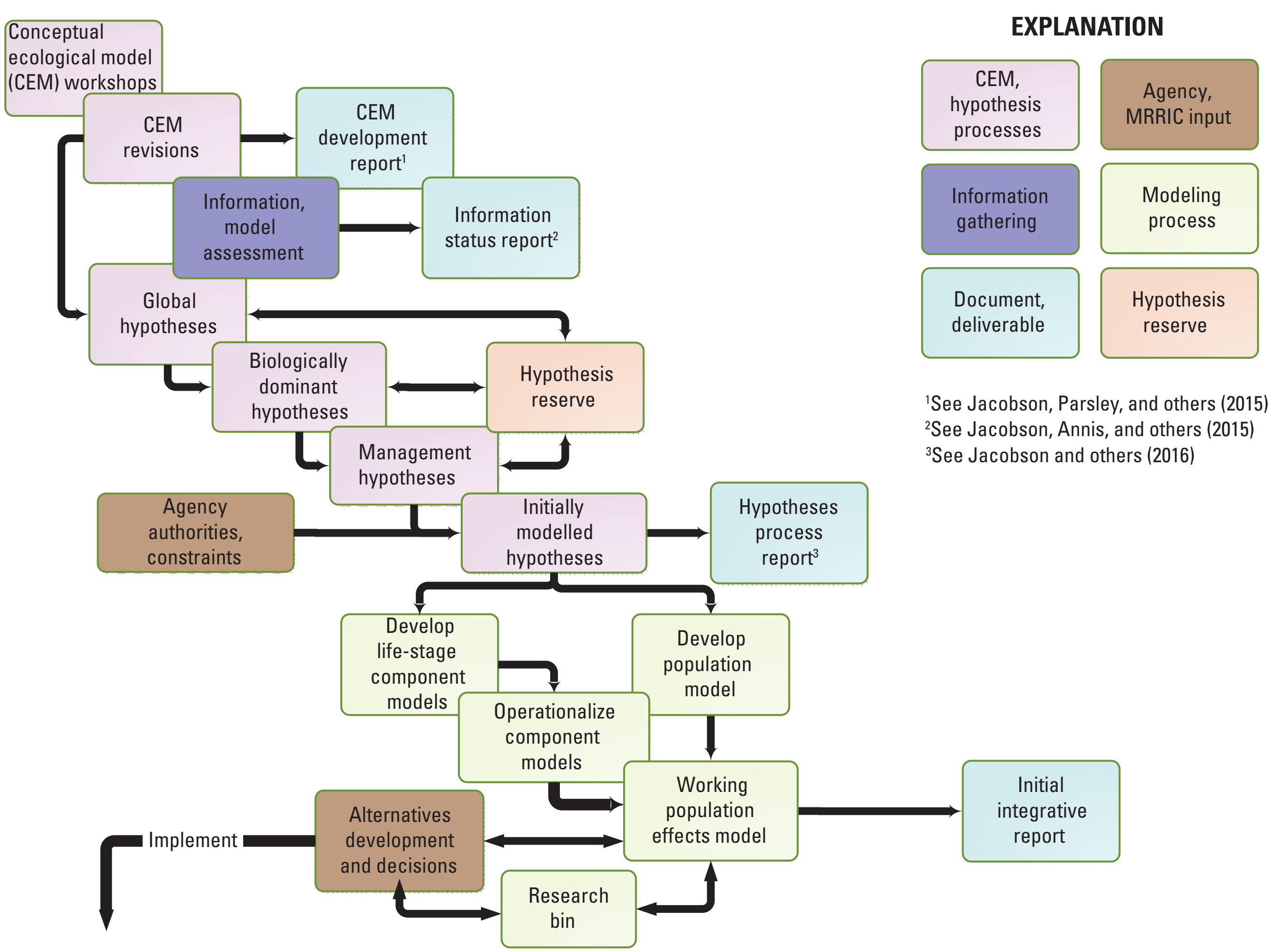


Figure 1. Sequence of tasks and timeline in phase 1 of the Missouri River Pallid Sturgeon Effects Analysis.

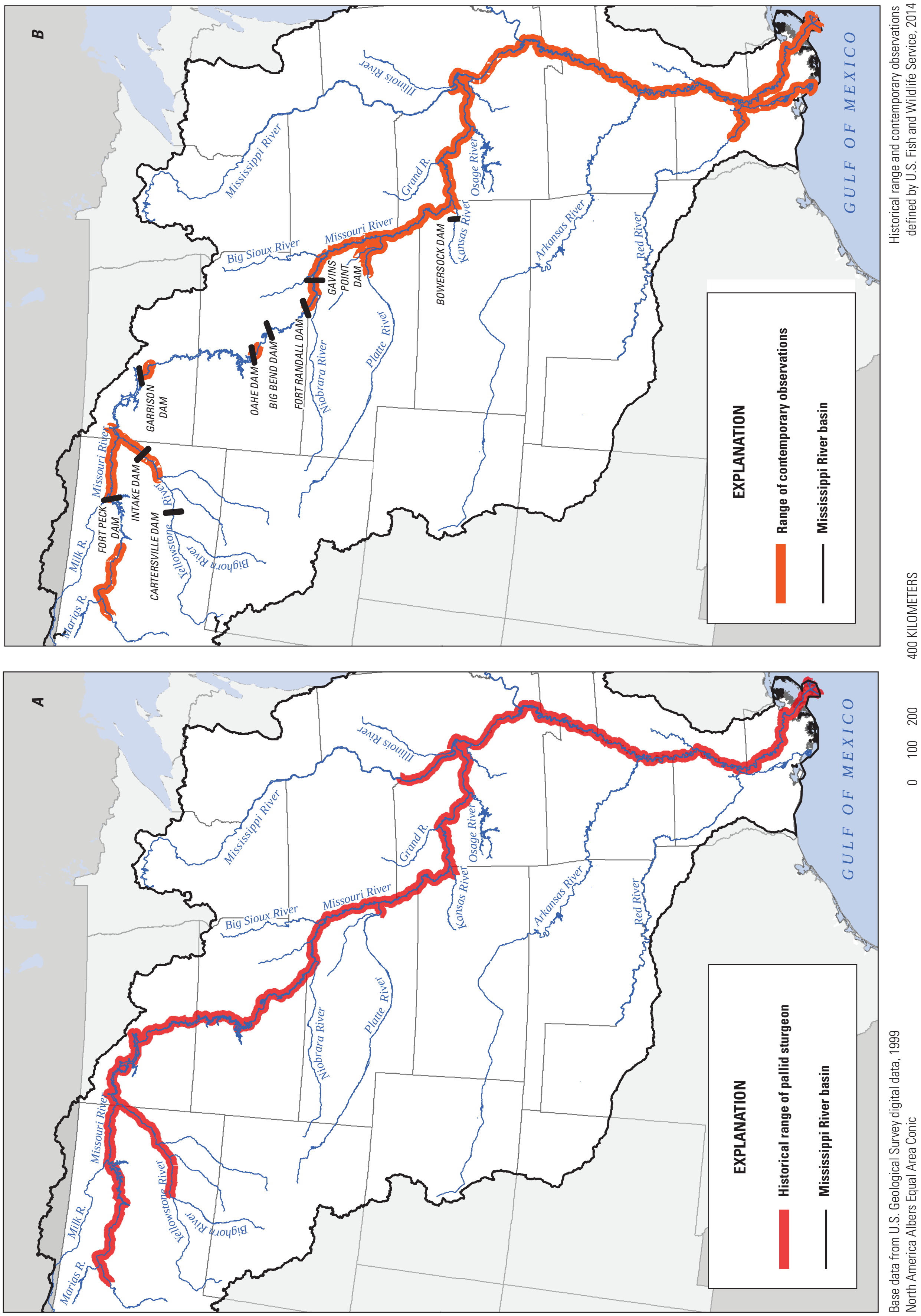


Figure 2. Range maps and management units for pallid sturgeon. *A*, Pre-dam, historically documented range of pallid sturgeon. *B*, Post-dams documented range of pallid sturgeon. *C*, Management units for the pallid sturgeon recovery plan. *D*, Missouri River and Mississippi River basins.

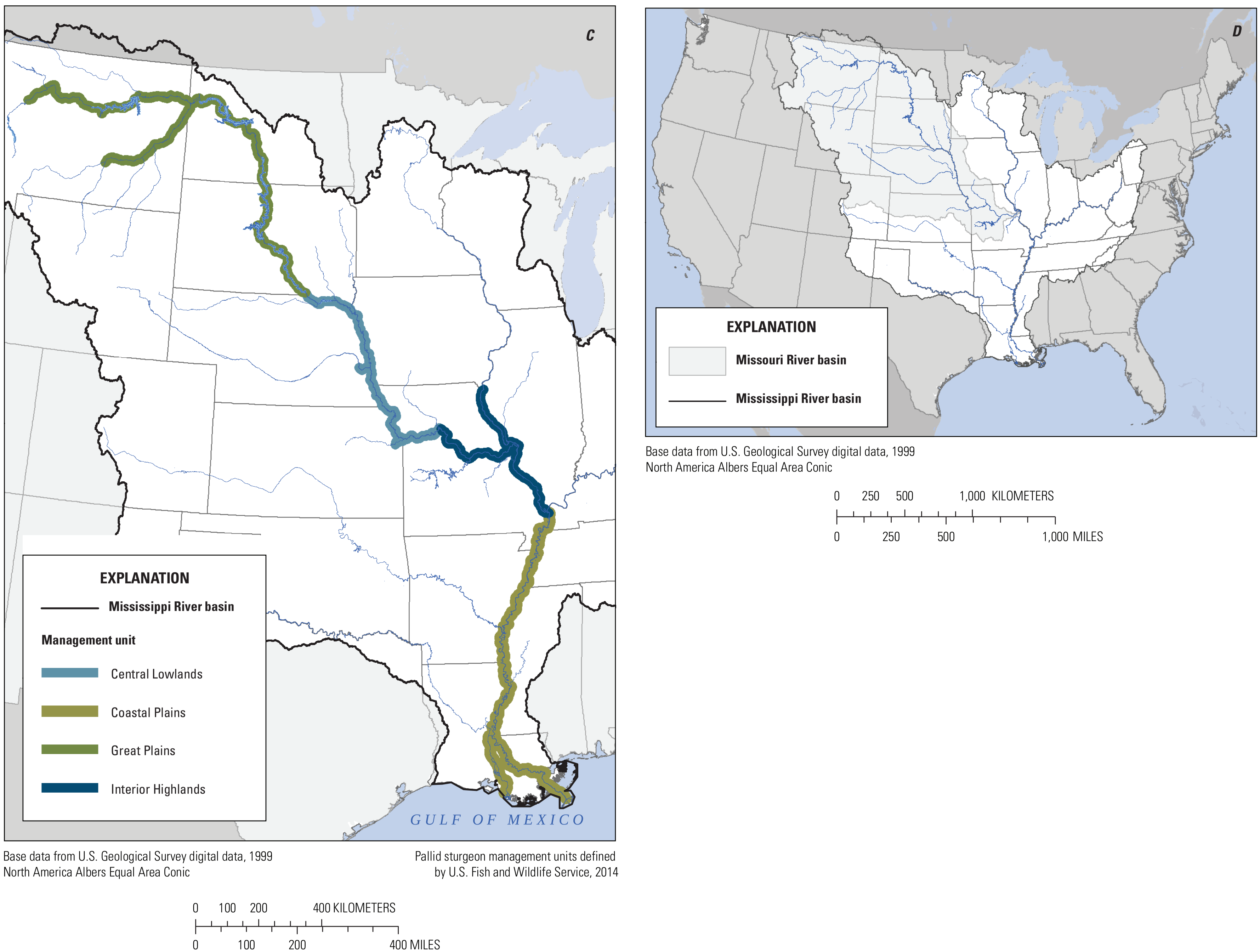


Figure 2. Range maps and management units for pallid sturgeon. *A*, Pre-dam, historically documented range of pallid sturgeon. *B*, Post-dams documented range of pallid sturgeon. *C*, Management units for the pallid sturgeon recovery plan. *D*, Missouri River and Mississippi River basins.—Continued

The purpose of this report is to document lines of evidence for the 21 working management hypotheses (table 1) developed through the EA process. The intended audience for the report consists of scientists and technical agency personnel who will be involved in developing and implementing AM of pallid sturgeon in the Missouri River (fig. 2). The intent is to develop rigorous, quantitative analyses, but the ability to quantify driver-stressor-response relations in pallid sturgeon is compromised by fundamental information gaps. As developed in more detail in this report, we provide useful models of the effects of management actions on survival of drifting free embryos in the upper river, and we can provide useful models of the effects of flow and channel reconfigurations on habitat availability in the lower river; however, the connections between habitat availability and survival can only be inferred. This report presents a population model that can be used to assess sensitivity of life stages, assess some hypotheses related to stocking decisions, and explore a limited number of management scenarios; however, information gaps prevent linkage of flow and channel reconfiguration actions directly to population responses. Some hypotheses are so information poor that lines of evidence are limited to theoretical deduction, inference from sparse empirical datasets, or expert opinion.

We emphasize development of three types of models as critical elements in planning, decision making, and AM of pallid sturgeon in the Missouri River (fig. 2). The first is a collaborative population dynamics model. The reference to collaboration denotes that we intend the model to be further developed, implemented, and maintained through a collaboration of pallid sturgeon scientists representing diverse institutions and agencies. Presently, this model is a work in progress with some limited forecasting ability, although the validity of forecasted dynamics is uncertain. In the future, the model may provide a general population viability framework to assess management actions, as envisioned in publications on EAs (Murphy and Weiland, 2011, 2014). Presently, it is applicable to understanding effects of stocking on population dynamics in the upper and lower river and exploring information needs through sensitivity analyses.

This report also discusses development of advection/dispersion models, as developed by Fischenich and others (2014) as part of the EA process, because of the importance of these models in assessment of drift and dispersal of free embryos. The advection/dispersion modeling framework allows for consideration of transport and fate of free embryos under the assumption that they act as passive particles. The models provide insights into management options on the Yellowstone and Upper Missouri Rivers (fig. 2) and the potential extent of interaction between the Lower Missouri and Mississippi River subpopulations.

Finally, this report also emphasizes development of two-dimensional (2D) hydrodynamic models for habitat assessments on the Lower Missouri River (fig. 2). The hydrodynamic models allow for integrative assessment of the effects of flow regime[6] and channel reconfigurations[7] on types and distributions of physical habitat units. In collaboration with the USACE (Fischenich and others, 2014), four models were developed on representative reaches of the Lower Missouri River; however, utility of the models depends to a large extent on the biological validity of functional habitat definitions. We developed definitions of functional habitat units from theoretical and empirical information on pallid sturgeon habitat selection and preference.

The quantitative model framework developed through the EA is intended to form part of the framework for future AM of species in the Missouri River (fig. 2). Although drafting of the AM plan is not complete as of the date of this publication, we anticipate that the plan will include an ongoing AM process whereby new learning from monitoring, assessment, and research efforts will be assimilated, assessed, and used to decrease uncertainties and improve management actions with time.

Background of the Missouri River and Pallid Sturgeon

The Missouri River (fig. 2) has been substantially altered since European exploration and settlement. The Missouri River was once a dynamic and diverse large-river ecosystem, but management for socioeconomic benefits has greatly altered its natural habitats and the fish and wildlife that rely upon them. *Scaphirhynchus albus* (Pallid sturgeon) is among the native species that have experienced an associated decline in population coinciding with substantial habitat alteration of the Missouri River for purposes of flood control, navigation, hydropower, water supply, water quality, irrigation, recreation, and fish and wildlife. Additional suggested contributors to the population decline have been intensive commercial fishing and exposure to contaminants from industrial, agricultural, and municipal sources. Adaptive management of habitat rehabilitation and hatchery augmentation is currently (2016) being implemented to prevent jeopardy of the pallid sturgeon[8].

[6] Flow regime refers to the time series of discharge in the river, occurring naturally or affected by reservoir releases. Flow regime is usually characterized in terms of magnitude, duration, frequency, rate of change, and timing of flows.

[7] Channel reconfiguration refers to the general process of re-engineering the channel and adjacent flood plain lands to provide greater habitat diversity and availability. It may include widening, alteration of channel-training structures (wing dikes, revetments), or construction of side-channel chutes or backwaters.

[8] We use the term “rehabilitation” to denote the process of restoring some of the ecological functions of the river-corridor ecosystem but not necessarily to a preconceived historical endpoint. This use of the term is similar to naturalization as defined by Rhoads and others (1999) in which the design objectives for rehabilitation are set by knowledge of natural system dynamics but defined by stakeholder wishes to balance ecological and socioeconomic returns.

Table 1. List of 21 working management hypotheses developed through the hypothesis filtering process.

Action	Number	Management hypothesis
		Upper Missouri River
Alter flow regime at Fort Peck Dam	1	Naturalized flow releases at Fort Peck Dam will result in increased productivity through increased hydrologic connections with low-lying land and flood plains in the spring, and decreased velocities and bioenergetic demands on exogenously feeding larvae and juveniles during low flows in summer and fall.
	2	Attractant flow releases at Fort Peck Dam will result in increased reproductive success through increased aggregation and spawning success of adults.
	3	Reduction of main stem Missouri River flows from Fort Peck Dam during free-embryo dispersal will decrease main stem velocities and drift distance, thereby decreasing mortality by decreasing numbers of free embryos transported into headwaters of Lake Sakakawea.
Temperature control, Fort Peck Dam	4	Warmer flow releases at Fort Peck Dam will increase system productivity and food resource availability, thereby increasing growth and condition of exogenously feeding larvae and juveniles.
	5	Warmer flow releases from Fort Peck Dam will increase growth rates, shorten drift distance, and decrease mortality by decreasing free embryos transported into headwaters of Lake Sakakawea.
Sediment augmentation, Fort Peck Dam	6	Installing sediment bypass at Fort Peck Dam will increase and naturalize turbidity levels, resulting in decreased predation on embryos, free embryos, and exogenously feeding larvae.
		Yellowstone River
Passage at Intake Diversion Dam	7	Fish passage at Intake Diversion Dam on the Yellowstone River will allow access to additional functional spawning sites, increasing spawning success and effective drift distance, and decreasing downstream mortality of free embryos and exogenously feeding larvae.
		Upper Missouri and Yellowstone Rivers
Upper basin propagation	8	Stocking at optimal size classes and in optimal numbers will increase growth rates and survival of exogenously feeding larvae and juveniles.
	9	Stocking with appropriate parentage and genetic diversity will result in increased survival of embryos, free embryos, exogenously feeding larvae, and juveniles.
		Lake Sakakawea
Drawdown, Lake Sakakawea	10	Drawdown of Lake Sakakawea will increase effective drift distance, decreasing downstream mortaliity of free embryos and exogenously feeding larvae.
		Lower Missouri River
Alter Flow regime at Gavins Point Dam	11	Naturalization of the flow regime at Gavins Point Dam will improve flow cues in spring for aggregation and spawning of reproductive adults, increasing reproductive success.
	12	Naturalization of the flow regime at Gavins Point Dam will improve connectivity with channel-margin habitats and low-lying flood plain lands, increase primary and secondary production, and increase growth, condition, and survival of exogenously feeding larvae and juveniles.
	13	Naturalization of the flow regime at Gavins Point Dam will decrease velocities and bioenergetic demands, resulting in increased growth, condition, and survival for exogenously feeding larvae and juveniles.
	14	Alteration of the flow regime at Gavins Point Dam can be optimized to decrease main stem velocities, decrease effective drift distance, and minimize mortality of free embryos.
Temperature management, Gavins Point Dam	15	Operation of a temperature management system at Fort Randall Dam and/or Gavins Point Dam will increase water temperature downstream from Gavins Point Dam, providing improved spawning cues for reproductive adults.

Table 1. List of 21 working management hypotheses developed through the hypothesis filtering process.—Continued

Action	Number	Management hypothesis
		Upper Missouri River
Channel reconfiguration	16	Re-engineering of channel morphology in selected reaches will create optimal spawning conditions—substrate, hydraulics, and geometry—to increase probability of successful spawning, fertilization, embryo incubation, and free-embryo retention.
	17	Re-engineering of channel morphology in selected reaches will increase channel complexity and bioenergetic conditions to increase prey density (invertebrates and native prey fish) for exogenously feeding larvae and juveniles.
	18	Re-engineering of channel morphology will increase channel complexity and minimize bioenergetic requirements for resting and foraging of exogenously feeding larvae and juveniles.
	19	Re-engineering of channel morphology in selected reaches will increase channel complexity and serve specifically to intercept and retain drifting free embryos in areas with sufficient prey for first feeding and for growth through juvenile stages.
Propagation lower basin	20	Stocking at optimal size classes and in optimal numbers will increase growth rates and survival of exogenously feeding larvae and juveniles.
	21	Stocking with appropriate parentage and genetic diversity will result in increased survival of embryos, free embryos, exogenously feeding larvae, and juveniles.

Missouri River Environmental History

The Missouri River is the longest river in the United States at 2,341 miles (mi) (fig. 2). Second only to the Mississippi River in drainage area, the Missouri River Basin drains one sixth of the area of the United States (Galat, Berry, Peter, and White, 2005). The Missouri River, or "Big Muddy" (so named because of its once-high sediment load), has played a prominent role in the history of the United States. It was home to more than 20 Native American Indian tribes that used the abundant fish and wildlife that inhabited the diverse river corridor. The Missouri River Basin was opened to European settlement (Galat, Berry, Peter, and White, 2005; Blevins, 2006) after the Louisiana Purchase of 1803 and Lewis and Clark Expedition of 1804–6. Settlement along the Missouri River resulted in substantial alterations to physical riverine processes, ecological processes, and fish and wildlife populations.

Before settlement of the Missouri River basin, the Missouri River (fig. 2) provided a diversity of habitats. Flood plains along the river provided a source of nutrients, organic matter, sediment, and woody debris during flood events. Forested flood plain patches were mixed with varied habitats, including wet prairies, chutes, sloughs, and side channels. These areas of variable depth and current provided refugia for a variety of aquatic animals (U.S. Fish and Wildlife Service, 1993, 2014). Areas of slow current velocity provided backwater habitats rich with organic matter and prey items, providing nursery and feeding areas for many aquatic species (Funk and Robinson, 1974). Natural flood flows connected these habitats to the main stem channel and each other, allowing for exchanges of water, energy, and nutrients, and access of flood plain-dependent fishes to spawning and rearing habitats.

As the United States population grew, new demands were placed on the Missouri River (fig. 2). Commercial fish harvests during the late 1800s and early 1900s began exploiting the river and its fisheries. As commercial fisheries began to decline and westward expansion grew, the Missouri River became an important factor in commerce. Channelization, snag removal, and bank stabilization began in the mid-1800s to support the steamboat industry. Through the early 20th century, several congressional authorizations resulted in progressive channelization and bank stabilization, culminating in the Bank Stabilization and Navigation Project (1912) and Rivers and Harbors Act (1945). The Rivers and Harbors Act (1945) authorized a 9-foot (ft) deep, 300-ft wide navigation channel 735 mi from Sioux City, Iowa, to the Mississippi River at St. Louis, Missouri (Ferrell, 1995). Wing dikes and revetments now stabilize 735 mi of riverbanks, while narrowing and focusing flow in the thalweg to maintain a self-dredging navigation channel. These engineering structures have created a narrow, swift, and deep channel from what was historically a shallow, shifting, braided river, resulting in the loss of as much as 400 square kilometers (km^2) of river corridor habitats (Funk and Robinson, 1974; Hallberg and others, 1979; Hesse and Sheets, 1993). In addition, Federal and private levees have been built to allow urban and agricultural development on productive accreted lands and flood plain soils. Levees allow for socioeconomic uses of the flood plains but interrupt the exchanges of water, energy, and nutrients that support a productive ecosystem.

Simultaneous with development of the river corridor, basin-wide hydrology has been altered by construction of multipurpose reservoirs. Reservoirs in the Missouri River Basin (fig. 2) now provide a total of more than 130 cubic kilometers (km^3) of storage; 91 km^3 of this storage is provided by the main stem system of six reservoirs that impounds 53 percent of the drainage basin. The six main stem reservoirs were constructed between 1937 and 1963, and operation as a system began in 1967 (U.S. Army Corps of Engineers, 2004). Galat and Lipkin (2000) documented substantial alteration to the annual hydrograph downstream from the reservoirs, including reduced intra-annual flow variability with generally decreased spring pulses and increased summer low flows. Hydrologic changes are especially severe just downstream from the dams and in inter-reservoir reaches where clear, cold water is released. The intensity of hydrologic alteration diminishes downstream from the dams as tributaries enter the Missouri River. The 360 mi downstream from the Kansas River confluence (at Kansas City, Mo.) has increased summer low flows relative to natural levels but retains substantial intra-annual variability, including spring–summer flow pulses. The reservoir system also fragmented the Missouri-Mississippi river system (fig. 2), potentially interrupting upstream and downstream migratory pathways.

In addition to flow-regime changes, the Missouri River (fig. 2) has been subjected to interacting changes in sediment regime and water quality. The sediment regime of the river has been substantially altered as a result of reservoir operations (Blevins, 2006; Jacobson, Blevins, and Bitner, 2009). At Hermann, Mo., the annual suspended sediment load is now 17 percent of the 326 million metric tons per year documented before the dams were closed. The decrease in sediment load also has been associated with decreases in turbidity that might directly affect native fish fauna (Galat, Berry, Gardner, and others, 2005). The reservoirs influence water quality for some distance downstream, generally resulting in decreased water temperatures, increased water clarity, and decreased nutrient and organic matter transport (Hesse and others, 1988; Hesse and Sheets, 1993; Blevins and Fairchild, 2001; Brown and others, 2011). Agricultural, industrial, mining, and urban development have also created potential for introduction of contaminants to the Missouri River (Petty and others, 1995, 1998; Echols and others, 2008).

Pallid Sturgeon History and Status

Pallid sturgeon are large, long-lived benthic fish that inhabit the turbid, fast-flowing rivers of the Missouri and Mississippi River Basins (fig. 2). Pallid sturgeon are often mistaken for the closely related, shovelnose sturgeon, which share their range. Their appearance and habitat preferences are so similar it was not until 1905 that pallid sturgeon was identified as a distinct species. Forbes and Richardson (1905) evaluated nine male sturgeon caught by commercial fisherman in the confluence of the Missouri and Mississippi Rivers. Finding distinct differences in the sturgeon, they classified the pallid as *Parascaphirhynchus albus*, assigning it a new genus. It was not until 1954 that Bailey and Cross (1954) reassigned the pallid into the *Scaphirhynchus* genus as *S. album*. In 1962, Bailey and Allum (1962) revised the pallid to its current name *S. albus*.

Scaphirhynchus spp. have evolved to inhabit turbid, fast-flowing waters. These species have elongated wide-spladed rostrums and heavily scuted dorso-ventrally compressed bodies with long thin caudal peduncles and wide pectoral fins. Small eyes are supplemented by four fleshy barbels and a protrusible mouth for detecting and capturing food items (Bailey and Cross, 1954; Pflieger, 1997). Morphological differences between the two *Scaphirhynchus* spp. are slight, and the two species have been differentiated historically only by the meristic and morphometric ratios developed by Bailey and Cross (1954). The larger pallid sturgeon is generally paler in color (white to light grey), does not have ossified scutes on its abdomen, has smaller eyes, and has a proportionally larger mouth width compared to the shovelnose sturgeon. Barbel placement and relative length also vary by species; pallid sturgeon have a concave alignment with the outer barbels more posteriorly placed than the inner barbels, whereas shovelnose sturgeon barbels are aligned in a straight row (Bailey and Cross, 1954; Pflieger, 1997). Hybrids or crosses of shovelnose and pallid sturgeon exhibit a mix of these characteristics or may more closely resemble one species or the other (Kuhajda and others, 2005). The recent advent of advanced genetic techniques has allowed more precise identification of shovelnose and pallid individuals, hybrid intermediates, and phenotypic variants (Schrey and Heist, 2007).

Although *Scaphirhynchus* spp. have a similarity of appearance and similar habitat requirements, many notable differences exist. Pallid sturgeon are slower to mature and attain a larger maximum size than shovelnose sturgeon (Mayden and Kuhajda, 1997; Wildhaber and others, 2007). Pallid sturgeon typically inhabit more turbid and swifter waters of predominantly sand-bedded rivers, whereas the smaller, quicker maturing shovelnose sturgeon have a wider distribution and geographic range, including large main stream rivers and smaller, clearer tributaries. As larvae and juveniles, pallid and shovelnose sturgeon share dietary preference for macroinvertebrates, but when pallid sturgeon reach the late juvenile to early adult stage (about 750 millimeters [mm] in length), they switch to a diet composed primarily of native cyprinids (Gerrity and others, 2006; Grohs and others, 2009; French, Graeb, Bertrand, and others, 2013).

The natural geographic range of the pallid sturgeon includes the Mississippi and Missouri River Basins (fig. 2) in which turbid, high-velocity waters flow over predominately sandy substrate. This natural geographic range includes the Yellowstone and Missouri Rivers downstream to the confluence with the Mississippi River, and the Mississippi River from Keokuk, Iowa, to the Gulf of Mexico (including the Atchafalaya River distributary). Also included are lower parts of some Missouri River tributaries, including the Milk River in Montana, Niobrara and Platte Rivers in Nebraska, Big Sioux River in Iowa, Kansas River in Kansas, and Grand and Osage Rivers in Missouri (fig. 2). Over this wide geographic range, phenotypic and genetic differences are visible. Notably, pallid sturgeon in the Upper Missouri and Yellowstone Rivers generally attain larger adult size compared to their Lower

Missouri River counterparts, and Mississippi River pallid sturgeon are the smallest (U.S. Fish and Wildlife Service, 1993). Murphy and others (2007) documented morphological differences between pallid sturgeon from the Upper Missouri River and the Mississippi and Atchafalaya Rivers. Extensive sampling indicates genetically distinct populations of pallid sturgeon are in the Upper Missouri, Lower Missouri, and Mississippi Rivers (Campton and others, 2000; Tranah and others, 2001, 2004; Schrey and others, 2006, 2011). The presence of genetic structure within the pallid sturgeon metapopulation is recognized in the 2014 recovery plan; and the plan speculates that, with additional sampling and genetic information, distinct population segments might be defined (U.S. Fish and Wildlife Service, 2014). It is notable that pallid sturgeon have been hypothesized to be more abundant in the Lower Mississippi and Atchafalaya Rivers compared to the Missouri River and have been considered for delisting by the specific management unit (MU) (U.S. Fish and Wildlife Service, 2012). Other scientists argue that sturgeon identified as pallid sturgeon in the Lower Mississippi and Atchafalaya Rivers are hybrids resulting from back-crossing between pallid and shovelnose sturgeon (Tranah and others, 2004; Elchelberger and others, 2014).

Decline of the Pallid Sturgeon

Because pallid sturgeon was not recognized as a species until 1905, little is known about its historical abundance (Pflieger, 1975). Early descriptions suggest pallid sturgeon were never common in their natural geographic range (Forbes and Richardson, 1905; Bailey, 1954). Information is limited, however, because commercial harvest records from the period did not discriminate among sturgeon species, and the habitats frequented by pallid sturgeon (deep, swift, and turbid waters) made sampling for them more difficult than for other native species, including the shovelnose sturgeon (Funk and Robinson, 1974; Kallemeyn, 1983). Only fisherman targeting sturgeon for caviar were likely to find the pallid sturgeon because shovelnose sturgeon were in higher abundance, particularly in areas of low turbidity. Commercial harvest records from the early 20th century near the Missouri and Mississippi River confluence (fig. 2) indicated a shovelnose to pallid sturgeon ratio of 500 to 1 (Forbes and Richardson, 1905) or 300 to 1 (Forbes and Richardson, 1909); ratios of shovelnose to pallid sturgeon generally decreased in more turbid water of the Lower Missouri River (Bailey, 1954).

Overharvesting has been implicated in diminished populations of several other North American sturgeon species. *Scaphirhynchus* spp., as well as *Acipenser fulvescens* (lake sturgeon), were intensively harvested during the late 1800s and early 1900s throughout the Missouri and Mississippi River Basins (fig. 2). The larger pallid and lake sturgeon were a highly sought source of caviar, and many of the smaller, more abundant shovelnose sturgeon were harvested as by catch. Recorded commercial harvest of undifferentiated sturgeon (lake, pallid, and shovelnose sturgeon together) reached a high of 195,450 kilograms (kg) in the early 1890s and declined to less than 9,100 kg by 1950 (Carlander, 1954). Such harvesting resulted in the extirpation of the lake sturgeon from the Missouri and lower Mississippi Rivers during the early part of the 20th century (Carlson and others, 1981). This notable decline in the sturgeon population indicated by commercial fishing records coincided with reservoir construction, channelization, and development in the Missouri River Basin, indicating that pallid sturgeon populations were subjected to multiple stressors.

Concern for the pallid sturgeon grew as surveys from management agencies in the late 20th century produced few pallid sturgeon (Schmulbach and others, 1975; Carlson and others, 1985). Low catches of pallid sturgeon and documented hybridization of the pallid sturgeon with the shovelnose sturgeon were taken as indications that populations were likely below self-sustaining levels. In 1990, the USFWS formally listed the pallid sturgeon as a Federally endangered species according to the Endangered Species Act of 1973. A species recovery plan was developed and released in 1993 (Dryer and Sandvol, 1993), a 5-year review of the species status was published in 2007 (U.S. Fish and Wildlife Service, 2007), and the species recovery plan was revised in 2014 (U.S. Fish and Wildlife Service, 2014). In 2010, the shovelnose sturgeon was listed by the U.S. Fish and Wildlife Service as a Federally threatened species under the Endangered Species Act of 1973 because of its similarity of appearance to the pallid sturgeon. This eliminated commercial harvest of the shovelnose sturgeon in the Missouri, middle Mississippi, and lower Mississippi Rivers (fig. 2) to prevent unintentional harvesting of pallid sturgeon in areas where both species are present. Illegal harvesting of pallid sturgeon reproductive females for caviar before this listing may have had a long-term effect on the population and the ability of the population to rebound.

Present and Future Estimates of Pallid Sturgeon Population Size

Estimates of current pallid sturgeon populations are limited and subject to considerable uncertainty. Duffy and others (1996) summarized the estimates of various studies, both published and unpublished, which suggested as few as 6,000 or as many as 12,000 wild pallid sturgeon existed throughout their natural geographic range. Estimates from mark-recapture studies on interreservoir populations indicate that the population between Fort Peck and Garrison Dams (fig. 2) may be 158 adults (Braaten and others, 2009) to 125 wild adults (Jaeger and others, 2009). A 1995 survey estimated 45 wild adult pallid sturgeon existed in the river upstream from Fort Peck Lake; however, only three wild pallid sturgeon were collected in this location from 2007 to 2013 (U.S. Fish and Wildlife Service, 2014). Steffensen and others (2012) estimated that the wild population of the Lower Missouri River downstream from Gavins Point Dam was 5,991 pallid sturgeon in 2012. Steffensen and others (2013a) indicated that the population seems to be stable because of supplemental stocking by the Pallid Sturgeon Conservation Augmentation Program but remains neither self-sustaining nor viable. Estimates for the middle Mississippi River (mouth of the Missouri River to the confluence with the Ohio River) suggest a population of 1,600 to 4,900 pallid sturgeon (Garvey and others, 2009). Population estimates from the remainder of the pallid sturgeons' natural geographic range are not available in published literature.

Historical (early 20th century) and current population sizes provide some understanding of trends in pallid sturgeon populations, but they do not necessarily indicate what would be a sustainable population under present river conditions. One approach to estimating a minimal sustainable population is based on calculating the population size needed to sustain genetic variation. The effective population size (N_e) indicates the number of successful breeding individuals that are actually contributing genes to the next generation. Where there are too few successful parents, genetic variation decreases with each generation; therefore, individuals become inbred and reduce the health and fitness of the population. The magnitude of N_e required to prevent a decrease in genetic variation is controversial and generally impractical to determine through theory. A sufficient N_e allows the genetic integrity of a species to be maintained and aids in limiting the threat of extinction (Frankham, 2005).

The N_e to the total adult population (N) ratio (N_e/N), however, has a high degree of variability (Lande, 1995; Frankham, 2005; Palstra and Ruzzante, 2008; Frankham and others, 2014). The N_e is typically smaller and sometimes orders of magnitude smaller than N. Frankham (2005) reports a N_e/N range for many species from 10^{-6} to 0.996 and a mean N_e/N of about 0.1. A review of 83 studies of 65 species by Palstra and Ruzzante (2008) generated a median N_e of 260 and median N_e/N of 0.14 . One of the assumptions necessary for $N_e=N$ is that the variance in reproductive success among adults equals two. Typically, the reproductive variance is much greater than two, and N_e is much less than N because a small number of adults produce far more than two offspring and most produce none. As a result, gene copies from a small number of successful parents become overrepresented, and the population's genetic variation decreases faster than a population with the same N but a reproductive variance of two.

Franklin (1980) suggested the "50/500 rule," which states that a minimum N_e of 50 in the short term (one to two generations) would prevent inbreeding but that a population needed a long-term N_e of 500 to preserve fitness over evolutionary time of three or more generations. The revised pallid sturgeon recovery plan (U.S. Fish and Wildlife Service, 2014) followed the 50/500 rule where it calls for a minimum N of 5,000 adults per MU, corresponding with a minimum N_e of 500 assuming that N_e/N=0.1. Frankham and others (2014), in contrast, argued in favor of a "100/1,000 rule," meaning a single generation N_e of 100 and a long-term N_e of 1,000, suggesting that a total adult population of 10,000 may be required assuming that N_e/N=0.1 in pallid sturgeon.

The determination that a particular number of pallid sturgeon adults corresponds with an acceptable N_e assumes that the population is self-sustaining through natural recruitment. Because there has been zero or extremely small natural recruitment of pallid sturgeon in the Missouri River Basin, the N_e of the wild stock is virtually zero; and unless natural reproduction returns, the stock will go extinct (that is, all genetic variation will be lost) without continued propagation. When fish are maintained under propagation, managers have the opportunity to select the number of breeders and control reproductive success; thus, N_e and N_e/N can be manipulated directly. Saltzgiver and others (2012) determined that based on the number of offspring produced from 43 female and 86 male wild pallid sturgeon (N=129), an N_e of 77 was achievable (N_e/N=0.6) for the Gavins Point National Fish Hatchery captive broodstock program. Heist and others (2013) recommended that until sufficient natural recruitment was restored, hatchery practices should be established such that *Ne* for future generations of the upper Missouri River Basin stock should be at least 100 and preferably 250.

The revised pallid sturgeon recovery plan estimates that a self-sustaining population of 5,000 adults is needed as a minimum in each of the three MUs (Great Plains, Central Lowlands, and Interior Highlands) (U.S. Fish and Wildlife Service, 2014). Although the pallid sturgeon population of the Great Plains MU (fig. 2) is substantively isolated from the others, it is not clear if genetically isolated subpopulations are delineated by the boundary between the Central Lowlands and Interior Highlands MUs. The boundary was determined based on the geographic distributions of small fish in tributaries to the Missouri River (fig. 2) rather than known ranges of the pallid sturgeon (U.S. Fish and Wildlife Service, 2014), whereas telemetry data indicate that some adult pallid sturgeon migrate between these two MUs (DeLonay and others, 2009). Based on simulations of continuously distributed populations by Neel and others (2013), estimates of N_e based on samples collected within a "genetic neighborhood" are generally representative of the N_e of the local population, whereas estimates based on samples that span multiple genetic neighborhoods are confounded by allele frequency differences among populations. A genetic neighborhood is defined based on the density and dispersal (that is, movement between birth and reproduction) of individuals such that about 87 percent of individuals breed within the genetic neighborhood in which they were born. Similarly, Waples (2010) determined that migration rates of as much as 10 percent did not substantially affect estimates of local N_e; thus, assuming that pallid sturgeon collected within a region do not span multiple genetic neighborhoods, estimates of N_e will be valid for the local population. Without a better understanding of the density and dispersal of pallid sturgeon, however, the geographical extent to which the N_e estimate applies will not be clear. Without resolution of these issues, and especially without a demonstration that pallid sturgeon are successfully recruiting in the wild, reasoning from N_e to population targets would be tenuous.

Implicated Stressors and Historical Mitigation

Development of the Missouri River (fig. 2) has progressed coincident with documented declines in many native fish species, including the pallid sturgeon (Dryer and Sandvol, 1993; Galat, Berry, Gardner, and others, 2005; U.S. Fish and Wildlife Service, 2014). The challenge has been to isolate which of many potential stressors, acting alone or in combination, are responsible for lack of population growth in the species.

The scale of channelization and intensity of hydrologic change have led many to hypothesize that changes in physical habitat in the Missouri River system have been instrumental in the decline of the pallid sturgeon (Quist and others, 2004; Bergman and others, 2008), but other stressors—including overharvest, contaminants, entrainment, removal, and hybridization—have not been ruled out and continue to be perceived as threats to population growth (U.S. Fish and Wildlife Service, 2014; Jacobson and others, 2016). The 2003 Biological Opinion stated, “Destruction and alteration of big river ecological functions and habitat that was once provided by the Missouri and Mississippi Rivers is believed to be the primary cause of declines in reproduction, growth, and survival of pallid sturgeon.” (U.S. Fish and Wildlife Service, 2003, p. 73). Of the more than 3,500 river miles (RM), which include the pallid sturgeon natural geographic range, no part is without substantial alteration from barriers to passage, including dams and impoundments, altered flows, or channelization and bank stabilization. The most notable alterations have been the main stem dams and their reservoirs, and channelization for commercial navigation and bank protection on the Lower Missouri River (fig. 2*B*). Such habitat alterations are hypothesized to interrupt the natural life cycle of the pallid sturgeon, including altering food availability, foraging habitats, dispersal dynamics, spawning cues, spawning habitats, and water quality (U.S. Fish and Wildlife, 1993, 2014).

Missouri River main stem dams (fig. 2*B*) have created physical barriers to migration, a factor of special importance for a fish that uses hundreds of kilometers of the river in reproductive migrations. Although it is not known which parts of the river were used historically by subpopulations and for which life-stage functions, it is probable that dams now prevent access to formerly used habitats—either directly or by imposing changes in water quality for some distance upstream or downstream from the dams. Main stem reservoirs, which are inhospitable to velocity-adapted fish, clearly present challenges to downstream-dispersing free embryos and may harbor lethal water-quality conditions (Braaten and others, 2008; Guy and others, 2015). Downstream from dams, changes in flow regime, sediment regime, water temperature, water clarity, and nutrient transport provide additional potential to affect pallid sturgeon and their reproductive ecology (Hesse, 1987; Hesse and others, 1988). Particular attention has been given to disruption of hydrologic cues for reproductive synchrony (“spring rises”) that have been implicated as necessary factors in reproduction of many fish species (Poff and Allan, 1995; Poff and others, 1997; Humphries and Lake, 2000). Specific application of spring rises to pallid sturgeon reproduction has been under intense investigation, but unambiguous associations between flow pulses and reproductive success have not been established (Doyle and others, 2011; Papoulias and others, 2011; DeLonay, Chojnacki, Jacobson, Albers, and others, 2016).

Channelization and bank stabilization on the Lower Missouri River (fig. 2*B*) have altered habitat complexity and diminished flood-plain connectivity, factors that are likely to have substantive effects on productivity and species distributions of the river (Funk and Robinson, 1974; Hallberg and others, 1979; Hesse and Sheets, 1993; Galat, Berry, Peter, and White, 2005; Jacobson and Galat, 2006). Channelization to increase velocities for sediment transport and maintenance of the navigation channel has also increased advection of nutrients and organic matter, decreasing residence time and availability for assimilation in the food web. Although effects of channelization on pallid sturgeon populations have been inferred (U.S. Fish and Wildlife Service, 2003, 2014) and the theoretical basis for such stressors in aquatic ecosystems is well established (Junk and others, 1989; Sparks, 1995; Tockner and others, 2000), specific linkages to pallid sturgeon populations remain elusive. Additional stressors—including increased water temperatures from outfalls and introduction of contaminants from industrial, agricultural, and municipal sources—may contribute to lack of recruitment by reduced egg quality and fitness of offspring, but the levels of contaminants associated with diminished fitness in the laboratory are substantially higher than those documented in field data (Buckler, 2011).

In 2000, the U.S. Fish and Wildlife Service published a biological opinion indicating that the USACE operations of the Missouri River (fig. 2) were likely to jeopardize the existence of the pallid sturgeon. This document, along with the 2003 amendment, defined reasonable and prudent alternatives to jeopardy for the Missouri River pallid sturgeon (U.S. Fish and Wildlife Service, 2000, 2003). The reasonable and prudent alternatives included implementation of AM, monitoring, and research; increased pallid sturgeon supplemental propagation; flow enhancements from Fort Peck and Gavins Point Dams; and rehabilitation of shallow-water habitats (SWHs) to a density of 20–30 acres per RM from Sioux City, Iowa, to St. Louis, Mo. Additional broad-scale mitigation has taken place under the Missouri River Bank Stabilization and Navigation Project Fish and Wildlife Mitigation Program (hereafter referred to as the “Mitigation Program”) to recover some of the habitat lost because of the Bank Stabilization and Navigation Program. The Mitigation Program’s goal is to enhance lost habitat diversity by restoring approximately 32 percent (166,675 acres) of the estimated lost channel, sandbar, and meander-belt habitat (U.S. Army Corps of Engineers, 2003). The Mitigation Program goals, and compliance with the amended biological opinion, were formally collected into the MRRP in the Water Resources Development Act of 2007 (WRDA 2007). The WRDA 2007 authorized mitigation projects for the main stem Upper Missouri River and allowed USACE funding to aid in the planning and implementation of fish passage around the Intake Diversion Dam on the Yellowstone River.

Rehabilitation activities of the Missouri River (fig. 2) have been guided by AM principles beginning with the adoption of the 2000 Biological Opinion (U.S. Fish and Wildlife Service, 2000) and the 2001 Master Manual revision (U.S. Army Corps of Engineers, 2001), and more formally with the WRDA 2007 creation of the Missouri River Recovery Implementation Committee and its subcommittees (Science and AM workgroup and Missouri River ISAP).

Relation of Effects Analysis to Previous Work

The EA is the most recent of multiple efforts to plan and prioritize information needs and recovery actions for pallid sturgeon. In 1993, the USFWS began recovery actions by publishing, with input from experts of the Pallid Sturgeon Recovery Team, a recovery plan for the pallid sturgeon. This collaboration provided background information regarding the history, ecology, and species status of the pallid sturgeon. Additionally, objectives and criteria for avoiding jeopardy were adopted (U.S. Fish and Wildlife Service, 1993). A revision to the recovery plan was published in 2014 (U.S. Fish and Wildlife Service, 2014).

Recovery objectives and science needs were also refined in 2004 with the first of two workshops mediated by the University of Wyoming William D. Ruckelhaus Institute of Environmental and Natural Resources. This workshop brought together experts from state and Federal agencies, stakeholders, and experts from outside the Missouri River Basin to identify critical research needs necessary for reducing uncertainty in the pallid sturgeon recovery effort (Quist and others, 2004). A follow up workshop was held in 2007 to update and prioritize research needs from throughout the natural geographic range (Bergman and others, 2008). The background information, recovery objectives, and research prioritization provided by these reports and workshops have been influential in guiding the pallid recovery efforts, including EA team efforts.

In summer 2013, the USACE and USFWS hosted workshops for sturgeon biologists, landscape ecologists, and Missouri River experts from state and Federal agencies to create CEMs that were intended to represent the Missouri River ecosystem and pallid sturgeon population dynamics. Missouri River pallid sturgeon CEMs provide graphical representations of complex components of the Missouri River ecosystem and how processes and interactions affect the survival of pallid sturgeon in various life stages. The CEMs are an important tool in the AM of the Missouri River because they enforce systematic thinking, allow stakeholders and scientists to visualize and share understanding, and provide a framework for generating testable hypotheses (Jacobson and Berkley, 2011).

Because of the distinctly different management needs and challenges of the Upper and Lower Missouri Rivers (fig. 2*B*), separate workshops were held for each river, but the workshop participants decided on a common model structure for both. The resulting CEM is a model in which hierarchical component-level models (Jacobson and Berkley, 2011) produce individual life-stage survival probabilities that are amenable to creating a stage-based population model (Wildhaber and others, 2007; Wildhaber, DeLonay, and others, 2011). Draft models were distributed to interested stakeholders and members of the public for technical review during a 30-day review period. The review comments were compiled by the MRRMP and, along with all pertinent materials, were given to the Pallid Sturgeon EA team for further refinement. While maintaining the general substance of the workshop CEMs, the Pallid Sturgeon EA team designed a general hierarchical structure for the component models, refined the graphical structure of the CEMs, and reconciled variation among the components and between models developed for the Upper and Lower Missouri Rivers.

The Pallid Sturgeon EA team used the CEMs as a basis to evaluate the importance of primary biotic responses to pallid sturgeon survival at various life stages. Biotic responses, which were considered important by an expert panel, were then used to create working dominant hypotheses that are likely to be relevant to pallid sturgeon population dynamics and also may have contributed to its population decline on the Missouri River (fig. 2). Through a modified Delphi expert-opinion process (Normand and others, 1998), these hypotheses were reduced to 23 working dominant hypotheses. The working dominant hypotheses were then matched to hypotheses about management actions that could influence the biotic outcomes. After an additional solicitation of expert opinion, 30 working management hypotheses were selected. These working management hypotheses were then filtered by the USACE and USFWS for actions that were within the agency's authority and jurisdiction, resulting in 21 working management hypotheses for initial modeling of linkages from management to pallid sturgeon population responses (table 1). During this process, the 9 filtered hypotheses were not discarded; they reside in reserve as alternative hypotheses should any of the working management hypotheses be falsified. No attempt was made to prioritize the 21 working management hypotheses. This was in part because the substantial uncertainties made prioritization impractical. In addition, we hypothesized it would provide additional flexibility if multiple management actions could be explored to achieve the same biological objectives. We discuss the interactions of management actions at the end of this report in terms of decision trees.

Quantitative Modeling Framework

A fundamental EA objective is to link management actions to pallid sturgeon population dynamics in, principally, a population viability analysis (Murphy and Weiland, 2011). The ideal situation would be a model that predicts how changes in system condition—for example, flow releases from dams—affect survival at relevant life stages, which would then propagate to a predicted population response. The ideal is illustrated in the population-level CEM (fig. 3), in which conditions and processes affect survival at critical life-stage transitions. Each life-stage transition is associated with a component CEM (fig. 4), which illustrates the abiotic and biotic factors that influence survival at that life stage.

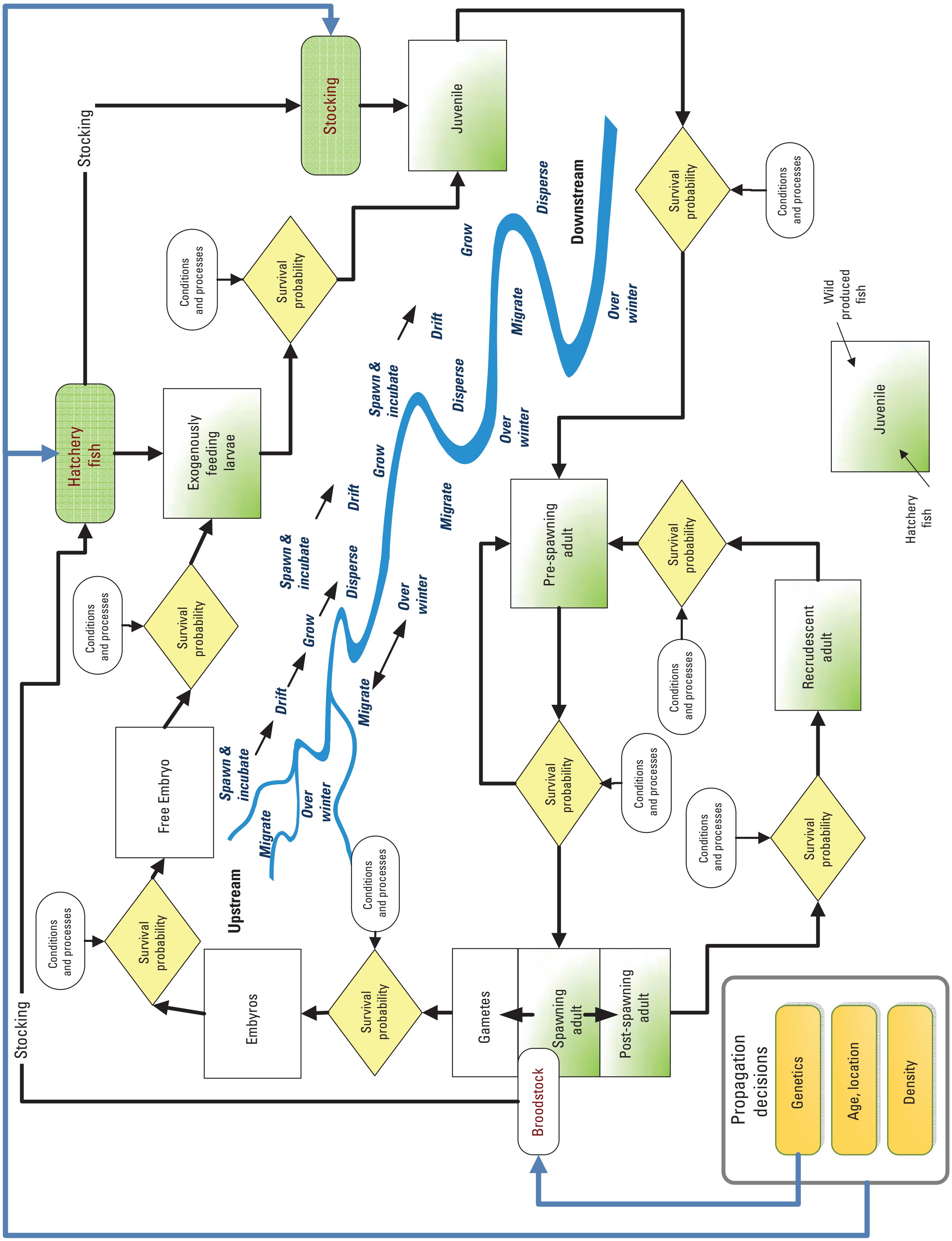


Figure 3. Generalized population-level conceptual ecological model showing life stages and geographic context of the pallid sturgeon reproductive cycle. Modified from Wildhaber and others (2007).

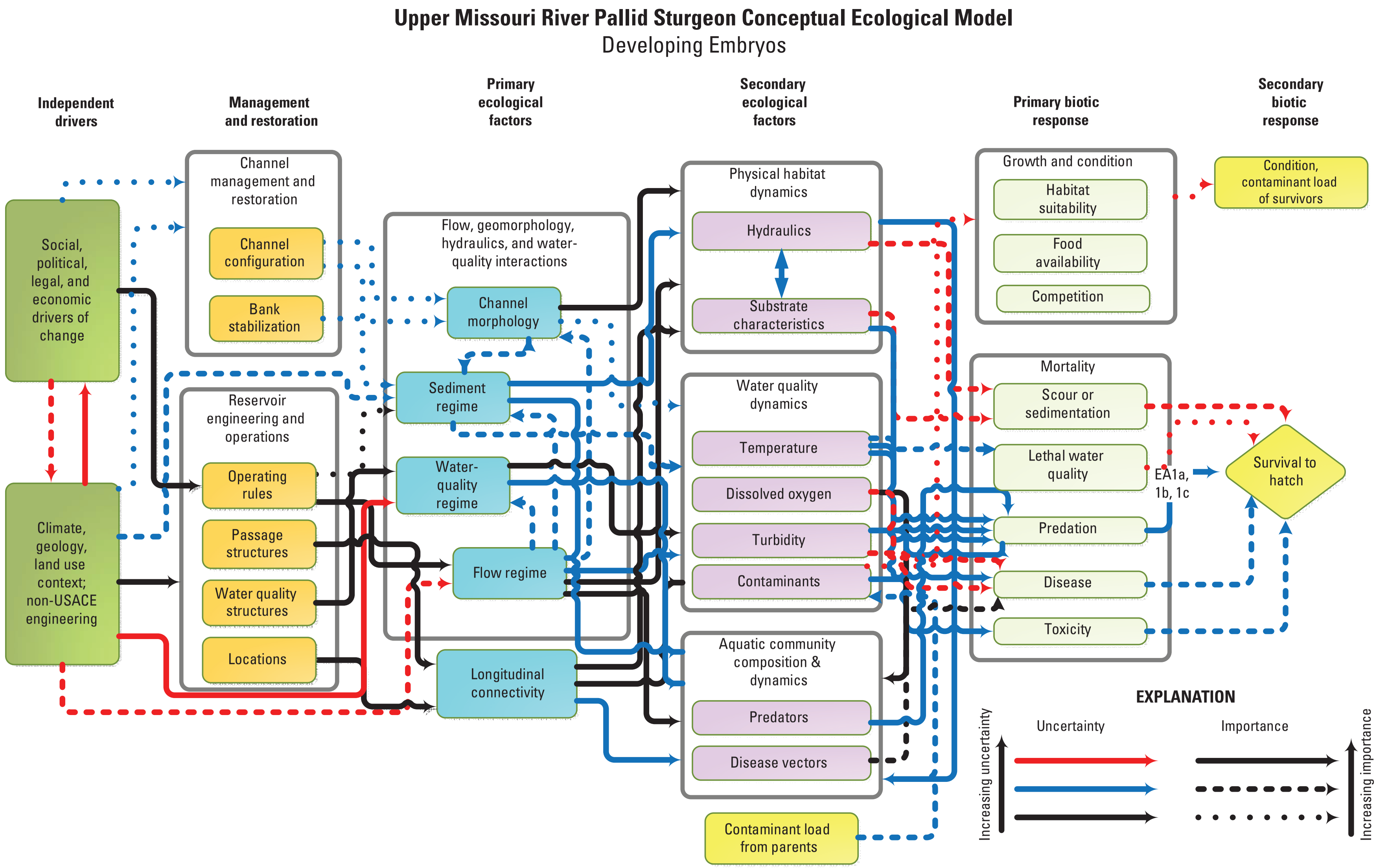


Figure 4. Example of a life-stage component conceptual ecological model showing the driver-stressor relations leading to survival to next life stage (Jacobson, Parsley, and others, 2015).

In reality, our ability to construct models that can provide useful predictions of population dynamics as a function of management actions is limited by information gaps in model structure and demographic parameter values (for example, growth, survival, fecundity, and sex ratios). A possible exception is in the upper river, where mortality seems to be closely linked to dispersal into Lake Sakakawea (fig. 2) based on inferences from documented lethal water-quality effects in the headwaters of Fort Peck Lake (Braaten and others, 2008; Guy and others, 2015). In this case, physical modeling of advection/dispersion of drifting free larvae is plausibly linked to survival probability and—if all other life-stage survival probabilities are known with sufficient certainty—can be used to calculate population responses. For other habitat-related hypotheses on the upper and lower river, the functional links between habitat and critical population demographic parameters are much less certain.

Quantitative Modeling Approach

Our approach to quantitative modeling in the EA acknowledges the gap between habitats and demographic parameters but advances understanding using a two-sided approach (fig. 5). For habitat-related hypotheses, we use a series of models that translate management actions into changes in flow regime, water quality, and channel configuration. Hydrologic and reservoir operation models (Hydrologic Engineering Center Reservoir Simulation Model [HEC–ResSim]) provide quantities of water, which are routed hydraulically downstream using one-dimensional (1D) models that conserve mass and energy and can be used to evaluate some habitat variables (Hydrologic Engineering Center River Analysis System [HEC–RAS]; Hydrologic Engineering Center Ecosystem Functions Model [HEC–EFM]). Implementation of the HEC–ResSim, HEC–RAS, and HEC–EFM models are documented in Fischenich and others (2014). The effects of management actions on the potential for free-embryo larvae to drift downstream to nonsupporting habitats are being addressed with 1D advection/dispersion models (Erwin and Jacobson, 2014; Fischenich and others, 2014). Detailed habitat inventories are addressed with high-resolution, 2D hydrodynamic models that can be used to simulate extent and patch structure of a wide variety of functional habitat definitions.

The critical dependency in this cascade is definition of functional habitats—what ranges of habitat conditions are best linked to population demographic variables? If functional habitats can be defined reliably, then the modeling process from management action to functional habitat units (fig. 5, left side) provides quantitative information that can be used to infer effects of management actions on pallid sturgeon population dynamics.

We are also approaching the modeling gap from the population side using a stage-structured population dynamics model to simulate population dynamics based on best-available information on model structure and statistical distributions of demographic parameters. This modeling effort—combined into the population-level model (fig. 5, right side)—allows us to evaluate population sensitivities to model structure and parameter values and provides for exploration of some specific hypotheses—for example, effects of changing stocking rates—albeit constrained by considerable uncertainties in demographic parameters.

Although this approach to quantitative modeling fails to provide the ideal cascade of causal links from management action to population responses, it is an accurate reflection of the present (2016) state of pallid sturgeon science. The habitat models quantify the relative contributions of flow and channel reconfiguration actions in determining habitat distributions, subject to the level of biological realism attained in defining those habitats. The population models quantify sensitivities and indicate which life-stage transitions are most important to population responses. The models provide a quantitative framework that identifies critical uncertainties. The models can be used to guide future research, select alternative hypotheses, design monitoring and evaluation programs, and structure learning under AM.

Component Conceptual Ecological Model Structure

The CEMs that underlie the EA are documented in detail in Jacobson, Parsley, and others (2015). The essential structure of each life-stage component CEM is a hierarchical arrangement of drivers, stressors, and responses (fig. 4, from left to right). Each pair of columns, from right to left, can be considered a driver-stressor pair, and the final column is the ultimate biotic response (secondary biotic response or change in survival probability). The columns categorize the hierarchy of factors into management and restoration, primary ecological factors, secondary ecological factors, and primary biotic response. An important feature of structure is that uncertainty in predictions, and biological relevance, generally increase to the right. The CEMs have nested boxes to group and provide additional levels of hierarchical organization within each column. During the summer 2013 workshops, pallid sturgeon experts assigned arrows to the relations between and among boxes to illustrate strength of process linkages and associated uncertainties (fig. 4; table 2).

Hypotheses were developed by experts through consideration of pathways of relations through the CEMs, starting with consideration of dominant biological hypotheses (right side), followed by consideration of management actions (left side). The CEMs and global hypotheses contained within them serve as the mind map for a very broad range of hypotheses for the links from management actions to population responses. Although subsequent steps in the hypothesis filtering process narrowed down the hypotheses to a dominant set for initial modeling and exploration, the CEMs serve as a reserve of alternative hypotheses that can be resurrected as needed to explain observed population responses.

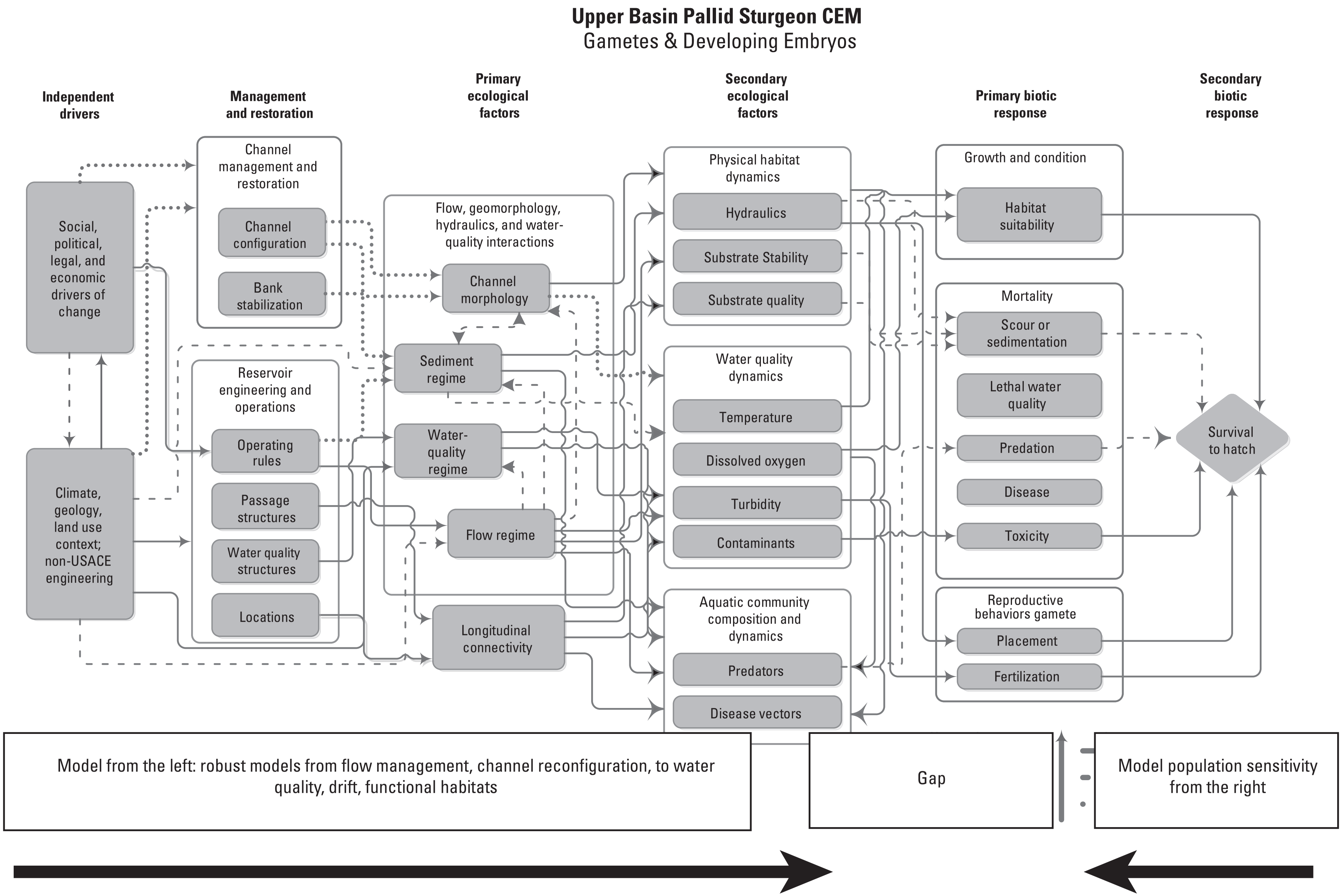


Figure 5. Diagram illustrating left to right and right to left approaches to turning conceptual ecological models into quantitative models.

Table 2. Descriptions of importance and uncertainty categories for conceptual ecological models.

Label	Description
	Importance
High	A link that is known or thought to have a direct and substantive effect in altering on another condition or process.
Moderate	A link that is known or thought to have an indirect, modifying effect on another condition or process.
Low	A link that is known or thought to have a small modifying effect on another condition or process.
	Uncertainty
High	A link with no published literature to support understanding.
Moderate	A link with some support from published studies on other species or rivers.
Low	A link supported by information from peer-reviewed studies specific to the question and species.

Working Pallid Sturgeon Population Model

The Pallid Sturgeon EA team recognized the importance of having a population dynamics model to serve as the framework for assessment. Once the component CEMs are operationalized and developed into quantitative models with useful parameter estimations, they will predict the effect of alternative management and rehabilitation actions on survival (secondary biotic responses). Stage-specific predictions of secondary biotic responses can then be coupled to a population model to evaluate management and rehabilitation actions on long-term population dynamics. This coupling will provide the necessary framework to objectively evaluate alternative management and rehabilitation strategies. A framework to achieve this requires a population model that accepts inputs from quantitative versions of the CEMs; therefore, a stage-based population model based on existing CEMs and the conceptual life-history model was developed to simulate population dynamics.

Objective of the Pallid Sturgeon Population Model

The population model structure was developed to meet three primary objectives: (1) provide a quantitative framework to forecast pallid sturgeon population dynamics given inputs from the CEMs described by Jacobson, Parsley, and others (2015), (2) provide a flexible model structure template that can be used to model several populations as part of a metapopulation (that is, upper river, lower river, and subpopulations if identified) and with varying spatial resolutions, and (3) account for whether pallid sturgeon were produced in the Missouri River (fig. 2) or hatchery system (fig. 6). An additional consideration in the development of the model structure was the availability of biological data commonly collected during population assessments (for example, size, weight, age, sex, and origin), which are necessary to parameterize and potentially calibrate the model. Do note that this population modeling effort is a work in progress and will be modified as needed to meet the needs of the Missouri River Pallid Sturgeon EA, Missouri River AM program, and community of scientists engaged in understanding pallid sturgeon population dynamics.

Approach to the Pallid Sturgeon Population Model

Four existing pallid sturgeon population dynamics models were identified as part of the EA process (Jacobson, Annis, and others, 2015). These models included the following: (1) an unpublished model developed by Reynolds and Tyre (2011) that predicted the effect of changes in processes or conditions on survival in terms of parameter elasticity (sensitivity of the parameter to change accounting for parameter magnitude), (2) a population viability analysis by Steffensen and others (2013a) that used an age-structured population model, (3) a population viability model developed by Wildhaber and others (2015) and, (4) an unpublished, partially developed population model by H. Jager (Environmental Sciences Division, Oak Ridge National Laboratory, written commun.). Common among these existing models is the use of age structure to simulate population dynamics. Additionally, three of these models, the exception being the model developed by Reynolds and Tyre (2011), were population viability models that predicted the pseudoextinction probability of the simulated population. The advantages of age-structured population viability models are that they can capture additional biological realism (that is, annual growth and increasing reproduction output with age), and the outputs are easily understood. Detailed summaries and comments of these models and related sturgeon population models are in table 1 of Jacobson, Annis, and others (2015).

Unfortunately, these existing models could not satisfy EA objectives because they are age structured, whereas the EA CEMs must be stage structured with an emphasis on survival probabilities within the first year of life. To simulate the effect of management and rehabilitation actions on population dynamics as captured in the CEMs, a   model is required (fig. 6). Using a stage-structured model does not preclude using existing parameters (for example, survival and fecundity) and functional relations from existing age-structured models. In many cases, we borrowed and used existing values and relations in the integrated population model when applicable; however, because existing quantitative models are age-based, borrowed demographic rates and functional relations were modified to account for the stage structure in the model.

Parameter estimates and functional relations are intended to be improved through future targeted research and assessments under AM of pallid sturgeon. Revision and refinement of the CEMs and population model probably will be an ongoing process, with iterative refinement as new data, information, and understanding become available.

Origin and Importance of Pallid Sturgeon Survival Data

Estimates of pallid sturgeon survival rates are required for the population model. The survival rates apply to transitions from one life stage to another. Rates are hypothesized to be influenced by management actions; for example, management actions are hypothesized to influence juvenile pallid sturgeon survival through varying pathways in the juvenile CEM, which in turn affects survival (fig. 7). Few reliable survival estimates exist, however, for pallid sturgeon, especially for early life stages. Some of these rates need to be borrowed from related sturgeon species, elicited from expert opinion, or tuned to produce biologically reasonable dynamics. We continue to compile demographic rates and characteristics for related sturgeon species, recognizing the importance of these values for parameterizing population models. Additionally, identifying these data gaps will provide guidance necessary for prioritizing future research.

Origin and Importance of Pallid Sturgeon Population Size and Structure Data

Information on current population size (abundance) and structure (age and size) is required to begin the population model to reflect the current system state. We have identified varying data sources and expertise that provided these inputs. Studies also have been completed that use back calculations to estimate current and historic population size for hatchery-origin fish; however, these studies are limited to specific areas within the Upper and Lower Missouri Rivers (fig. 2). Braaten and others (2009), for example, reconstructed historical abundances for recovery priority management area 2, which includes the Missouri River upstream from Lake Sakakawea to Fort Peck Dam and the Yellowstone River upstream to the confluence with the Tongue River. Recent estimates of naturally produced adult pallid sturgeon were 158 individuals (95-percent confidence interval of 129–193) in 2004. Studies completed by Rotella (2013) provided segment-specific estimates of population abundance of hatchery-origin pallid sturgeon. Estimated abundance values are stage specific, typically for juvenile or adult fish.

The Pallid Sturgeon Population Assessment Project (PSPAP) collects standardized monitoring data for pallid sturgeon and other native fishes. Standardized sampling is generally completed during a 7-month period (April–October). The PSPAP also collects pallid sturgeon broodstock data during spring and targeted, nonstandard pallid sturgeon data throughout the monitoring period. Broodstock sampling is much more intensive and completed during a much shorter period (2–4 weeks) than standardized sampling. A combination of standard and nonstandard (that is, broodstock and targeted sampling) PSPAP data were used to generate the first survival estimates for the upper (Hadley and Rotella, 2009; Rotella, 2013) and lower (Steffensen and others, 2010) Missouri River Basins. This same combination of data was used to develop the first regional population estimates for pallid sturgeon in the Lower Missouri River (fig. 2*B*) (Steffensen and others, 2012; Winders and Steffensen, 2014). The PSPAP data also have been used to characterize pallid sturgeon demographics, such as gender ratio, age-at-maturity, fecundity, reproductive readiness (Steffensen and others, 2013a, 2013b), and growth (Shuman and others, 2011).

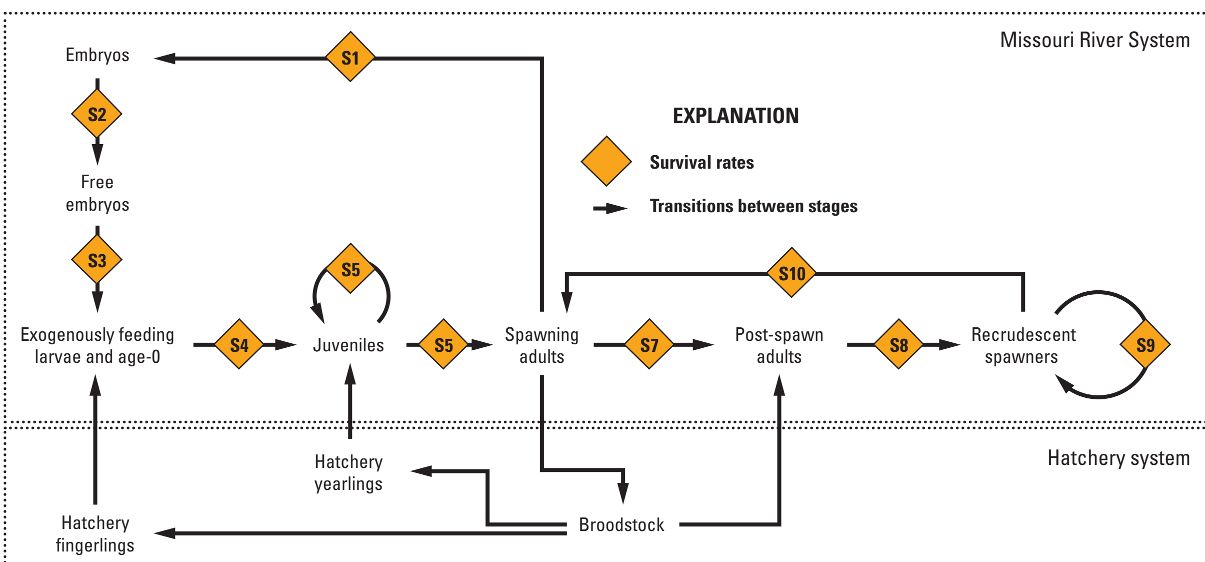


Figure 6. Generalized stage-based conceptual ecological model used to develop a quantitative pallid sturgeon population model.

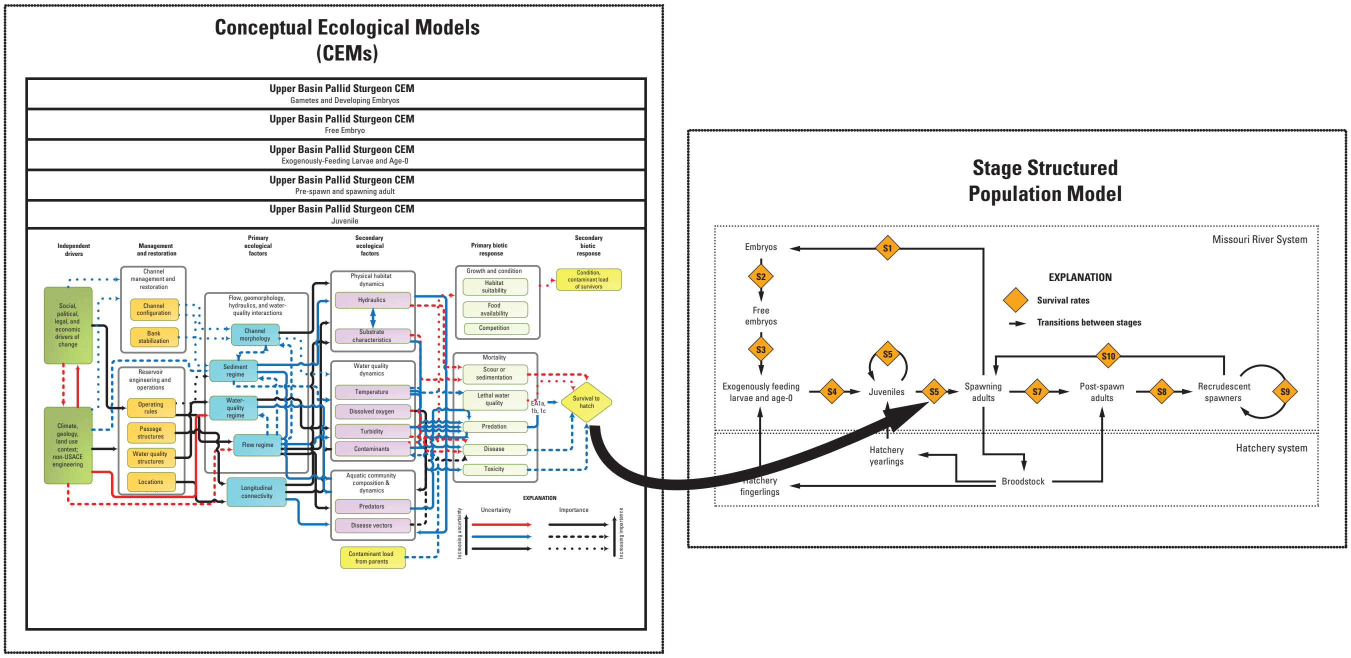


Figure 7. Life-stage specific conceptual ecological model predicting survival (left side), coupled with the generalized stage-structured population model, illustrating stage transitions (right side). The arrow illustrates how the predictions of secondary biotic responses from conceptual ecological models can be coupled dynamics.

A Stage-Structured Organization of Pallid Sturgeon Life History

Stages.—Stages were used to organize pallid sturgeon life history and as a framework to model population dynamics. Seven stages were used in the model to capture biologically important pallid sturgeon stage transitions similar to those identified in Wildhaber, DeLonay, and others (2011) and correspond to life stage-specific CEMs (Jacobson, Parsley, and others, 2015) (table 3). Pallid sturgeon life history in the Missouri River system was organized into the following seven stages (development rates provided are estimates and depend on factors like water temperature and diet):

1. *Embryo (E; 5–8 days).*—Period from fertilization to hatching.

2. *Free embryo (FE; 8–12 days post-hatch [dph]).*—Period from hatching until the larval fish begins feeding.

3. *Exogenously feeding larvae and age-0 (EFL; 8–12 dph to June 1).*—Period from full development of fin rays during the winter until June 1 of the following year. June 1 was selected as a fixed time to demarcate age-0 stages compared to age-1+ fish, which were simulated on an annual period.

4. *Juvenile (J; age-1 to age-9).*—Period of pallid sturgeon sexual immaturity; a fish can remain in this stage until age-9.

5. *Spawning adult (SP; age-7 to age-41).*—This stage includes juvenile fish that have become sexually mature and are ready to spawn and adult fish that have already spawned and are ready to spawn again.

6. *Post-spawn adult (PS).*—An adult fish that has released its gametes. The model assumes fish remain in this state until June 1 of the following year.

7. *Recrudescent adult (R).*—A post-spawn adult fish that is replenishing gametes. The fish may remain in this state for as much as 4 years.

Table 3. Demographic values, symbols, descriptions, and sources used in modeling population dynamics for Upper and Lower Missouri River Basin pallid sturgeon populations.

Symbol	Description	Value	Source
	Indices		
t	Time	Varies	None.
a	Age	Varies	None.
o	Hatchery or natural origin	Varies	None.
j	Time since spawning	Varies	None.
	State variables		
E	Number of fish in embryo stage	Varies	Calculated at initialization.
FE	Number of fish in free embryo stage	Varies	Calculated at initialization.
EFL	Number of fish in exogenously feeding larvae and age-0 stage	Varies	Calculated at initialization.
J	Number of fish in juvenile stage	Varies	Calculated at initialization.
Fingerlings	Number of hatchery-origin fingerling fish stocked	Varies	Calculated at initialization.
Yearlings	Number of hatchery-origin yearling fish stocked	Varies	Calculated at initialization..
SP	Number of fish in spawning stage	Varies	Calculated at initialization
R	Number of fish in recrudescent adult stage	Varies	Model input.
H	Number of fish taken to hatchery for broodstock	Varies	Calculated at initialization.
PS	Number of fish in post-spawn stage	Varies	Calculated at initialization.
	Demographic rates		
$S1$	Probability an oocyte is fertilized and gamete produced	Varies	Presently calibrated in each basin such that population is in equilibrium.
$S2$	Probability that an embryo survives ad transitions to a free embryo	Varies	Calculated at initialization.
$S3$	Probability that a free embryo survives and transitions to an exogenously feeding larva	Varies	Calculated at initialization.
$S4$	Probability that an exogenously feeding larvae survives and transitions to a juvenile	Varies	See table 5.
$S5$	Probability that a juvenile survives and transitions to adult stage	Varies	See table 5.
	Demographic values		
F	Female fecundity	Varies	See equation 13 and fig. 9.
M	Age-specific probability that a juvenile fish becomes sexually mature and transitions to the spawning stage	Varies	See fig. 9.
$M_{R,J}$	Probability of a recrudenscent adult returning to spawning stage given the years since last spawn	Varies	See fig. 10.
A_{max}	Maximum age	41	Keenlyne and others (1992).
Sex_{ratio}	Sex ration of adult pallid sturgeon	0.33	Steffensen and others (2013b).
α	Intercept for linear relationship of fecundity and fork length	-43678	Steffensen and others (2013b).
β	Slope term for relationship of fecundity and fork length	72.7	Steffensen and others (2013b).

Table 3. Demographic values, symbols, descriptions, and sources used in modeling population dynamics for Upper and Lower Missouri River Basin pallid sturgeon populations.—Continued

Symbol	Description	Value	Source
Demographic values—Continued			
FL	Average maximum fork length	1,683	Reynolds and Tyre (2011); Keenlyne and Jenkins (1993).
K	Growth coefficient	0.036	Reynolds and Tyre (2011); Keenlyne and Jenkins (1993).
t_0	Theoretical size at age-0	-5.9	Reynolds and Tyre (2011); Keenlyne and Jenkins (1993).

Each stage represents an important part of pallid sturgeon life history, varying in duration from days to years. The effect of hatchery operations on the population was accounted for with the addition of three stages specific to the hatchery system (fig. 6). These stages include the following:

1. *Broodstock (B).*—Sexually mature fish ready to spawn that are removed from the Missouri River system and used as a source of eggs and sperm to produce offspring in a controlled environment in a hatchery system.

2. *Fingerlings (F).*—Fish hatched and reared for 3–4 months in a hatchery system and released back into the Missouri River system.

3. *Yearlings (Y).*—Fish hatched and reared for 10–12 months in a hatchery system and released back into the Missouri River system.

Within the model, fish transitioning from one stage to another in a directed fashion is illustrated as arrows among text boxes in figure 6; for example, juvenile pallid sturgeon can remain at the juvenile stage or move into a spawning adult stage. Spawning adults can transition into three states: a post-spawn adult stage, removal from the population to enter hatchery broodstock, or removal because of mortality. Stages are further organized by hatchery- and natural-origin fish to account for hatchery operations within the system. Sexually mature fish can be removed from the spawning stage and become hatchery broodstock (fig. 6). These fish are then spawned and returned to the Missouri River system as post-spawn adults. The offspring of these fish are reared in the hatchery system and stocked into the Missouri River system as fingerlings or yearlings. The model allows for hatchery-origin fish to be stocked into the Missouri River system where they interact and may eventually spawn in the wild, resulting in naturally produced offspring.

The stage structure of the population model captures additional biological realism, specifically accounting for age-dependent demographic rates and values (for example, fecundity) (fig. 8). Within the larger age structure of the model, pallid sturgeon life-history stages were organized within the following age structure: (1) age-0—embryo, free embryo, and exogenously feeding larvae; (2) age-1 to age-9—juvenile, spawn, post-spawn, and recrudescent; and (3) age-7 to age-41—spawn, post-spawn, and recrudescent. Including age structure within the existing stage structure provided similarity with existing age-structured population viability models (Steffensen and others, 2013a; Bajer and Wildhaber, 2007).

Although uncertainties are substantial, in its present form the model provides a framework to simulate and explore pallid sturgeon dynamics and also to identify informational gaps. The model is limited in its predictive capability and should be used with the understanding that numerous caveats and conditions are warranted.

Pallid Sturgeon Population Model Specification

Embryos

Embryos represent the successful fertilization of an oocyte by a spermatocyte. The number of embryos at time (t) was modeled as:

$$E_t = S1 \cdot \sum_{A=1}^{A_{max}} F_a \left(Sex_{ratio} \cdot (SP_{a,t} - H_{a,t}) \right) \qquad (1)$$

where

- E_t is the number of fish in embryo stage at time (t),
- $S1$ is the probability an oocyte is fertilized and gamete produced,
- A_{max} is the maximum age (41; Keenlyne and others, 1992),
- A is the age,
- F_a is the female fecundity at age (a),
- Sex_{ratio} is the sex ratio of adult pallid sturgeon (0.33; Steffensen and others, 2013b),
- $SP_{a,t}$ is the number of fish in spawning stage at t and a, and
- $H_{a,t}$ is the number of fish taken to a hatchery for broodstock at t and a.

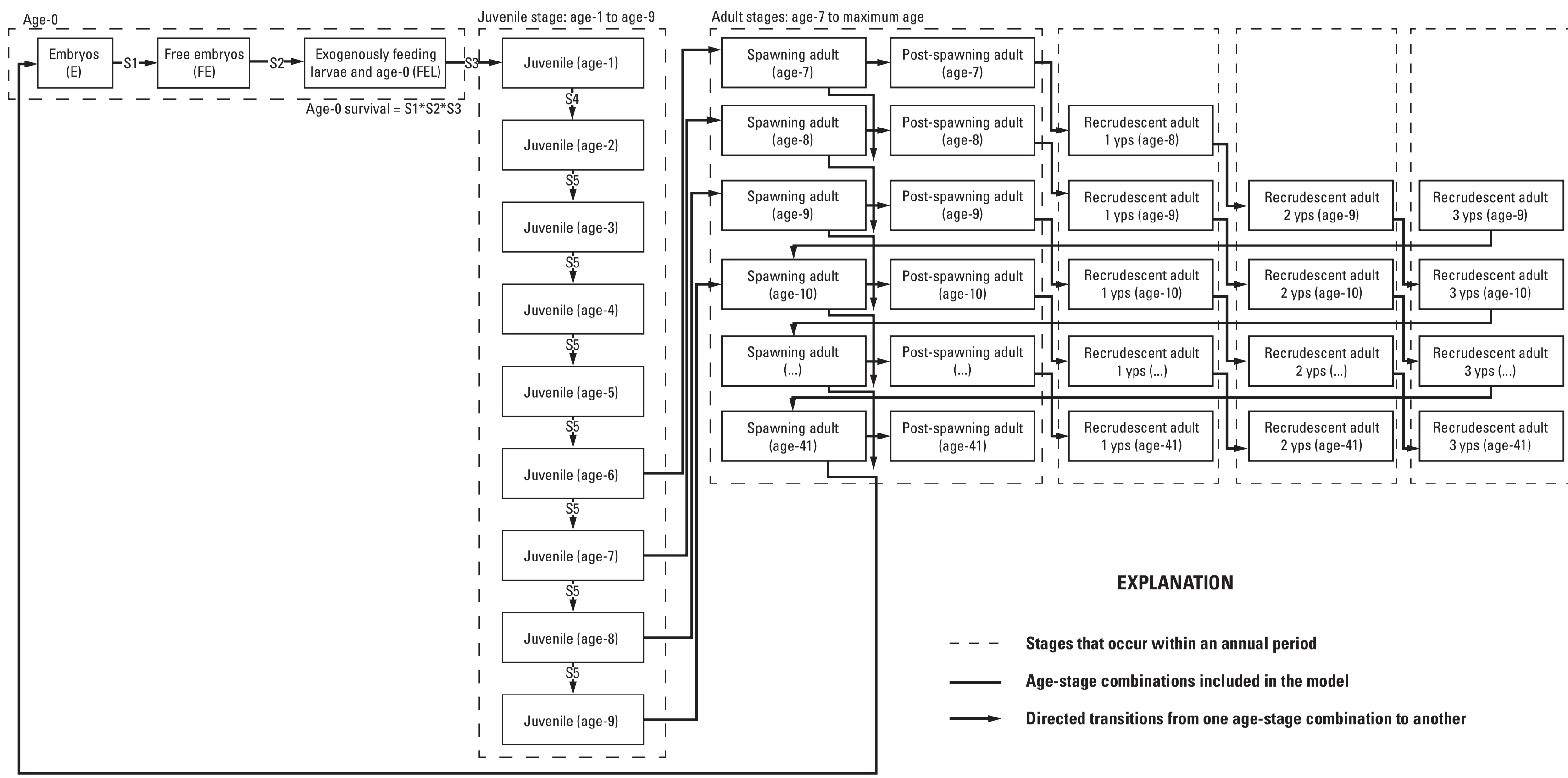


Figure 8. Conceptual ecological model illustrating additional age-structure added to the stage-structured pallid sturgeon population illustrated in figure 6.

Free Embryos

Free embryos are embryos that have escaped various sources of mortality, have hatched, and are living off of their yolk-sac reserves as they disperse until transition to first feeding as exogenously feeding larvae. These dynamics happen within a short period of days to weeks; therefore, the number of embryos at t is a function of the number of embryos at t, modeled as:

$$FE_t = S2 \cdot E_t \,, \tag{2}$$

where

- FE_t is the number of fish in free-embryo stage at time t,
- E_t is the number of fish in embryo stage at time t, and
- $S2$ is probability that an embryo survives and transitions to a free embryo.

Exogenously Feeding Larvae and Age-0

Exogenously feeding larvae and age-0 pallid sturgeon represent the longest life stage (lasting several months) modeled during the first year of life. These fish have transitioned to feeding in their environment. This life stage, however, still happens within the first year of life; therefore, the number of exogenously feeding larvae and age-0 at t is a function of the number of free embryos at t, modeled as:

$$EFL_t = S3 \cdot FE_t \,, \tag{3}$$

where

- EFL_t is the number of fish in exogenously feeding larvae and age-0 stage at time t,
- $S3$ is the probability that a free embryo survives and transitions to an exogenously feeding larvae, and
- FE_t is the number of fish in embryo stage at time t.

Juvenile (Age-1)

Pallid sturgeon can remain in the juvenile stage for many years. Additionally, this stage is typically the recipient of population supplementation in the form of hatchery stockings of fingerlings (age-0) and yearlings (age-1). It is at this stage that differentiation between natural- and hatchery-origin pallid sturgeon is recognized in the model. Specifically, the model assumes that natural-origin pallid sturgeon were spawned, fertilized, and hatched in the Missouri River system, whereas hatchery-origin pallid sturgeon received external input from a hatchery system. The number of natural-origin age-1 juveniles was modeled as a function of exogenously feeding larvae and age-0 as:

$$J_{a=1,t,o=natural} = S4 \cdot EFL_t \,, \tag{4}$$

where

- J is the number of fish in juvenile stage,
- a is the age,
- t is the time,
- o is hatchery or natural origin,
- $S4$ is the probability that an exogenously feeding larvae survives and transitions to the juvenile stage, and
- EFL_t is the number of fish in exogenously feeding larvae and age-0 stage at t.

The number of hatchery-origin juveniles at t was a function of hatchery inputs and modeled as:

$$J_{a=1,t,o=hatchery} = S4 \cdot Fingerlings_t \,, \tag{5}$$

where

- J is the number of fish in juvenile stage,
- a is the age,
- t is the time,
- o is hatchery or natural origin, and
- $Fingerlings_t$ is the number of hatchery origin fingerling fish stocked at t.

The model assumes that fingerlings are added after a period of substantial mortality and, therefore, transition to the juvenile stage with no additional mortality.

Juvenile (Age-2)

Pallid sturgeon juveniles exceeding 2 years of age have effectively escaped the demographic bottleneck of low survival associated with preceding early life-history stages. Annual survival is estimated to exceed 0.9 in the upper river and 0.91 in the lower river (table 5). Similar to age-1 juveniles, the model accounts for hatchery- and natural-origin pallid sturgeon with the additional accounting for yearlings stocked in the system as:

$$J_{a=2,t,\, o=hatchery} = S5 \cdot J_{a=1,t,o=hatchery} + Yearlings_t \,, \tag{6}$$

where

- J is the number of fish in juvenile stage,
- a is the age,
- t is the time,
- o is hatchery or natural origin,
- $S5$ is the probability that fish in the juvenile stage survive and transition to the adult stage, and
- $Yearlings_t$ is the number of hatchery origin yearlings at time t.

Natural-origin age-2 juveniles were modeled as:

$$J_{a=2,t,\ o=natural} = S5 \cdot J_{a=1,t,o=natural}\ , \qquad (7)$$

where
- J is the number of fish in juvenile stage,
- a is the age,
- t is the time,
- o is hatchery or natural origin, and
- $S5$ is the probability that fish in the juvenile stage survive and transition to the adult stage.

Juvenile (Greater Than Age-2)

The remaining age classes contained within the juvenile stage are modeled in the same manner regardless of origin, with the future number of juveniles being a function of the current number of juveniles less those juveniles that became sexually mature and transitioned into the spawning stage or died. The annual transition from one age to another was modeled as:

$$J_{a+1,t+1,o} = \left(1 - M_{Juvenile,\ a}\right) \cdot \left(S5 \cdot J_{a,t,o}\right), \qquad (8)$$

where
- J is the number of fish in juvenile stage,
- a is the age,
- t is the time,
- o is hatchery or natural origin,
- $M_{Juvenile}$ is the age-specific probability that a juvenile fish becomes sexually mature and transitions to the spawning stage, and
- $S5$ is the probability that fish in the juvenile stage survive and transition to the adult stage.

Spawning Adults

The spawning adult stage represents pallid sturgeon that are sexually mature, either as juvenile fish that finally achieve sexual maturity or adult fish that have previously spawned and are returning to sexual maturity after gamete regeneration. This process was modeled as:

$$SP_{a+1,t+1} = M_{Juvenile,\ a} \cdot J_{a,t} + \sum_{i=1}^{4} M_{R,j} \cdot R_{i,a,t}\ , \qquad (9)$$

where
- SP is the number of fish in spawning stage,
- a is the age,
- t is the time,
- $M_{Juvenile}$ is the age-specific probability that a juvenile fish becomes sexually mature and transitions to the spawning stage,
- J is the number of fish in juvenile stage,
- i is a counter for number of years,
- $M_{R,j}$ is the probability of a recrudescent adult returning to spawning stage given the years since last spawn, and
- R is the number of fish in a recrudescent state.

Post-Spawn Adults

Once sexually mature pallid sturgeon spawn, they transition into a post-spawn stage in the same annual period. Additionally, sexually mature fish that were removed from the spawning population during broodstock collection are returned to the population in a post-spawn stage. Formally, this within-year dynamic was represented as:

$$PS_{a,\ t,o} = SP_{a,t,o} + H_{a,t,o}\ , \qquad (10)$$

where
- PS is the number of fish in the post-spawn stage,
- a is the age,
- t is the time,
- o is hatchery or natural origin,
- SP is the number of fish in spawning stage,
- H is the number of fish taken to a hatchery for broodstock.

Equation (10) assumes no mortality happens during the spawning period and broodstock collection operations; this assumption can be relaxed if mortality is determined to be substantial.

Recrudescent Adult (1 Year Post-Spawn)

Pallid sturgeon spawning in year t transition to a recrudescent adult stage in year t+1. During this stage, fish are actively replenishing gametes, typically remaining in a recrudescent stage for as much as 4 years. One year post-spawning, fish transition from a post-spawn stage to a recrudescent stage as:

$$R_{j=1,a+1,\ t+1,o} = PS_{a,t,o} - \left(1 - S5\right) \cdot PS_{a,t}\ , \qquad (11)$$

where
- R is the number of fish in a recrudescent state,
- j is the time since spawning,
- a is the age,
- t is the time,
- o is hatchery or natural origin,
- PS is the number of fish in the post-spawn stage, and
- $S5$ is the probability that fish in the juvenile stage survive and transition to the adult stage.

Recrudescent Adult (Greater Than 1 Year Post-Spawn)

Pallid sturgeon recrudescent adults that are greater than 1 year post-spawn were modeled as a linear function of the number of recrudescent adults in the previous year and age that survived and did not return to a spawning state. Formally, this relation was expressed as:

$$R_{j+1,\,a+1,\,t+1,o} = \left(1 - M_{R,\,j}\right) \cdot \left(S5 \cdot R_{j,a,\,t,o}\right), \tag{12}$$

where

- R is the number of fish in a recrudescent state,
- j is the time since spawning,
- a is the age,
- t is the time,
- o is hatchery or natural origin,
- $M_{R,j}$ is the probability of a recrudescent adult returning to spawning stage given the years since last spawn, and
- $S5$ is the probability that fish in the juvenile stage survive and transition to the adult stage.

Pallid Sturgeon Population Model Values

A variety of sources were used to determine values required by equations 1–12 to simulate pallid sturgeon population dynamics. Four types of data were required: (1) initial population abundances, (2) demographic values (for example, sex ratio), (3) demographic rates (for example, survival), and (4) demographic functions (for example, maturity and fecundity). Functions relating demographic values to age were developed using existing data, relations, and expert opinion.

Initial stage-specific abundances for upper and lower river natural- and hatchery-origin populations are used to stochastically begin the population model from an empirically derived triangular distribution (table 4). Survival rates were also stochastically drawn from triangular distributions given empirical estimates and associated ranges of uncertainties (table 5). Additional demographic values (for example, sex ratio), uncertainties, and data sources are in table 3.

Functions relating age or time since an event were required to predict additional age- or time-dependent demographic rates. In the simulation model, fecundity (eggs per female) was predicted as a function of age (fig. 9) using the following:

$$Fecundity = \alpha + \left(FL_{\infty} \cdot \left(1 - e^{-K \cdot A - t_0}\right)\right)^{\beta}, \tag{13}$$

where

- α is the intercept for the linear relation of fecundity and fork length (Steffenson and others, 2013b),
- FL_{∞} is the average maximum fork length (Reynolds and Tyre, 2011; Keenlyne and Jenkins, 1993),
- e is a constant, the base of the natural logarithm,
- K is the growth coefficient (Reynolds and Tyre, 2011; Keenlyne and Jenkins, 1993),
- A is the age,
- t_0 is the theoretical size at age-0 (Reynolds and Tyre, 2011; Keenlyne and Jenkins, 1993), and
- β is the slope term for the relation of fecundity and fork length (Steffensen and others, 2013b).

Table 4. Stage- and origin-specific initial abundance used in modeling population dynamics for Upper and Lower Missouri River Basin pallid sturgeon populations.

[Minimum, maximum, and expected values were used to parametrize a triangular distribution from which initial abundance values were stochastically drawn from for simulations.]

Stage	Basin	Origin	Value			Source
			Minimum	Expected	Maximum	
Juvenile	Lower Missouri River Basin	Hatchery	3,750	4,000	4,250	K. Steffensen, written commun.
		Natural	0	500	1,000	K. Steffensen, written commun.
	Upper Missouri River Basin	Hatchery	73,439	97,220	121,025	Rotella (2013)
		Natural	0	500	1,000	Unknown (assumed to be similar abundances to the Lower Missouri River Basin)
Adult	Lower Missouri River Basin	Hatchery	18,000	21,500	25,000	K. Steffensen, written commun.
		Natural	0	500	1,000	K. Steffensen, written commun.
	Upper Missouri River Basin	Hatchery	275	480	687	Rotella (2013)
		Natural	129	158	193	Braaten and others (2009)

Table 5. Stage- and origin-specific survival rates used in modeling population dynamics for Upper and Lower Missouri River Basin pallid sturgeon populations.

[Minimum, maximum, and expected values were used to parametrize a triangular distribution from which survival values were stochastically drawn from for simulations.

Basin	Survival	Value			Source
		Minimum	Expected	Maximum	
Lower Missouri River Basin	S0	0.02	0.051	0.1	Steffensen and others (2013b)
	S_a = 1	0.6	0.686	0.75	Steffensen and others (2013b)
	S_a≥2	0.9	0.922	0.95	Steffensen and others (2013b)
Upper Missouri River Basin	Age-0[a]	0.02	0.051	0.1	Steffensen and others (2013b)
	Age-1[b]	0.423	0.633	0.83	Hadley and Rotella (2009)
	Age-2[b]	0.64	0.81	0.97	Hadley and Rotella (2009)
	Age-3[b]	0.82	0.92	1	Hadley and Rotella (2009)
	Age-4+[b]	0.71	0.82	0.94	Hadley and Rotella (2009)

[a]Age-0 survival estimates were unavailable, therefore lower basin estimates used

[b]Survival values are average of values reported for RPMA1, RPMA2, and RPMA3

A sexual maturity function, which calculated the probability of a juvenile fish transitioning to an adult fish as a function of age (fig. 9), was parameterized to reflect the minimum and maximum age at sexual maturity reported by Keenlyne (1997). Similarly, the probability of a recrudescent adult returning to sexual maturity was predicted as a function of years post-spawning (fig. 10). These probabilities were selected to estimate a spawning interval of 2.5 years (Steffensen and others, 2013a).

Beginning the Pallid Sturgeon Population Model

Beginning the pallid sturgeon population model required three steps: (1) stochastically selecting stage-specific demographic rates from an empirically based distribution, (2) stochastically selecting stage-specific abundances (also from an empirically based distribution), and (3) allocating stage-specific abundance among age classes. Demographic rates were stochastically generated from triangular distributions representing the minimum, most likely, and maximum values for each parameter. For early life-history stages where no survival estimates exist, survivals were randomly selected subject to the constraint that the product of early life-stage survival rates equaled an estimate of age-0 survival. Stage-specific initial abundances were randomly selected from triangular distributions. Age-specific abundances within each age class were then stochastically generated assuming a stable age distribution. Specifically, the cumulative age-specific survival was calculated for each age and used to allocate fish among ages assuming multinomial distribution. Once fish were allocated to age-classes within the adult stage, they were uniformly allocated among spawning and recrudescent stages.

Analysis—Simulating Pallid Sturgeon Population Dynamics

Sensitivity

A sensitivity analysis was used to evaluate the effect of parameter uncertainty on pallid sturgeon population dynamics simulated for the lower and upper river. The sensitivity analysis was performed by randomly drawing parameters within parameter extremes assuming a triangular distribution. Randomly selected values were used to begin the population model and the population simulated during a 100-year period. Population abundances at year 100 were simulated for juvenile and adult stages of hatchery- and natural-origin pallid sturgeon. This process was replicated 10,000 times to capture parameter variability. Yearling stocking was set to the basin-specific average value. Model parameter values were then assigned to quantiles (0–25, 25–50, 50–75, and 75–100 percent). Stage- and origin-specific mean abundances were calculated for each quantile and used to construct tornado plots to visualize how parameter uncertainty contributes to variation in abundances at year 100.

Modeled Conditions

The parameterized model was also used to evaluate several conditions and address three questions regarding the upper and lower river pallid sturgeon populations.

1. What is the population growth rate (lamda [λ]) under (A) present stocking conditions and (B) no stocking?

This condition was evaluated using the same steps of the sensitivity analysis with the exception that a condition was added in which yearling stocking was set to zero and simulated for the upper and lower river populations.

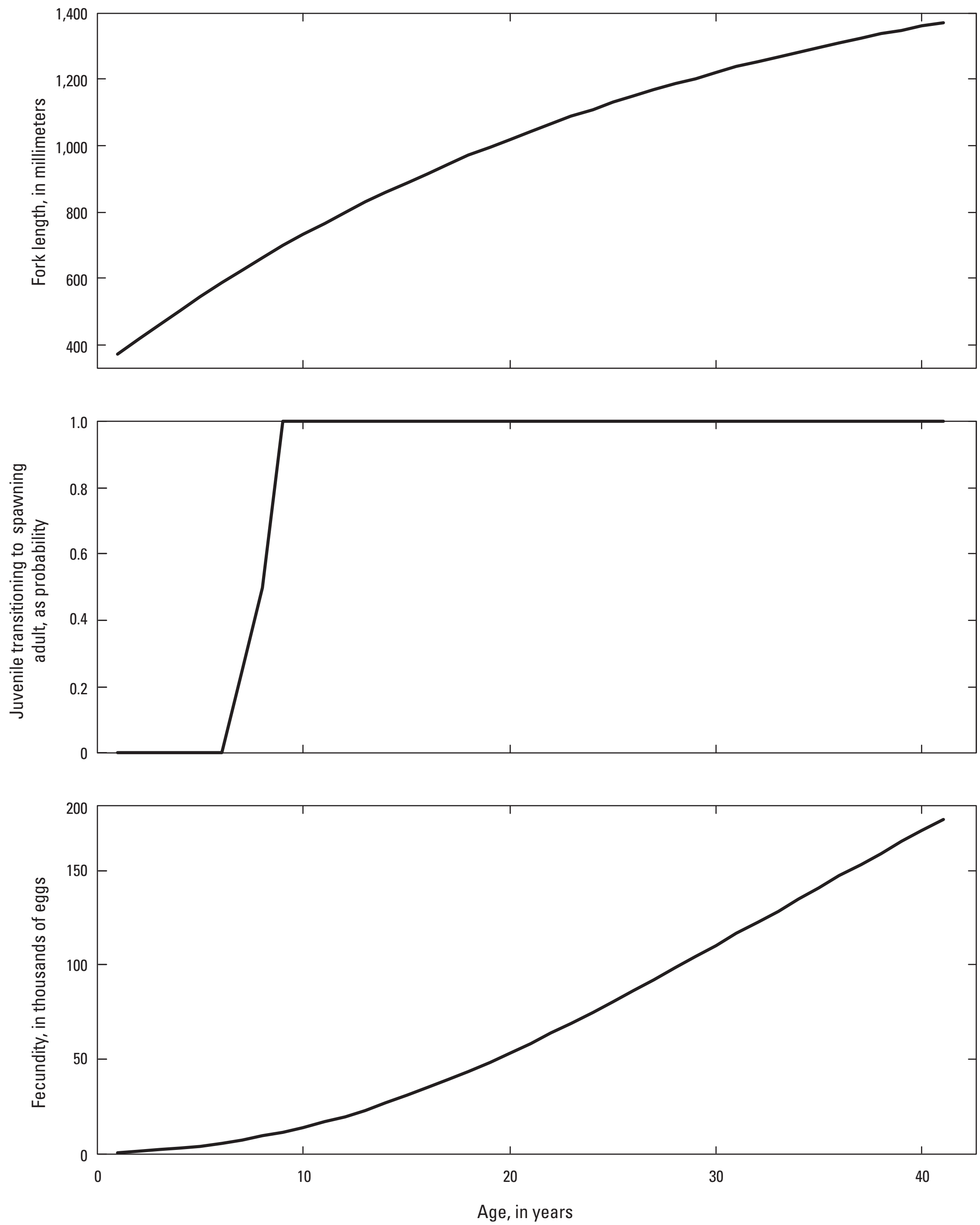


Figure 9. Fork length, probability of a juvenile stage fish becoming sexually mature, and fecundity versus age for pallid sturgeon in the Missouri River System.

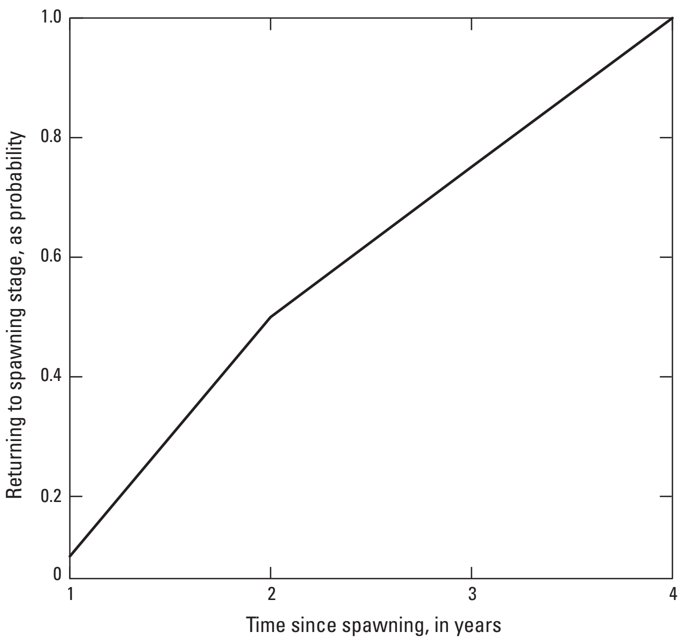


Figure 10. Probability of a recrudescent adult returning to spawning stage by years since last spawning.

A stochastic growth rate λ was calculated for each of the 10,000 replicates as the geometric mean of annual growth rates for each replicate.

2. How much would early life-history survival need to increase to achieve λ greater than or equal to (≥) 1 (a growing population) without stocking?

Early life-history survival is an important determinant of population growth rate and dynamics in many fish populations. The use of population supplementation can circumvent poor survival of early life-history stages and maintain population abundances. In this condition, the question is "how high does early life-history survival need to be to maintain or increase the population (that is, λ≥1)?" This question was evaluated by performing a grid search of values for $S1$ and $S_{A=0}$($S_{A=0}$=$S2$×$S3$×$S4$). Specifically, $S1$ was evaluated for values of 0.001 to 0.003 by increments of 0.0002, and $S_{A=0}$ was evaluated for values of 0.01 to 0.1 by increments of 0.01 for the upper and lower river populations. Stocking values were set at 0 and the population simulated for a 100-year period, and we simulated 100 replicate model runs for each unique combination of $S1$ and $S_{A=0}$. The mean stochastic λ and proportion of the 100 replicates with a mean stochastic λ≥1 were calculated for each combination of $S1$ and $S_{A=0}$.

3. Is the population sensitive to a depensation effect and what population size is needed to get past critical depensation?

Spawning population abundance is hypothesized to limit embryo production. The mechanism underlying this hypothesis relates to the likelihood of spawning aggregations, especially when spawning abundances are low and sexually mature fish may have difficulties finding one another in the highly altered Lower Missouri River (fig. 2*B*). To explore this hypothesis, we substituted $S1$ in equation 1 with a model that predicts $S1$ as a sigmoidal function of spawning adult population numbers as:

$$S1 = \beta_{max} \cdot \left(1 + e^{-d\cdot(SP - SP_{50})}\right)^{-1}, \tag{14}$$

where

- $S1$ is the probability that an oocyte is fertilized and gamete produced,
- β_{max} is the maximum probability of transitioning to a fertilized embryo,
- e is a constant, the base of the natural logarithm,
- d is a parameter indicating how quickly the function approaches β_{max},
- SP is the number of fish in spawning stage, and
- SP_{50} is the number of spawning fish that reach 50 percent of β_{max}.

The relation reduces the probability of eggs becoming embryos, especially at low spawning population abundances (that is, Allee or depensation effect) (fig. 11). The probability increases with increasing spawning population abundance until a maximum probability is reached. A visual analysis of the previous stocking scenarios (average stocking and no stocking) accounting for the hypothesized depensation effect is used to illustrate the analysis. Results of this analysis are not meaningful at this time because the underlying depensatory relation and parameters needed to predict embryo production are unknown. This analysis is provided only to illustrate model capabilities if useful data were to become available in the future.

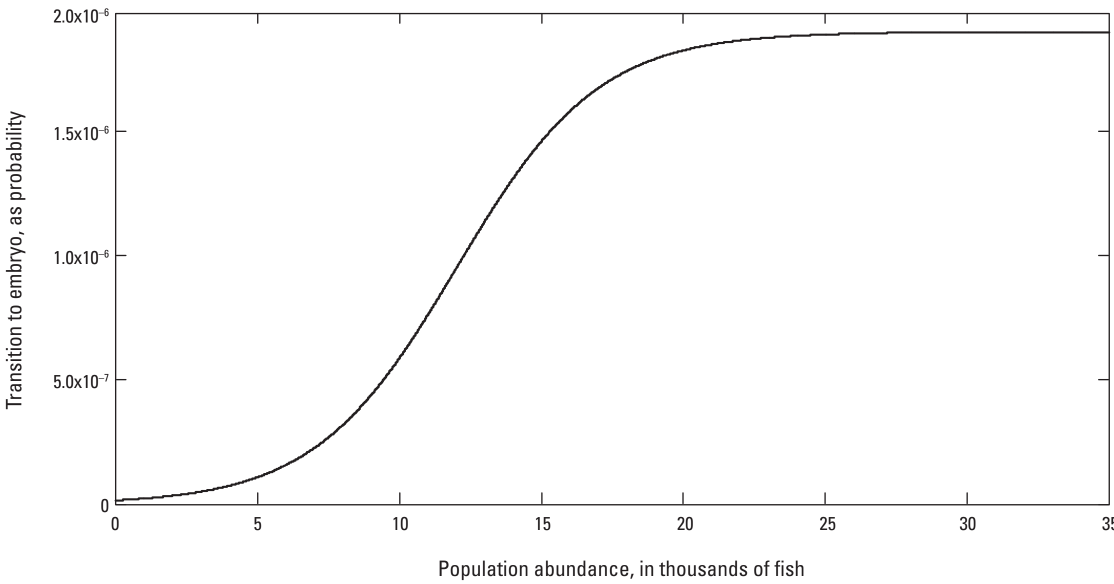


Figure 11. Number of fertilized embryos produced versus population abundance. The nonlinear function relating abundance to embryos accounts for a depensatory response (that is, an allee effect) where the number of fertilized embryos is lower at low population abundance, representing hypothesized reduced likelihood of spawning adult aggregations.

Preliminary Results—Simulating Pallid Sturgeon Population Dynamics

Sensitivities

Stage-specific sensitivity analyses for population abundance in year 100 varied between Upper and Lower Missouri River (fig. 2*B*) populations (figs. 12–16). The number of natural-origin pallid sturgeon adults in year 100 was most sensitive to early life-history survival (age-0 to age-1) for the upper river; and a mix of hatchery-origin adult abundance, early life-history survivals, and sex ratio (fig. 12). Similar patterns of parameter sensitivity resulted for natural-origin juveniles (fig. 13). Hatchery-origin adults and juvenile sensitivities also varied between the upper and lower rivers, and juvenile survival played a role in upper-river population dynamics and a mix of factors in the lower river (figs. 14 and 15). Similarly, sensitivity results varied between river sections for total population abundance; there was a stronger influence of hatchery supplementation in the lower river, followed by early life-history survival, sex ratio, and adult abundance (that is, factors linked in embryo production) (fig. 15), whereas the upper river dynamics were sensitive to early life-history survival and sex ratio. Sensitivity results for the total populations in the upper and lower rivers are shown in figure 16.

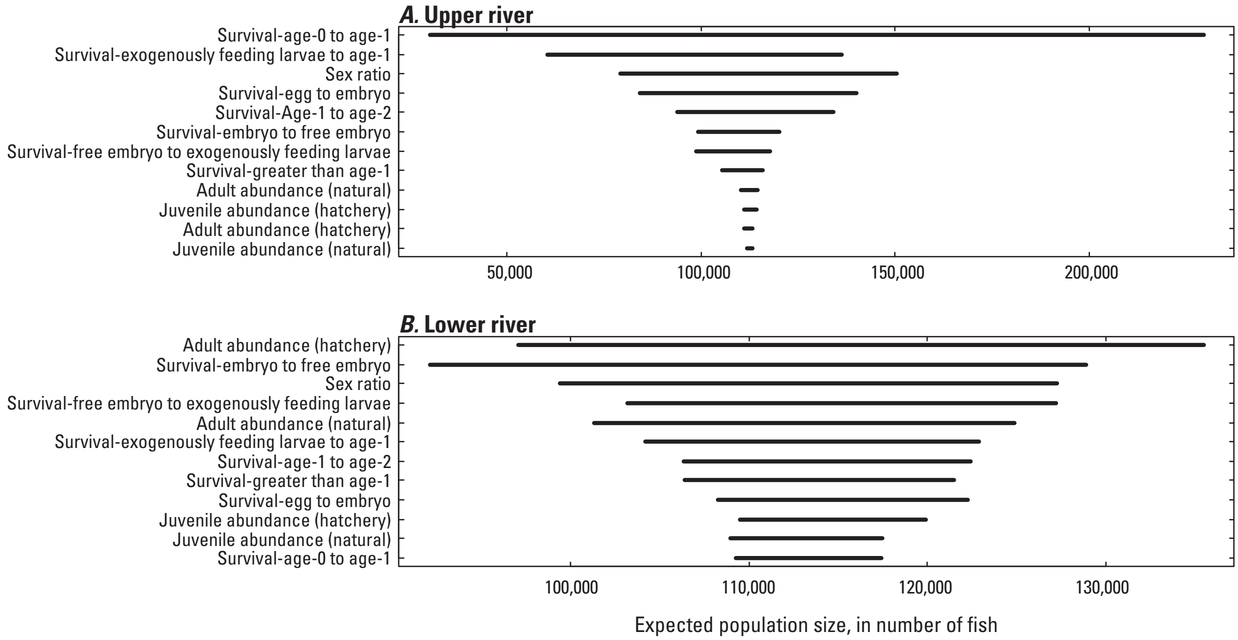


Figure 12. Tornado diagram of sensitivity of population abundance in year 100 for natural-origin adults in the upper river, *A*, and lower river, *B*. Sensitivity of population abundances in year 100 increases with horizontal bar width, therefore parameter sensitivity increases along the *y*-axis.

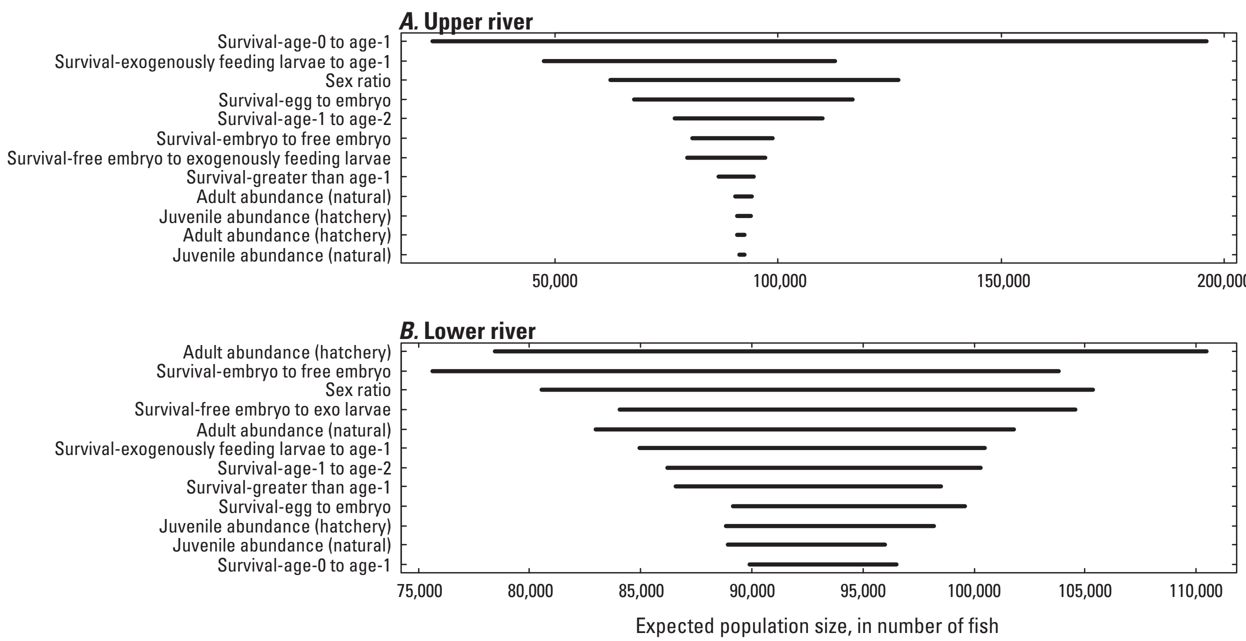


Figure 13. Tornado diagram of sensitivity of population abundance in year 100 for natural-origin juveniles in the upper river, *A*, and lower river, *B*. Sensitivity of population abundances in year 100 increases with horizontal bar width, therefore parameter sensitivity increases along the *y*-axis.

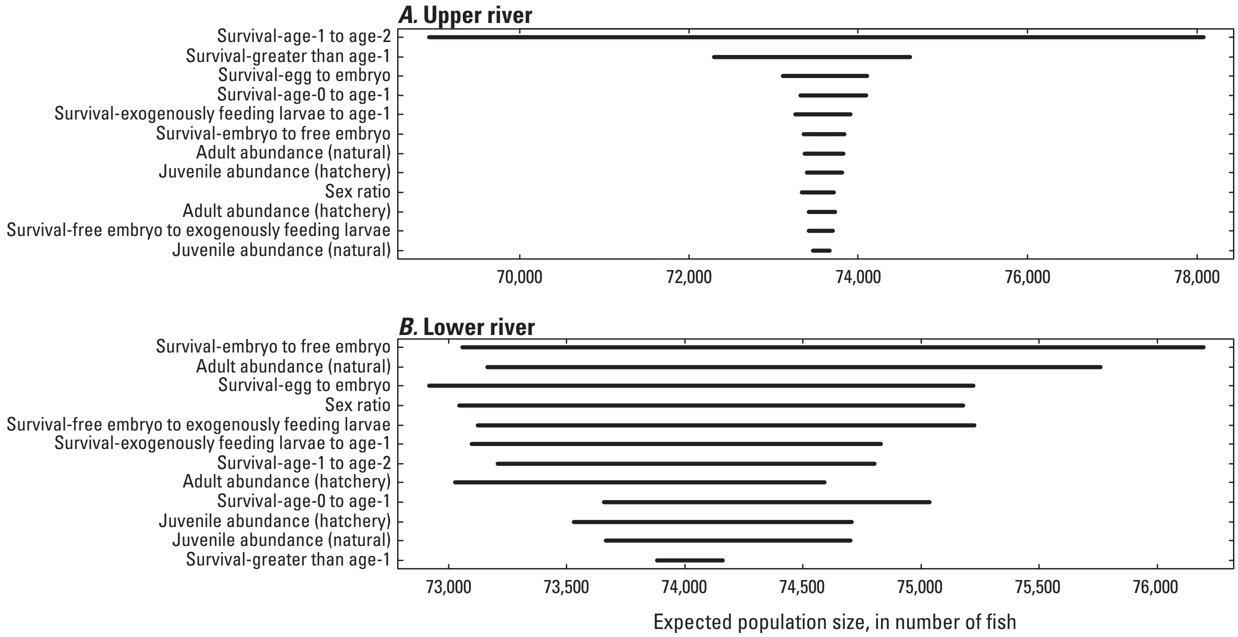


Figure 14. Tornado diagram of sensitivity of population abundance in year 100 for hatchery-origin adults in the upper river, *A,* and lower river, *B*. Sensitivity of population abundances in year 100 increases with horizontal bar width, therefore parameter sensitivity increases along the *y*-axis.

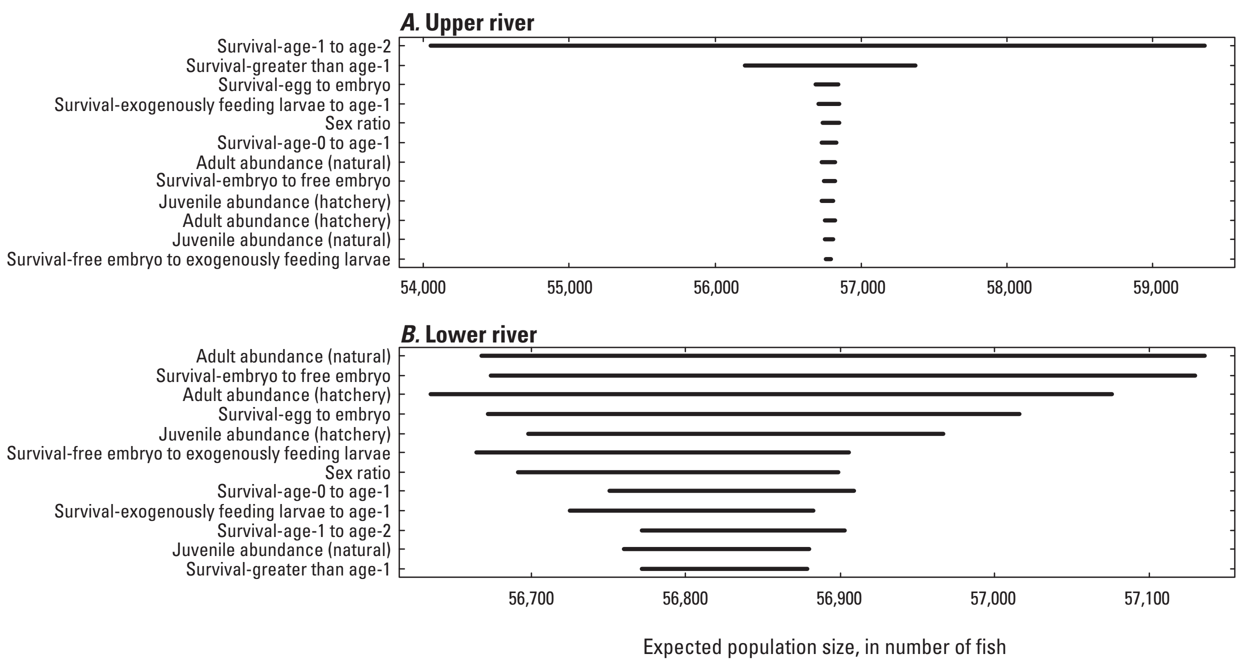


Figure 15. Tornado diagram of sensitivity of population abundance in year 100 for hatchery-origin juveniles in the upper river, *A,* and lower river, *B*. Sensitivity of population abundances in year 100 increases with horizontal bar width, therefore parameter sensitivity increases along the *y*-axis.

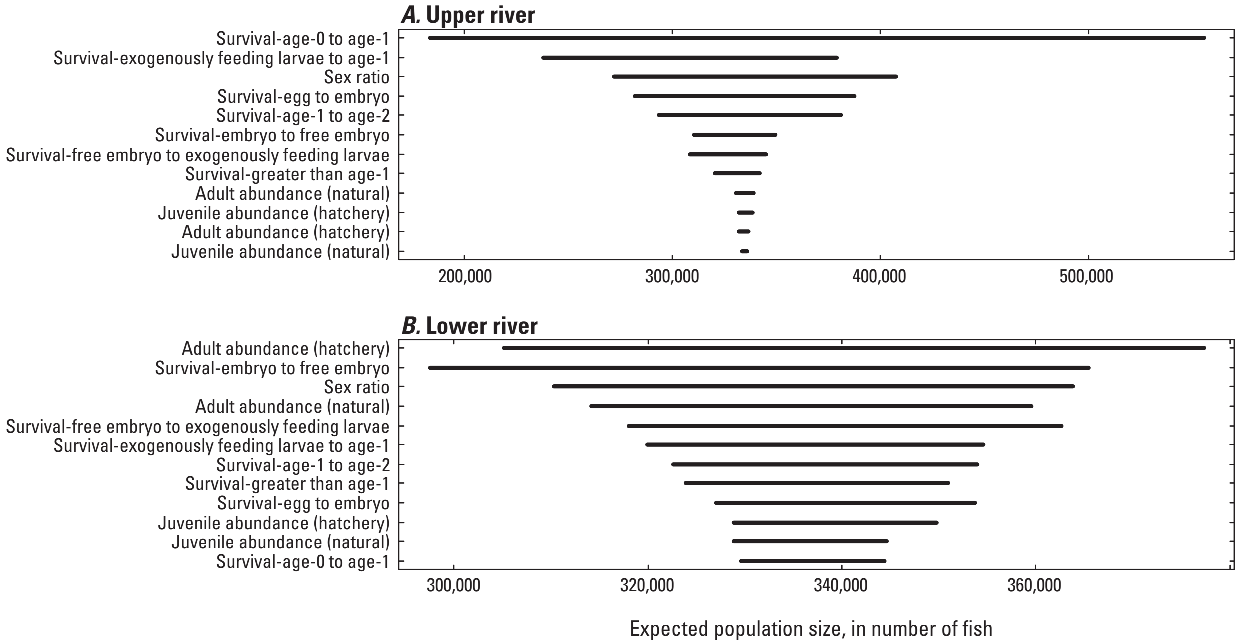


Figure 16. Tornado diagram of sensitivity of population abundance in year 100 for all stages and origins (total population) for upper river, *A*, and lower river, *B*, population simulations. Sensitivity of population abundances in year 100 increases with horizontal bar width, therefore parameter sensitivity increases along the *y*-axis.

Modeled Conditions

1. What is the population growth rate (λ) under (A) present stocking conditions and (B) no stocking?

Population dynamics exhibited high variability among runs, which was not unexpected given the degree of uncertainties in model parameters. In average stocking scenarios, populations tended to increase for all stages in the upper and lower rivers (figs. 17–20). This is not an unexpected result given high survival rates of stocked fish greater than age-0 and the lack of density dependence in the model. In reality, lack of food or space would be expected to increase mortality at some point and regulate maximum population size; density dependent processes may be included in future iterations of the model. In conditions of no stocking, most replicates tended to decline during the 100-year simulations for natural-origin juveniles and adults as existing hatchery-origin fish senesced out of the population (figs. 17–18). There were certain rare parameter combinations of high early-life stage survivals that resulted in increasing abundance of natural-origin fish under no-stocking conditions. As expected, hatchery-origin fish abundance declined to 0 during the 100-year simulations when no fish were stocked (figs. 19 and 20). All populations and stages are shown in figure 21. Evaluating distributions of growth rates (λ) for each scenario, all stocking scenarios had a growth rate greater than 1 (fig. 22). With the cessation of stocking, upper river simulations were more likely to have a growth rate less than 1, and most simulations for the lower river had population growth rates less than 1.

2. How much would early life-history survival need to increase to achieve λ≥1 without stocking?

There was uncertainty in how much critical survival parameters need to increase to achieve a population growth rate (λ) greater than 1. In particular, varying combinations of $S1$ and $S_{A=0}$ can achieve a population growth rate greater than 1 given the parameters used to model the population. In general, simulations indicated that combinations of $S1$ exceeding 0.0012 and $S_{A=0}$ exceeding 0.02 for the upper river, and $S1$ exceeding 0.001 and $S_{A=0}$ exceeding 0.02 for the lower river, resulted in positive population growth in no stocking conditions (fig. 23).

3. Is population sensitive to a depensation effect and what population size is needed to get past critical depensation?

The structure of the population model accommodated evaluation of a depensation scenario relating spawning population abundance to embryo production; however, it is important to reiterate that the underlying functional relation of a depensatory effect of spawning population abundance on embryo production is uncertain; and results are, therefore, highly uncertain. Relative to average stocking rates and no stocking rates, simulating the same conditions including a depensatory effect of population size on embryo production resulted in lower total population abundances and reduced population growth rates (fig. 24).

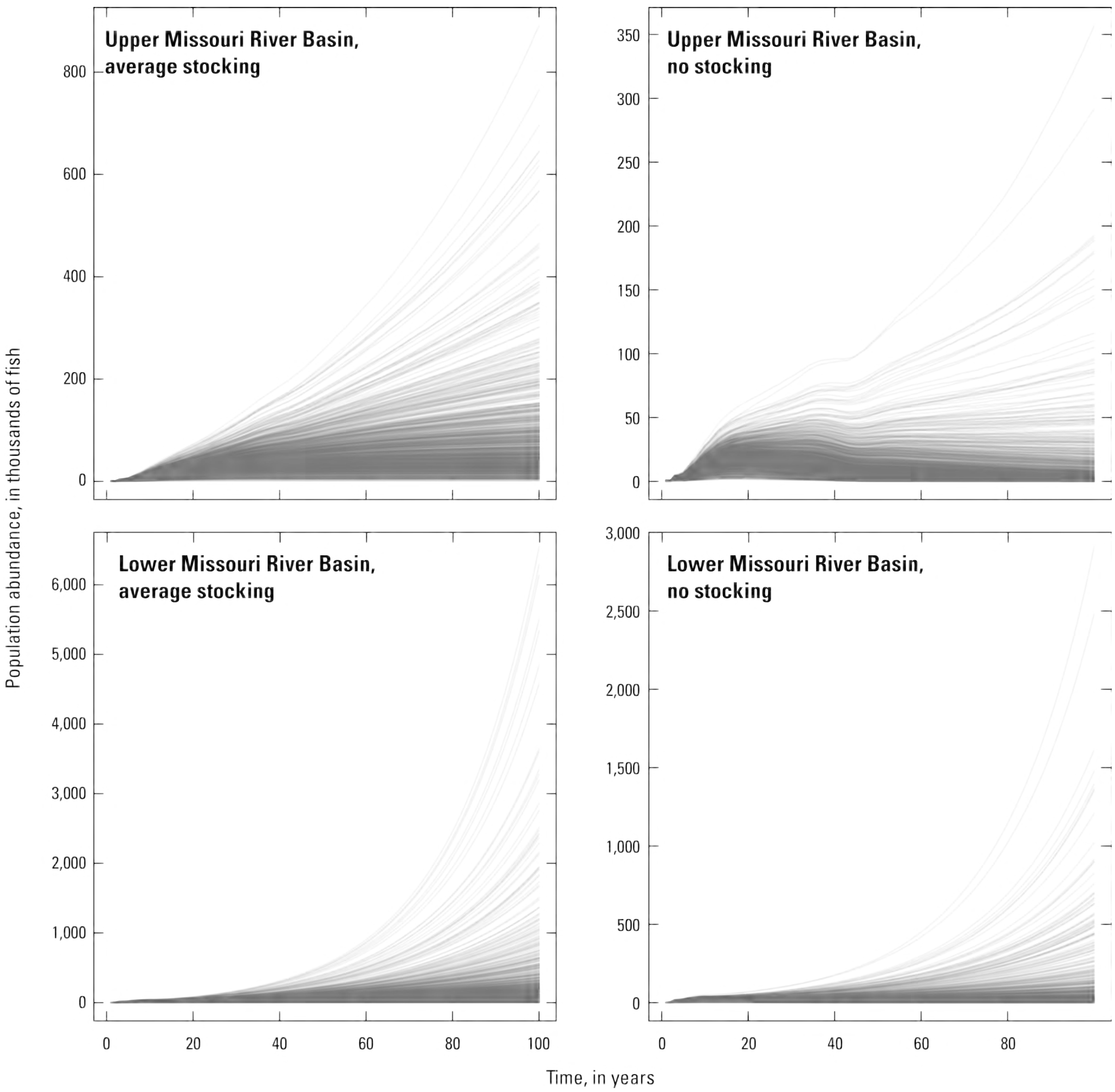


Figure 17. Simulated population abundance for natural-origin juveniles for the Upper and Lower Missouri River Basins for scenarios representing average stocking conditions and no stocking. Darker areas represent higher simulation densities.

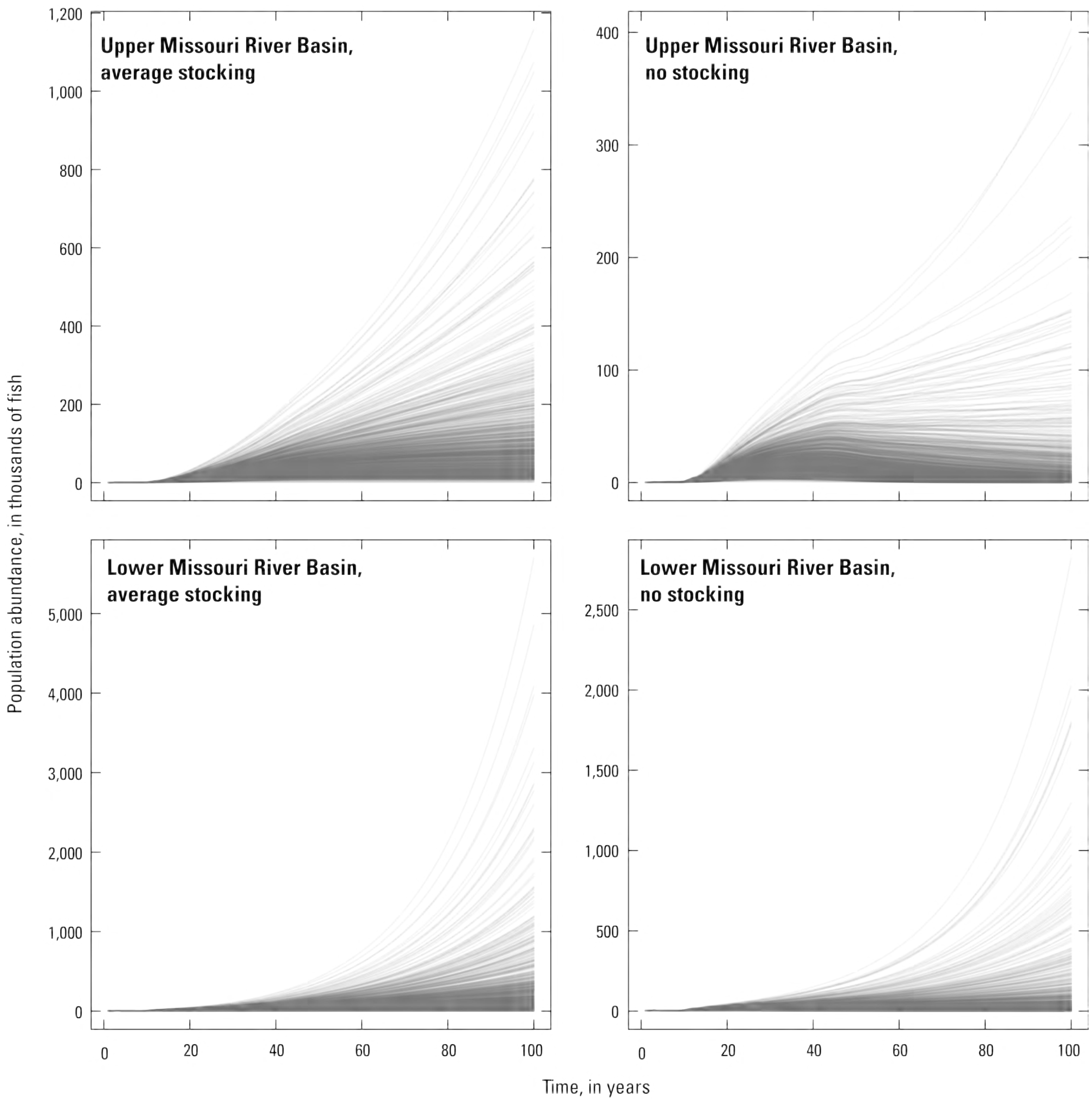


Figure 18. Simulated population abundance for natural-origin adults for the Upper and Lower Missouri River Basins for scenarios representing average stocking conditions and no stocking. Darker areas represent higher simulation densities.

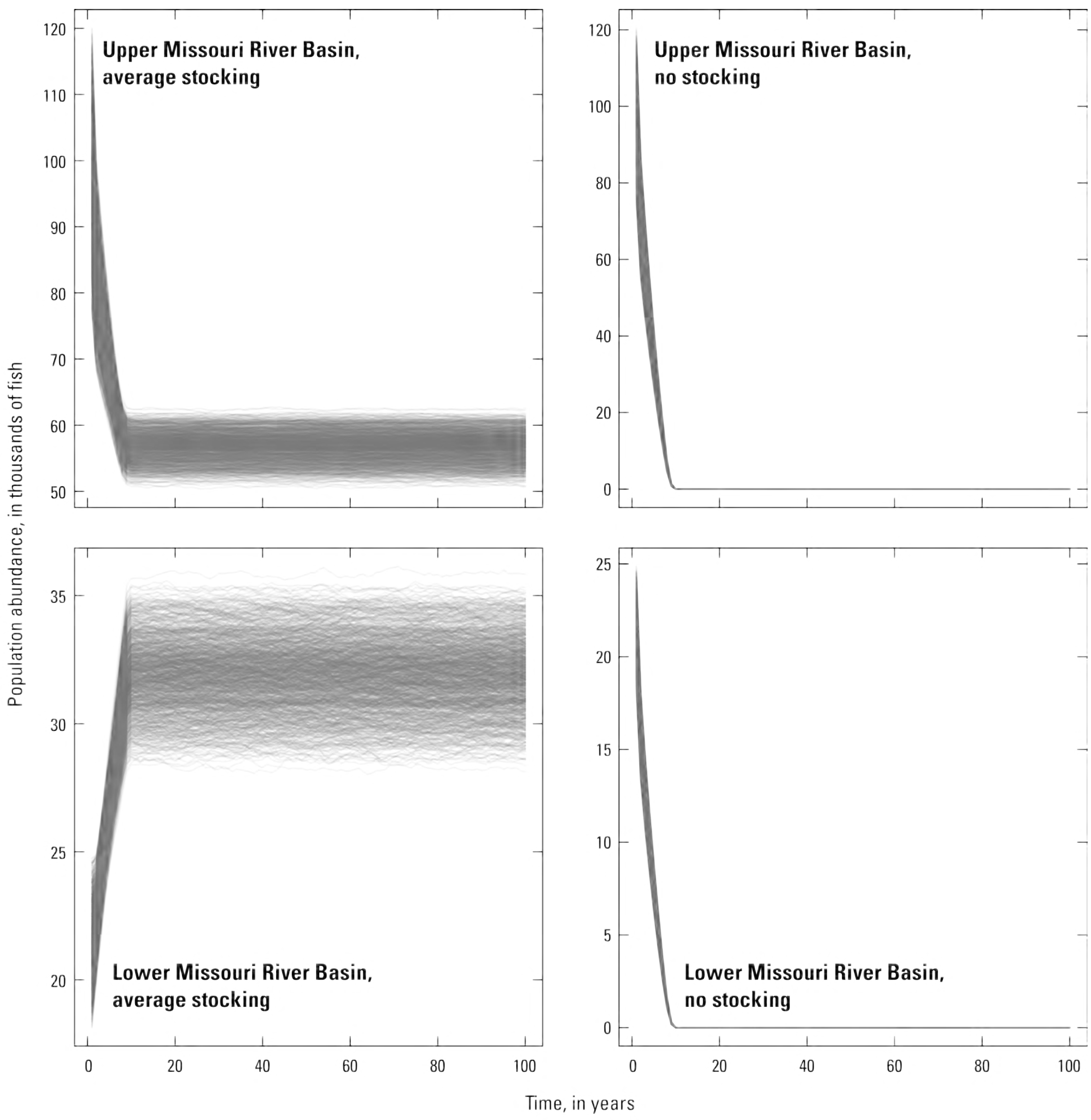


Figure 19. Simulated population abundance for hatchery-origin juveniles for the Upper and Lower Missouri River Basins for scenarios representing average stocking conditions and no stocking. Darker areas represent higher simulation densities.

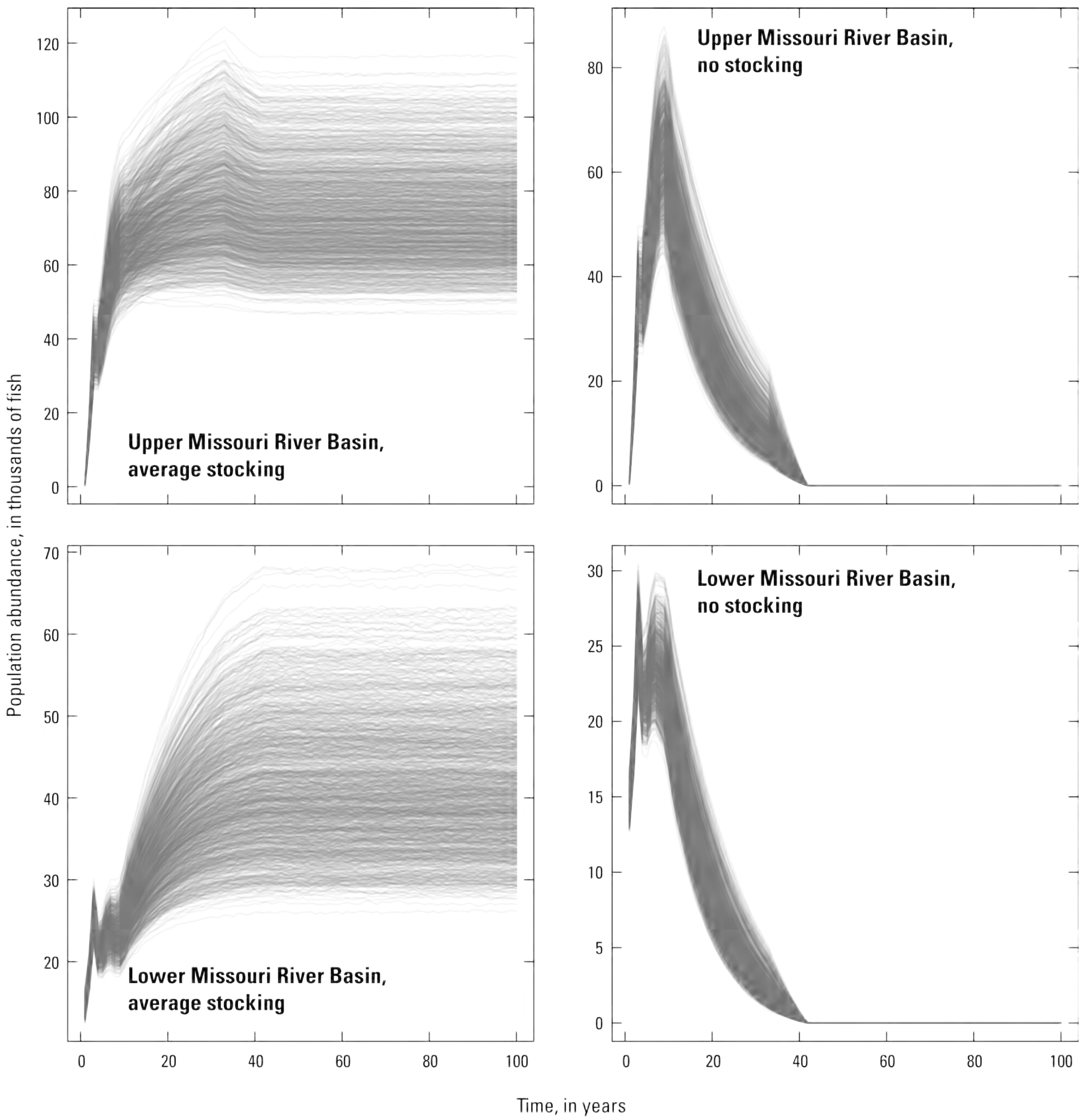


Figure 20. Simulated population abundance for hatchery-origin adults for the Upper and Lower Missouri River Basins for scenarios representing average stocking conditions and no stocking. Darker areas represent higher simulation densities.

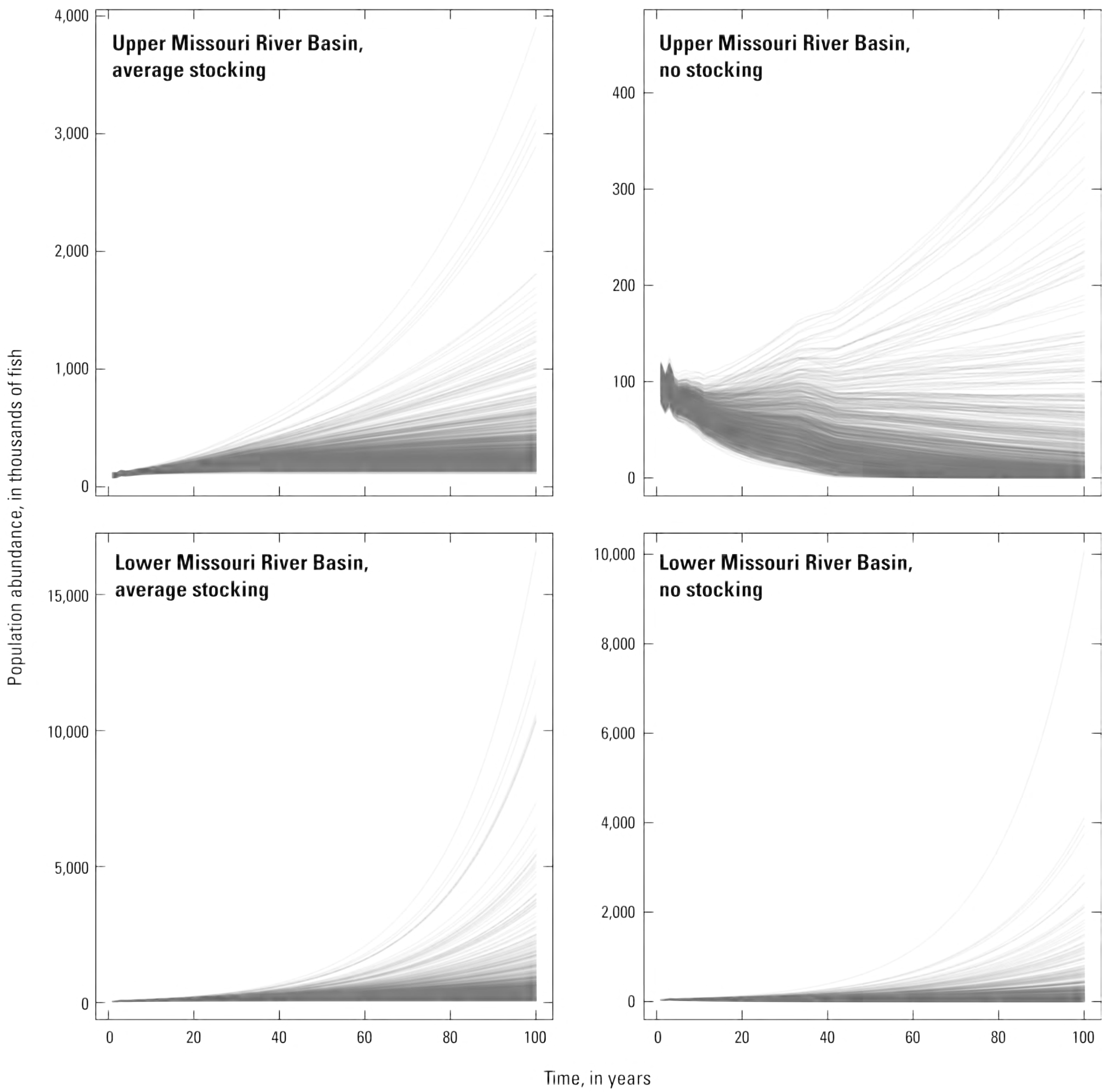


Figure 21. Simulated population abundance for all origins and stages (total population) for the Upper and Lower Missouri River Basins for scenarios representing average stocking conditions and no stocking. Darker areas represent higher simulation densities.

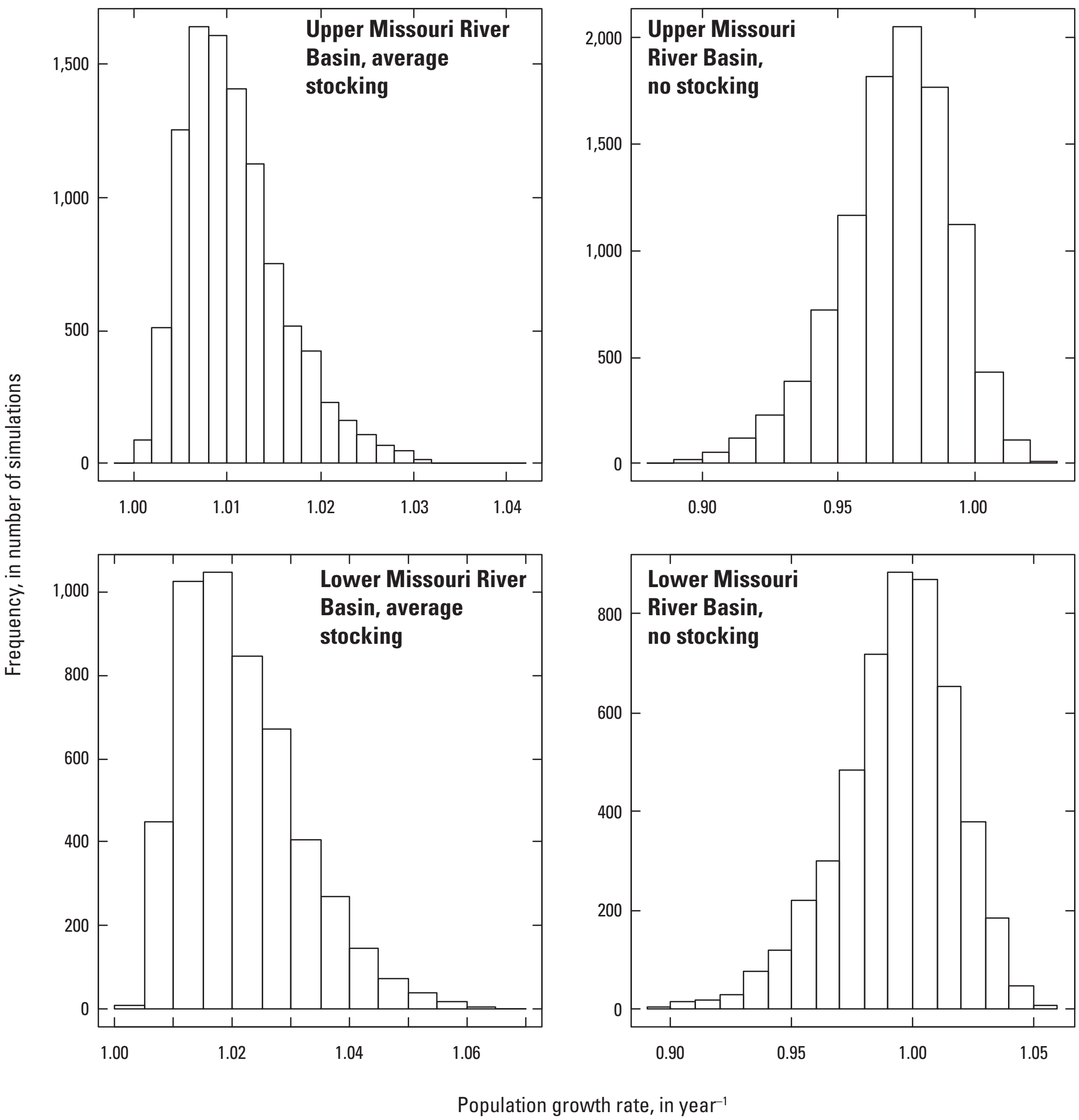


Figure 22. Distribution of population growth rates for average stocking and no stocking conditions simulated for the Upper and Lower Missouri River pallid sturgeon populations. Histograms represent the distribution of stochastic growth rates calculated for each 10,000 replicated simulated for each scenario.

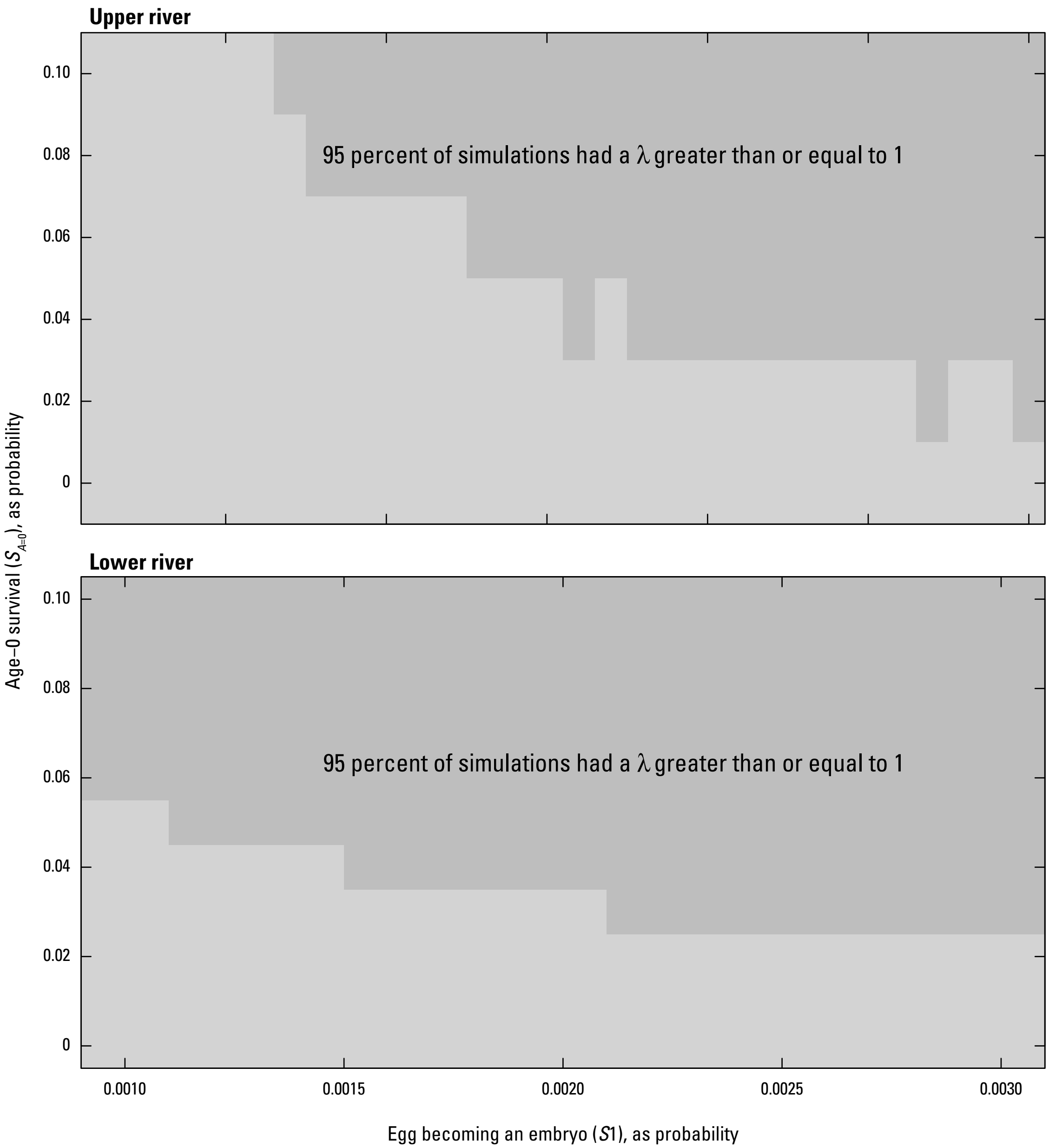


Figure 23. Graphs showing combinations of survival parameters resulting in positive population growth for no stocking conditions.

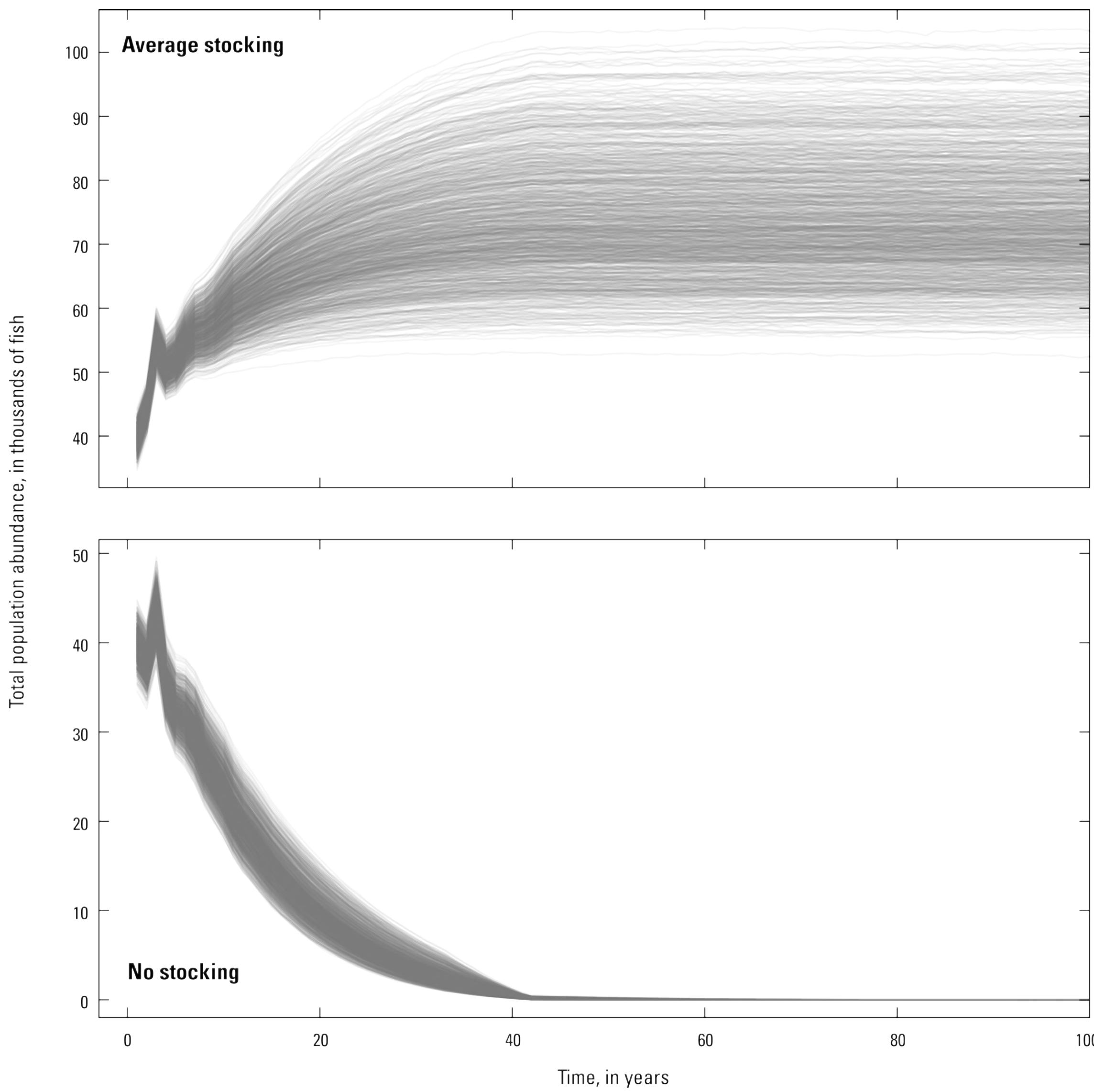


Figure 24. Simulated population abundance for all origins and stages (total population) for the Upper Missouri River Basin for average and no stocking conditions. Underlying these scenarios was a depensatory effect illustrated in figure 11.

Discussion

Confirmed Sensitivities

Sensitivity analysis results were similar between upper and lower river populations. In both cases, simulated populations were determined by early life-history survival. This is common for some fish species, especially for long-lived species like pallid sturgeon because survival at later life stages must be high to reach older ages; for example, to have high probability of fish surviving to age-41, annual survival would need to be high—exceeding 90 percent (this number makes several assumptions and is for illustrative purposes only)—which is congruent with adult survival estimates for the upper and lower river populations. Regardless of what life-history stage is evaluated, population abundance at year 100 is especially sensitive to early life-history survivals. Relative to the model parameters, stage-specific abundance was not as important as early life-stage survival in the upper and lower river population simulations.

Sensitivities did vary between hatchery- and natural-origin population dynamics. In particular, the survival of age-1 to age-2 is most sensitive for upper river hatchery-origin juveniles and moderately sensitive for lower river hatchery-origin juveniles. This makes biological sense because yearlings are stocked at age-1, thereby circumventing what is hypothesized to be early life-history demographic bottlenecks in the wild (table 5). This pattern was generally similar between upper and lower rivers and juvenile and adult life stages. The sensitivity of total population abundance resulted in a different set of model variables being important to population abundance, which varied between river sections for reasons that are uncertain and require further examination. Overall, the sensitivity analyses demonstrated where leverage points exist in the population model. Although it is still uncertain how performance of management and rehabilitation actions will be evaluated (for example, population abundance, growth rates, and survival rates), these sensitivity analyses demonstrate how the model can be used to evaluate biological and decision uncertainty and guide research, monitoring, and assessment.

Initial Exploration of Stocking Conditions

The stocking conditions evaluated represent initial exploratory analyses to evaluate how the effect of population supplementation may be evaluated using the population model. The condition results were as expected with population abundances declining with the cessation of stocking. These results warrant caution because demographic rates, $S1$ in particular, were calibrated such that the population was in approximate equilibrium (that is, $\lambda \sim 1$) with average stocking rates. Additionally, the true magnitude of $S2$, $S3$, and $S4$ are unknown, but we were able to constrain the probabilities such that the product of the three equaled $S_{A=0}$. Given these uncertainties, it was clear that stocking pallid sturgeon had an effect, and cessation would likely result in population declines similar to the results of Steffensen and others (2013a).

We also explored how the model could be used to identify critical population sizes needed to alleviate depensatory effects. In contrast to the simple stocking condition, there is much greater structural uncertainty in depensatory effects, and the results are much less useful for decision making. In particular, the shape of the functional response predicting $S1$ is unknown. Although we assumed a sigmoidal relation, there is no information to support this. Secondly, the sigmoidal relation we assumed reached a maximum, which was equal to the calibrated section-specific value of $S1$. Calibration of $S1$ is difficult because of the lack of ability to identify among $S1$, $S2$, $S3$, and $S4$. Specifically, there are no known estimates of $S1$, $S2$, $S3$, and $S4$, and these rates are in varying times scales. Although we can constrain $S2$, $S3$, and $S4$ to equal $S_{A=0}$, as was done in this analysis, there are varying combinations of $S2$, $S3$, and $S4$ whose product equals $S_{A=0}$. Efforts to estimate, constrain, or calibrate these variables with existing monitoring data will be an ongoing challenge. This example shows the flexibility of the population model framework to address management questions but underlines the need for additional reliable scientific information to achieve useful predictions.

Framework for Future Adaptive Management

In concept, the population model framework provides a critical link relating the effect of management actions on stage-specific survival, as described in the CEMs, to population dynamics. Sensitivity analysis of the model indicates where investment in research, monitoring, and assessment will provide the greatest returns by reducing uncertainty in population abundance with time. Population dynamics, for example, were sensitive to survival of early life-history stages; therefore, research on how to estimate survival and factors associated with survival may be prioritized. In some cases, population dynamics were sensitive to stage-specific abundance, which would support continued monitoring and assessment such that accurate and precise estimates of current abundances are available.

The modeling process described here provides a framework to couple CEMs with population dynamics as would be necessary to evaluate management and rehabilitation alternatives objectively and build an AM program. The current structure of the model is a tradeoff between simplicity and biological realism, and the present results should be considered preliminary and subject to modification. There are several assumptions made in the current model that may be modified to achieve greater biological realism as research and AM proceed. Notable assumptions in the present model are that survival does not differ between hatchery- and natural-origin fish, sex differences are unimportant, emigration and immigration can be neglected, and the spatial extent modeled is sufficient to meet the EA needs. These and other assumptions will be revisited and relaxed as more information becomes available or if needed to meet the objectives of the EA.

Drift and Dispersal Models Using Advection/Dispersion

Drift and dispersal modeling is used in the EA to assess transport and fate of free embryos during their early embryonic development. These so-called advection/dispersion models are potentially useful to quantify early life-stage survival on the upper river and indicate where age-0 larvae are likely to settle on the lower river.

When pallid sturgeon embryos hatch at 5 to 8 days after fertilization, they may drift immediately, or they may reside in substrate interstices for some time before drifting. There is active debate about the relative merits of the two hypotheses and application to Missouri River recruitment failure (DeLonay, Chojnacki, Jacobson, Albers, and others, 2016). After hatch, free embryos are resident in substrate or drift for 9 to 11 or more days, depending on water temperature, which affects development rate. If interstitial residency happens, the drift period may be as short as 4 days or, if not, as long as 11 or more days. During this period, free embryos are developing ontogenetically, progressively developing the ability to position themselves in the water column and laterally, while using up their yolk-sac food reserves.

Although some ability to position themselves in the water column has been documented in observations, most free embryos are collected close to the bottom of the river despite vigorous turbulence (Braaten and others, 2008, 2010; DeLonay, Chojnacki, Jacobson, Albers, and others, 2016). A preliminary, useful approach to evaluating potential for downstream dispersal is to treat free embryos as passive, neutrally buoyant particles subject to a combination of advection and dispersion. Treatment of free embryo dispersion as a passive transport process is a broad assumption that may be discarded as more information becomes available. For the present, the assumption of passive transport provides useful constraints on understanding of downstream dispersal.

Laboratory studies have indicated that free embryos have some ability to position themselves in the current, especially after 5–8 dph. Documented movements in laboratory studies have been mostly “swim up” behavior, a periodic vertical movement that has been interpreted as a mechanism to maintain downstream dispersal during this life stage (Kynard and others, 2007). These laboratory studies document that free embryos 5–11 dph progressively acquire the ability to hold themselves in the current, but holding ability was limited as current velocities approached 0.3 meter per second (m/s) (Kynard and others, 2002, 2007). Notably, mean column velocities in the Yellowstone, Upper Missouri, and Lower Missouri Rivers (fig. 2) (1.5–2 m/s) are substantially higher than those used in laboratory experiments (0.1–0.5 m/s). River velocity fields are also fully turbulent and typically characterized by macroturbulent flow structures that would be expected to be highly influential in modifying transport of free embryos. Velocity fields on the Lower Missouri River especially have extensive macroturbulence associated with bedforms and navigation structures (Jamieson and others, 2011). On the Lower Missouri River, multidimensional hydrodynamic models using particle tracking illustrate the high transport efficiency of the channelized river such that particles introduced in the navigation channel tend to stay in the channel (Jacobson, Lindner, and others, 2015).

Actual velocity fields experienced by free embryos in the field are unknown because it has not been possible to document dispersal patterns at the reach scale. In field-based drift experiments, most free embryos were captured within 0.5 meter (m) of the bottom (Braaten and others, 2008; Braaten, Fuller, Lott, Haddix, and others, 2012), indicative of a combination of physical and biological processes that concentrates free embryos near the bottom. Concentration near the bottom of the channel would presumably be the net result of their physical fall velocity (based on a specific gravity greater than 1, which would tend to keep them close to the bottom) and turbulence plus their inherent swim up behaviors (which would tend to keep them in suspension throughout the water column).

Existing laboratory- and field-based observations indicate that drift is most likely passive in the first 4–5 dph, but the ability to move and hold position in the current develops progressively through transition to first feeding (Braaten, Fuller, Lott, Ruggles, and others, 2012). The disjunction between laboratory and field conditions makes it tenuous to extrapolate directly from laboratory conditions to the field. High velocities and turbulence in the upper and lower rivers indicate that passive drift models may provide useful information through most of the free-embryo stage.

Even if drift is dominantly passive, hydraulic conditions in the rivers may act to retard drift rates compared to the water in which they are being transported. Virtual particle velocities (that is, the net downstream movement rate of free embryos) will vary with where the particles are in the water column. Those that spend more time closer to the bottom potentially will be transported at substantially slower rates than those higher in the water column, depending on the vertical particle-concentration gradient and the vertical water-velocity profile. The magnitude of water-column differential transport is unknown at this time because the net result of fall velocity, turbulence, and biological positioning has not been resolved. Water-column differential transport may explain the result of Braaten, Fuller, Lott, Ruggles, and others (2012) that virtual particle velocity was measured at 0.9 times mean water velocity during an Upper Missouri River drift experiment.

Reach-scale hydraulic factors may also contribute to retarded drift. Particles may be exchanged between the main flow and channel-margin eddies and backwaters. If the particles eventually re-enter the main flow, their virtual velocity will be substantially slower than those that remained in the main flow. Theoretically, contributions to retarded drift can be modeled through the dispersion coefficient in advection/dispersion models. This requires robust calibration and a modeling framework with sufficient resolution to capture the scale of geomorphic features that would create eddies and backwaters. In cases where velocity fields promote retention of the particles, the particle is lost to the transport flux. The reality of this situation for a drifting free embryo and eventual probability of recruitment will vary depending on if the retention environment supports growth and survival.

At the end of the drift phase, free embryos "settle" and must begin to feed. This transition to exogenously feeding status has been called the "critical period" because larvae are highly susceptible to mortality if the proper food is not available within a short time (Gisbert and Williot, 1997; Gisbert and Doroshov, 2003). Little is known about the settling process beyond laboratory observations, which are difficult to extrapolate to field conditions. Settling may involve long-term residency in a specific macrohabitat of the river, or it may instead involve progressive downstream dispersal at a slower rate as the larvae seek supporting habitats.

Advection/dispersion models are common in consideration of contaminant transport and have been implemented in HEC–RAS for the Yellowstone, Upper Missouri, and Lower Missouri Rivers (fig. 2) as part of the EA (Fischenich and others, 2014); clearly, these models are subject to uncertainties about interstitial residency and other physical and biological processes that may retard drift.

Objectives of Advection/Dispersion Modeling

The objectives of advection/dispersion modeling are to evaluate the physical controls on potential downstream drift of pallid sturgeon free embryos and assess effectiveness of management actions in altering drift and survival.

Dispersal of Free Embryos in Pallid Sturgeon Population Processes

Downstream dispersal of pallid sturgeon free embryos is a critical process in the upper and lower rivers. The linkage of free-embryo survival to dispersal is hypothesized to be most critical in the upper river because of limited available drift distance between impediments to upstream migration of adults and the headwaters of Lake Sakakawea (fig. 25). In the Lower Missouri River (fig. 2*B*), dispersal processes and distance determine where free embryos are likely to settle out of the drift and, therefore, where specific supporting habitats could be targeted for rehabilitation. Dispersal distance on the Lower Missouri River may also indicate the extent to which genetic subpopulations are subject to mixing by enhanced downstream advection.

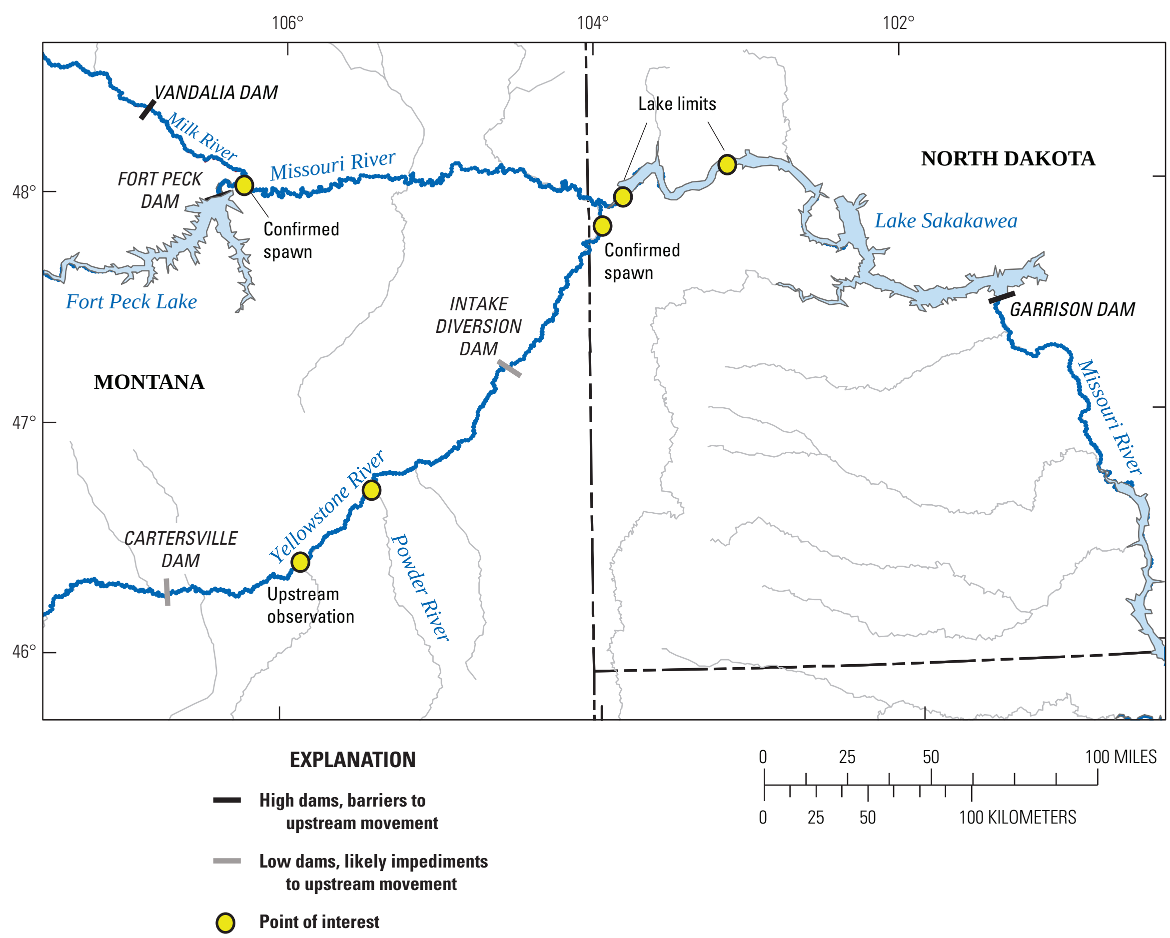


Figure 25. The Yellowstone and Upper Missouri Rivers, major tributaries, dams, reservoirs, and points of interest.

Operationally, we define the time required for drift as the interval until yolk-plug expulsion. This is the development event indicating when the yolk sac has been used up and the free embryo must begin first feeding. Time to yolk-plug expulsion is temperature dependent (table 6). Free-embryo mortality results if they drift into river locations with lethal habitats, predators, or where they lack proper food at transition to the exogenously feeding stage. Recent studies have documented lethal anoxic conditions in bottom sediments of the headwaters of Fort Peck Lake (Guy and others, 2015); although the extent and lethality of anoxia have not been documented for the headwaters of Lake Sakakawea, it is likely that some combination of habitat conditions in Lake Sakakawea is lethal to free embryos (Braaten and others, 2008). Mortality can also result if the free embryo is unable to exit from the drift when its yolk sac is depleted, cannot find proper food and, therefore, starves (Candrl and others, 2009).

Based on the assumption that locations within Lake Sakakawea are lethal, combinations of spawning locations, discharge, and temperature that result in free embryos being retained upstream from the lake are considered to be indicative of survival, and their proportion can be considered an estimate of survival probability.

Application to Management Actions

Management actions that can influence drift vary between the upper and lower rivers. Lack of recruitment in the upper river is consistent with the inference that the headwaters of Lake Sakakawea are lethal to pallid sturgeon free embryos; current information supports the hypothesis that the headwaters are anoxic, similar to Fort Peck Lake (Guy and others, 2015). Adequacy of drift distance upstream from Lake Sakakawea is determined in part by the migration pathway and upstream distance achieved by reproductive adults—including selections of the Upper Missouri River, Lower Yellowstone River, or other tributaries—and constraints imposed by dams, including Fort Peck Dam, Intake Diversion Dam (Yellowstone River), Cartersville Dam (Yellowstone River), and Vandalia Dam (Milk River) (fig. 25). Adequacy is additionally determined by the degree of interstitial residency, other factors that may retard drift, advection (mean rate of downstream particle velocity, closely related to prevailing discharge), dispersion (degree of longitudinal spread of the drifting free-embryo mass, closely related to channel morphology and complexity), and water temperature (which determines development rate). Dispersion also has a biological element because progressive development during drift may allow free embryos to seek slower velocities or food-producing habitats with increasing efficiency as drift progresses.

Table 6. Water temperatures and mean days and hours post-hatch for yolk-plug expulsion.

Water temperature, in degrees Celsius	Mean days post-hatch	Mean hours post-hatch
14	14	336
15	12	288
16	11	264
17	11	264
18	10	240
19	10	240
20	9	216

Management actions in the Upper Missouri River include changes in discharge characteristics from Fort Peck Dam and drawdown of Lake Sakakawea. Relevant discharge actions at Fort Peck Dam would be to decrease discharge and associated velocities to decrease drift distance or increase temperature to increase development rate. The relevance of actions on the Missouri River are dependent, however, on how pallid sturgeon elect to use the Yellowstone River, including whether they bypass Intake Diversion Dam successfully and in sufficient numbers and how far upstream they migrate to spawn. If pallid sturgeon use the Yellowstone River, discharge or temperature actions at Fort Peck Dam will not be relevant, but depending on how far up the Yellowstone River the pallid sturgeon spawn, drawdown of Lake Sakakawea may continue to be a management option to increase chances for survival.

Management actions on the Lower Missouri River to achieve hypothesized responses include lowering discharges from Gavins Point Dam to decrease advection or increase temperature of releases. These actions would slow drift or shorten the drift distance, resulting in settling at shorter distances downstream from spawning sites. Notably, there is no evidence to support the idea that survival of free embryos would be differentially affected by settling location on the lower river, so the primary importance of understanding of drift dynamics is to determine optimal locations for channel habitat rehabilitation projects. Channel reconfigurations to increase interception of drifting free embryos may be indicated to address the hypothesis that free embryos are incapable of moving from the highly engineered thalweg to supportive, channel-marginal habitats before starvation as they transition to first feeding.

Approach to Advection/Dispersion Modeling

Advection/dispersion modeling uses the 1D HEC–RAS framework and can be used with steady or unsteady flows (Fischenich and others, 2014). In addition to the calibrated 1D HEC–RAS model, the advection/dispersion implementation requires estimated longitudinal dispersion coefficients, which predict the spread of the embryos around the mean advection velocity. In this implementation, the longitudinal dispersion coefficients are being estimated in HEC–RAS for each cross section (Fischenich and others, 2014).

Extension of advection/dispersion modeling to useful predictions of free embryo dispersal requires several additional assumptions and involves related increases in uncertainty (Erwin and Jacobson, 2014). Braaten and others (2008) documented in a field experiment that pallid sturgeon free embryos drifted at nearly the same rate as mean water-column velocity, ranging from 0.03 to 0.07 m/s slower, for 1–11 dph; 17 dph free embryos drifted as much as 0.20 m/s slower, indicating that late-stage free embryos or exogenously feeding larvae had progressively developed the ability to move within the water column (possibly seeking slower velocities). To the extent that free embryos develop the ability to move to slower velocities during late stages, the advection/dispersion models may over-predict downstream advection.

An important source of potential error and uncertainty is the extent to which newly hatched free embryos exhibit interstitial residency. If free embryos drift immediately, they will disperse the maximum distance. For each day they may spend in interstices, the total downstream distance decreases by 40–80 mi (Fischenich and others, 2014). Similarly, if other combinations of biological behaviors and physical processes serve to retard drift rates—such as episodic retention in channel-marginal eddies or in flow-separation zones associated with dunes—the advection/dispersion models will overpredict downstream dispersal. Recent evidence from experimental streams supports a model of immediate drift for pallid sturgeon (DeLonay and others, 2015) although lack of residency has not been established for all potential combinations of field conditions.

Effects of varying hydrology can be incorporated in the advection/dispersion modeling in three ways. The most basic is to evaluate discharge variation using historical records to evaluate if the range of historical variation has been effective in altering drift dynamics. We address this by assuming steady flow conditions and using quantiles of historical flows, summarized as flow exceedances for June and July in the upper river and May and June in the lower river. The quantile approach is amenable to comparison with other time series datasets (for example, quantiles of Lake Sakakawea levels). The second approach to incorporating hydrology is to evaluate unsteady flow effects by exploring selected historical flood events during drift periods to evaluate how unsteady flow may affect fate of free embryos. The third approach is to compare advection/dispersion results using system-wide flow scenarios. To evaluate effectiveness of changes in flow scenarios, we use models of 100 years of daily flows that were previously produced using the USACE Daily Routing Model (DRM; U.S. Army Corps of Engineers, 1998). The DRM scenarios (table 7; figs. 26 and 27) illustrate a range of flow approaches; and although they may differ substantially from future flow scenarios developed through the MRRMP, they serve to explore the effectiveness of flow in management actions. The 100 years of data present a wide range of hydroclimatic conditions and can be used as a time series from which distributions of drift distance can be calculated.

Table 7. Daily Routing Model flow scenarios (figs. 26 and 27) used for comparisons in advection/dispersion and functional habitat models.

[Scenarios were developed during 1998–2005 by the U.S. Army Corps of Engineers to explore flow scenarios for revision of the Missouri River Master Water Control Manual (U.S. Army Corps of Engineers, 2006) and for consideration under adaptive management provisions of the Biological Opinion (U.S. Fish and Wildlife Service, 2003). The Daily Routing Model uses 100 years (or more) of daily input flow data and calculates reservoir releases based on rules and constraints (U.S. Army Corps of Engineers, 1998). Flow scenarios are illustrated in figures 26 and 27]

Scenario	Description
CWCP	Current water control plan prior to the 2006 revision of the Master Manual; no spring rise, no summer low flow.
EVQ2	Run-of-the-river, modeled with reservoirs full and input flows routed directly through. An approximation of the natural flow regime.
M540F0	The current water control plan after incorporation of the spring rise technical criteria, calling for March and May spring pulses at Gavins Point Dam.
FW22	A flow scenario introduced in the 2000 Biological Opinion with one spring rise and a summer low flow.
MR1528	A flow scenario with moderate March and May spring pulses and target summer flow release of 28,000 cubic feet per second.
MR2021	A flow scenario similar to MR1528 but with somewhat higher spring pulses and a summer low flow target release of 21,000 cubic feet per second.

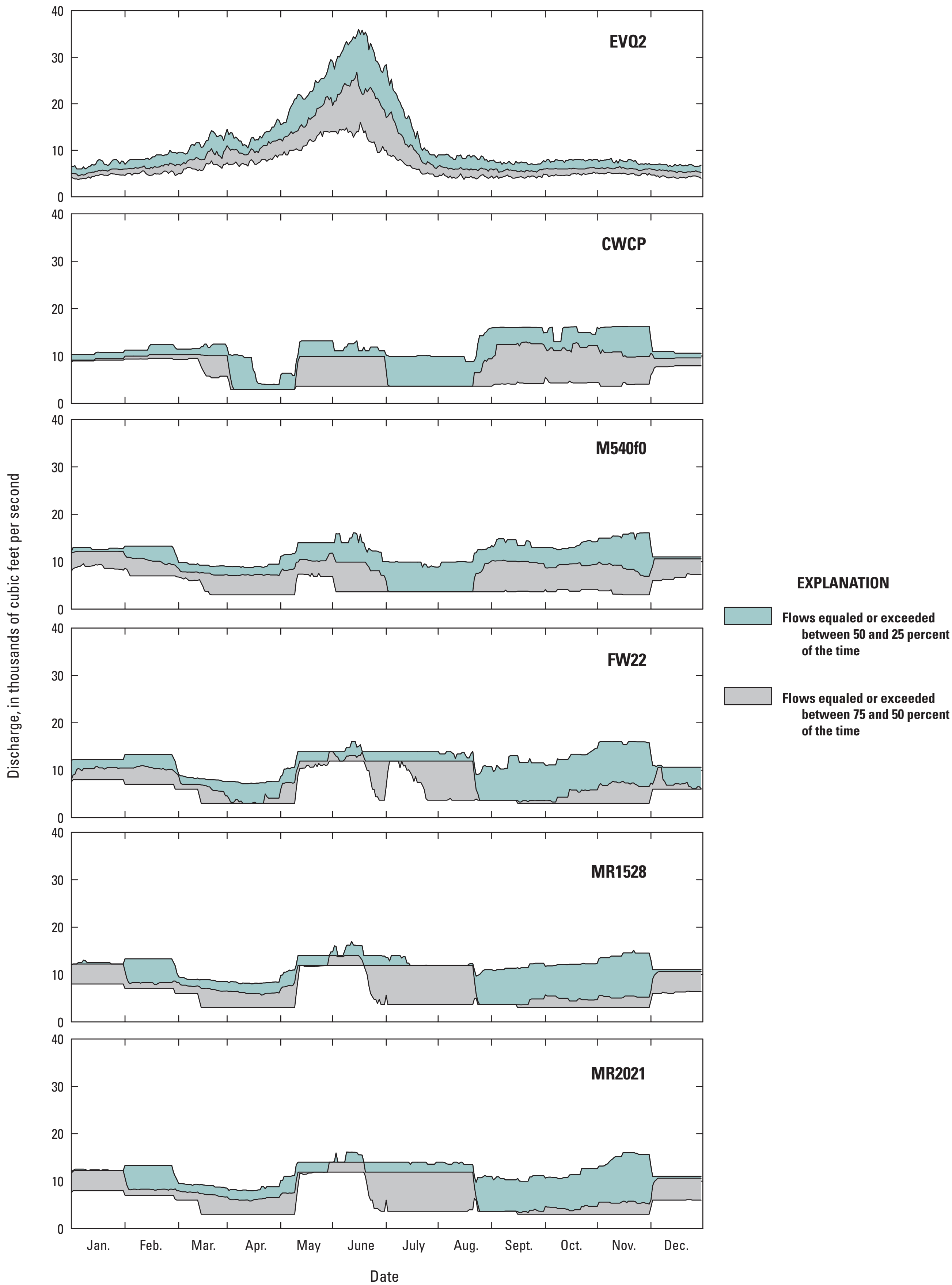


Figure 26. Flow-duration hydrographs for Fort Peck Dam for the six flow scenarios used for comparisons. Data are calculated from Daily Routing Model time series, 1898–1997 (U.S. Army Corps of Engineers, 1998).

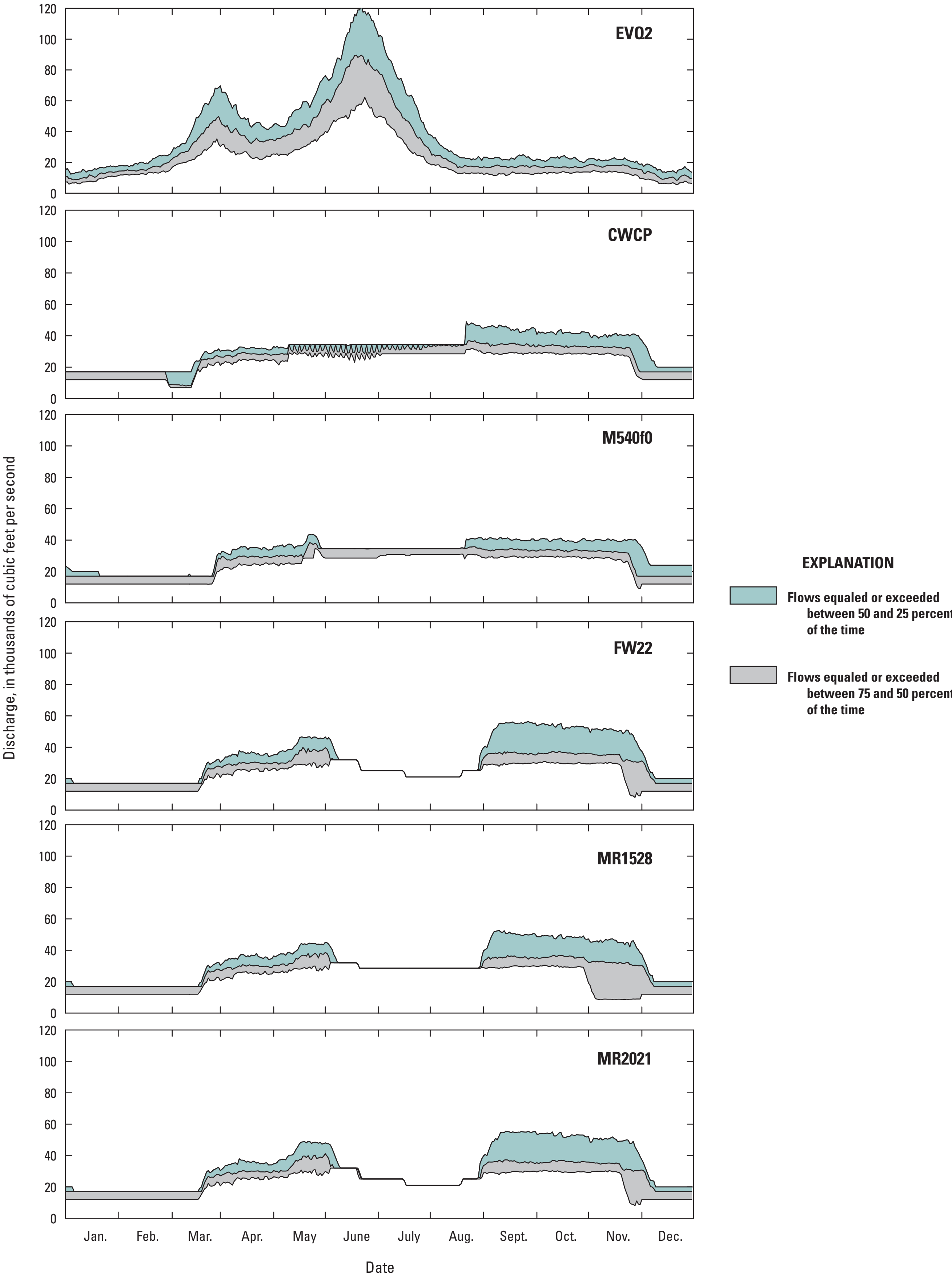


Figure 27. Flow-duration hydrographs for Gavins Point Dam for the six flow scenarios used for comparisons. Data are calculated from Daily Routing Model time series, 1898–1997 (U.S. Army Corps of Engineers, 1998).

Advection/Dispersion Modeling Results

Upper River

Modeled results for the upper river in Montana are intended to illustrate scenarios and test effectiveness of management actions. For these scenarios, we assume spawning takes place just downstream from the Fort Peck Dam spillway, at the mouth of the Milk River (fig. 2) where pallid sturgeon spawning was implicated in 2011 (DeLonay and others, 2014). This is as far upstream as reproductive sturgeon could migrate in the main stem of the Upper Missouri River, although additional migration up the Milk River could be possible. In the quantile analysis we use a combination of flow exceedances and lake-level exceedances (percent of time a discharge or lake level is equaled or exceeded) using recent historical records (1967–2013; table 8) to explore general effectiveness of flow and drawdown actions. The additional effect of water temperature in determining developmental rate and distance dispersed can be considered by assessing the number of days required to develop to yolk-plug expulsion—higher temperatures result in a lower number of days (table 6).

We also examined the effects of flow-regime scenarios on survival by using time series of discharges for June and July for the six flow scenarios. It should be noted that these flow scenarios were designed mostly to satisfy system requirements downstream from Gavins Point Dam. They were not intended to optimize drift and dispersal downstream from Fort Peck Dam; nevertheless, the six flow scenarios illustrate a range of potential reservoir release policies and serve to illustrate effectiveness (fig. 26).

Table 8. Percent survival of free embryos predicted from advection/dispersion modeling, assuming spawning near the mouth of the Milk River, Montana.

[Survival is shown as joint function of flow exceedance and Lake Sakakawea pool levels; —, not applicable; NGVD 29, National Geodetic Vertical Datum of 1929]

Drift days	Percent exceedance	Fort Peck Dam discharge, in cubic feet per second	Lake Sakakawea pool level, in feet above the NGVD 29					
			Historical minimum	Minimum	90	50	10	Maximum
			1,805	1,812.6	1,821.6	1,843.2	1,850.4	1,856
12	Minimum	3,000	2.6%	5.6%	1.5%	1.2%	0.3%	0.6%
	95	5,500	1.1%	2.3%	0.7%	0.5%	0.1%	0.3%
	90	6,100	0.7%	1.5%	0.5%	0.0%	0.0%	0.2%
	75	7,150	0.4%	0.8%	0.2%	0.1%	0.0%	0.1%
	50	8,600	0.2%	0.3%	0.1%	0.1%	0.0%	0.2%
	25	11,000	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%
	10	14,400	0.0%	0.0%	0.0%	0.0%	0.3%	0.0%
	5	16,100	0.0%	0.0%	0.0%	0.0%	0.3%	0.0%
	Maximum	65,900	—	—	—	—	—	—
10	Minimum	3,000	21.3%	18.9%	5.6%	3.2%	0.9%	0.9%
	95	5,500	3.6%	4.5%	1.5%	1.0%	0.2%	0.4%
	90	6,100	0.0%	3.0%	1.0%	0.0%	0.1%	0.3%
	75	7,150	1.1%	1.4%	0.6%	0.3%	0.1%	0.2%
	50	8,600	0.5%	0.5%	0.3%	0.1%	0.1%	0.3%
	25	11,000	0.1%	0.1%	0.0%	0.0%	0.0%	0.0%
	10	14,400	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%
	5	16,100	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%
	Maximum	65,900	—	—	—	—	—	—
8	Minimum	3,000	91.6%	85.3%	59.5%	26.1%	7.4%	3.0%
	95	5,500	53.4%	40.6%	13.9%	6.3%	0.8%	0.9%
	90	6,100	46.9%	33.8%	10.7%	4.2%	0.4%	0.5%
	75	7,150	29.5%	20.1%	5.8%	1.7%	0.2%	0.3%
	50	8,600	16.5%	10.6%	3.0%	0.7%	0.2%	0.7%
	25	11,000	12.5%	7.9%	2.5%	0.3%	0.0%	0.1%
	Maximum	65,900	—	—	—	—	—	—

Table 8. Percent survival of free embryos predicted from advection/dispersion modeling, assuming spawning near the mouth of the Milk River, Montana.—Continued

[Survival is shown as joint function of flow exceedance and Lake Sakakawea pool levels; –, not applicable; NGVD 29, National Geodetic Vertical Datum of 1929]

Drift days	Percent exceedance	Fort Peck Dam discharge, in cubic feet per second	Lake Sakakawea Pool Level, in feet above the NGVD 29					
			Historical minimum	Minimum	90	50	10	Maximum
			1,805	1,812.6	1,821.6	1,843.2	1,850.4	1,856
6	Mimimum	3,000	99.9%	99.9%	99.8%	98.2%	85.1%	70.1%
	95	5,500	99.8%	99.6%	96.8%	80.0%	32.7%	22.4%
	90	6,100	99.8%	99.4%	95.8%	75.4%	23.0%	13.9%
	75	7,150	99.4%	98.3%	90.7%	60.4%	11.1%	6.1%
	50	8,600	98.5%	96.2%	85.4%	49.4%	5.8%	4.4%
	25	11,000	97.5%	94.4%	82.6%	44.3%	3.4%	1.2%
	10	14,400	92.1%	85.6%	68.2%	29.9%	2.0%	0.3%
	5	16,100	85.3%	76.4%	56.5%	20.4%	1.1%	0.1%
	Maximum	65,900	–	–	–	–	–	–
4	Mimimum	3,000	99.9%	99.9%	99.9%	99.9%	99.9%	99.9%
	95	5,500	99.8%	99.8%	99.8%	99.8%	99.8%	99.8%
	90	6,100	99.8%	99.8%	99.8%	99.8%	99.8%	99.7%
	75	7,150	99.6%	99.6%	99.6%	99.6%	99.5%	99.2%
	50	8,600	99.3%	99.3%	99.3%	99.3%	98.9%	97.0%
	25	11,000	99.6%	99.6%	99.6%	99.6%	98.0%	92.5%
	10	14,400	99.5%	99.5%	99.5%	99.5%	94.7%	80.1%
	5	16,100	99.6%	99.6%	99.6%	99.5%	88.8%	62.7%
	Maximum	65,900	–	–	–	–	–	–
2	Mimimum	3,000	99.9%	99.9%	99.9%	99.9%	99.9%	99.9%
	95	5,500	99.9%	99.9%	99.9%	99.9%	99.9%	99.9%
	90	6,100	99.9%	99.9%	99.9%	99.9%	99.9%	99.9%
	75	7,150	99.9%	99.9%	99.9%	99.9%	99.7%	99.7%
	50	8,600	99.9%	99.9%	99.9%	99.9%	99.6%	99.6%
	25	11,000	99.9%	99.9%	99.9%	99.9%	100.0%	100.0%
	10	14,400	99.9%	99.9%	99.9%	99.9%	100.0%	100.0%
	5	16,100	99.9%	99.9%	99.9%	99.9%	100.0%	100.0%
	Maximum	65,900	–	–	–	–	–	–

Advection/dispersion models on the Yellowstone River address sensitivity of drift to discharge exceedance, assuming pallid sturgeon spawn at Miles City, Montana, at Yellowstone River RM 184 (Fischenich and others, 2014). This location is near the upstream-most historical documented location for pallid sturgeon (RM 183) (Anders and others, 2009). Application of the advection/dispersion model indicates that advection is high on the Yellowstone River, and dispersion is relatively low. Even at historical minimum discharge, few free embryos would remain in the Yellowstone River after 5 days; and at median discharge, few would remain after 2 days (table 9) .

Lower River

Advection/dispersion models developed for the lower river are intended to illustrate the amount of river that pallid sturgeon are likely to use. Unlike the upper river, there is no information to indicate that drift to any particular location on the Lower Missouri or Mississippi Rivers (fig. 2) is more or less beneficial to free embryos. Instead, the value of the advection/dispersion modeling on the Lower Missouri River is in its potential relevance to indicate optimal siting for channel reconfiguration projects and potentially to indicate the degree of mixing between Missouri and Mississippi River pallid sturgeon populations.

The model results are shown using quantiles of flow for the historical period (1967–2013) and by scenarios of two potential spawning locations (table 10). Telemetry studies of reproductive pallid sturgeon on the Lower Missouri River have documented 29 spawning events based on migrations, recaptures, and demonstration that females no longer had eggs (DeLonay, Chojnacki, Jacobson, Albers, and others, 2016). These observations also indicate that spawning events have been distributed broadly within this river segment rather than being concentrated in specific locations (fig. 28). Because clear site affinities for spawning have not been documented, the potential spawning locations to begin advection/dispersion modeling purposes have been distributed through the Lower Missouri River.

Table 9. Percentage of passively drifting free embryos remaining in the Yellowstone River by days of drift and flow exceedance.

[Assumes spawning at river mile 184 of the Yellowstone River near Miles City, Montana. Data from Fischenich and others, 2014]

Days in the Yellowstone River	Flow exceedance, in percent							
	Min	95	90	75	50	25	10	5
1	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0
2	100.0	100.0	100.0	100.0	99.0	95.0	70.0	60.0
3	100.0	100.0	90.0	58.0	5.0	0.0	0.0	0.0
4	92.0	70.0	12.0	1.0	0.0	0.0	0.0	0.0
5	42.0	5.0	0.0	0.0	0.0	0.0	0.0	0.0
6	5.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
10	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

Table 10. Percentage of passively drifting free embryos remaining in the Lower Missouri River by spawning river mile, days of drift and flow exceedance.

[Data from Fischenich and others, 2014]

Days in the Missouri River	Flow exceedance, in percent						
	95	90	75	50	25	10	5
River mile 800							
1	100.0	100.0	100.0	100.0	100.0	100.0	100.0
2	100.0	100.0	100.0	100.0	100.0	100.0	100.0
3	100.0	100.0	100.0	100.0	100.0	100.0	100.0
4	100.0	100.0	100.0	100.0	100.0	100.0	100.0
5	100.0	100.0	100.0	100.0	100.0	100.0	100.0
6	100.0	100.0	100.0	100.0	100.0	100.0	100.0
7	100.0	100.0	100.0	100.0	100.0	100.0	100.0
8	100.0	100.0	100.0	100.0	100.0	100.0	100.0
9	100.0	100.0	100.0	100.0	100.0	85.0	80.0
10	100.0	100.0	100.0	100.0	80.0	15.0	5.0
11	100.0	100.0	95.0	70.0	10.0	0.0	0.0
12	90.0	85.0	40.0	10.0	0.0	0.0	0.0
13	50.0	30.0	5.0	0.0	0.0	0.0	0.0
14	0.0	0.0	0.0	0.0	0.0	0.0	0.0
River mile 595							
1	100.0	100.0	100.0	100.0	100.0	100.0	100.0
2	100.0	100.0	100.0	100.0	100.0	100.0	100.0
3	100.0	100.0	100.0	100.0	100.0	100.0	100.0
4	100.0	100.0	100.0	100.0	100.0	100.0	100.0
5	100.0	100.0	100.0	100.0	100.0	100.0	100.0
6	100.0	100.0	100.0	100.0	100.0	90.0	76.0
7	100.0	100.0	100.0	92.0	50.0	15.0	5.0
8	95.0	85.0	70.0	20.0	2.0	0.0	0.0
9	40.0	30.0	10.0	1.0	0.0	0.0	0.0
10	5.0	2.0	0.0	0.0	0.0	0.0	0.0
11	0.0	0.0	0.0	0.0	0.0	0.0	0.0
12	0.0	0.0	0.0	0.0	0.0	0.0	0.0
13	0.0	0.0	0.0	0.0	0.0	0.0	0.0
14	0.0	0.0	0.0	0.0	0.0	0.0	0.0

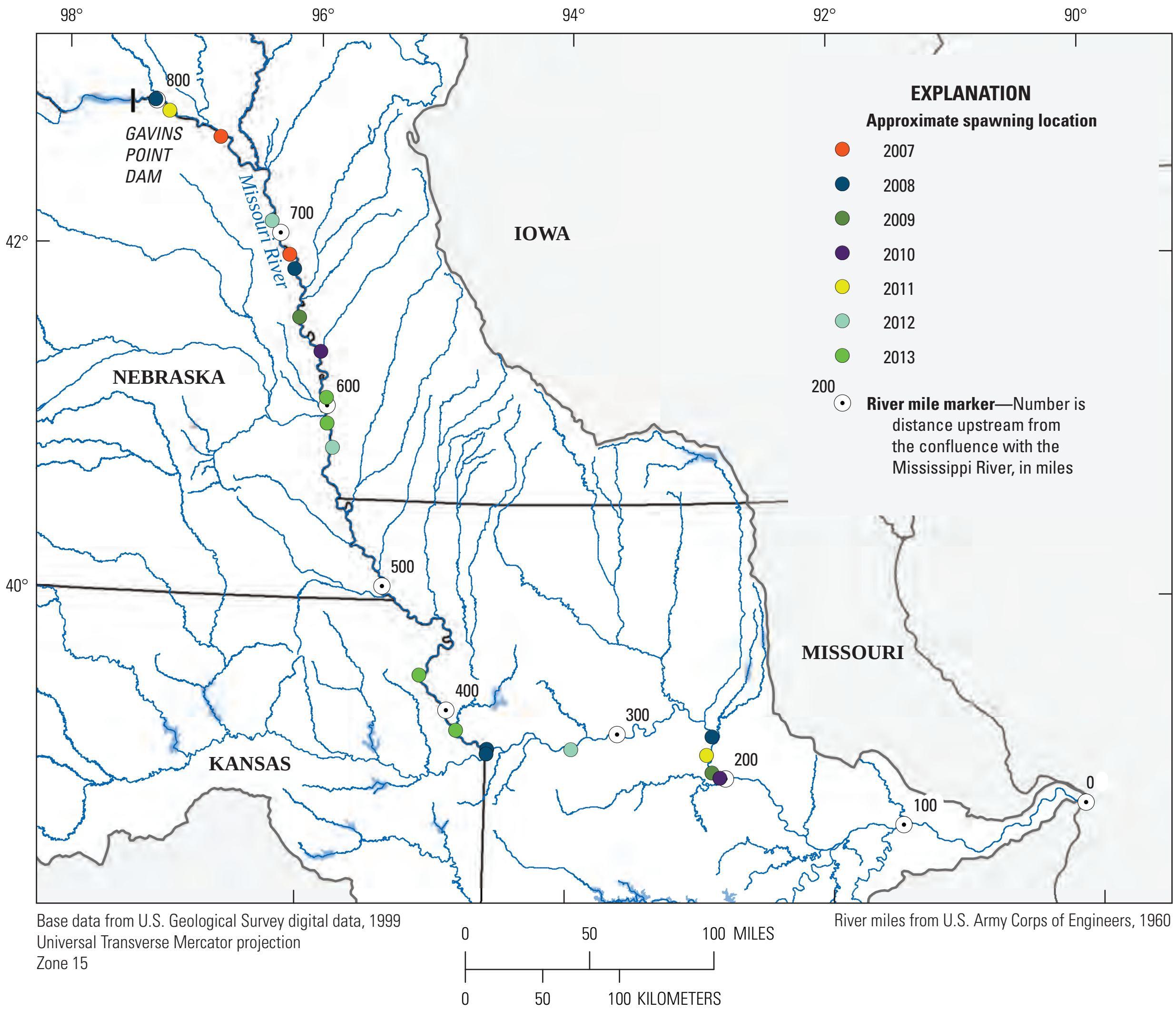


Figure 28. Map of documented spawning sites in the Lower Missouri River, 2007–2013 (DeLonay, Chojnacki, Jacobson, Braaten, and others, 2016).

Discussion

The implications of drift and dispersal modeling are discussed in later sections on individual management actions. In the upper river, the results document sensitivity of survival to flow regime and temperature management actions at Fort Peck Dam (fig. 2) and drawdown of Lake Sakakawea. In the Yellowstone River, the results indicate that fast velocities and low dispersion result in short retention at even very low flows. In the lower river, the results indicate sensitivity of drift and dispersal to flow management at Gavins Point Dam and the likelihood that free embryos will be retained in the Missouri River.

Functional Habitat Models

The concept of habitat is fundamental to ecological understanding of rivers because it describes the template of conditions occupied by organisms. In the Missouri River (fig. 2*A*), the recognition that physical habitat has been highly altered through reservoir management and channelization has motivated a special emphasis on restoring physical habitat as part of the MRRP (U.S. Fish and Wildlife Service, 2000, 2003). Although rehabilitation under the MRRP is focused on species objectives, most pathways to avoiding jeopardy involve manipulating habitats or habitat conditions (fig. 4).

Habitat can be defined broadly as “the resources and conditions present in an area that produce occupancy—including survival and reproduction—by a given organism” (Hall and others, 1997, p. 175), which is a definition that includes all physical, chemical, and biological conditions that might be related to occupancy. Frequently, the concept of habitat is reduced to physical components or components that are specific to support for particular life stages, such as spawning habitat or larval-rearing habitat. Aquatic habitats are dynamic because they change with discharge, sediment transport, and varying water quality and biotic conditions. The spatial dimensions and arrangements of habitats may also be important for species like pallid sturgeon because some habitat patches may need to be upstream or adjacent to others to provide conditions necessary for growth, survival, and reproduction. At a fundamental level, physical habitat is created from the interaction of flow regime with channel morphology, resulting in a dynamic mosaic of physical patches with varying biophysical capacity (Jacobson and Galat, 2006; Jacobson, 2013).

Since the 2000 Biological Opinion (U.S. Fish and Wildlife Service, 2000) Missouri River habitat rehabilitation has focused on SWH variably defined as 0–5 ft (0–1.5 m) deep and 0–2.5 feet per second (ft/s) (0–0.76 m/s) or 0–2.0 ft/s (0–0.61 m/s), and measured during mid-July to mid-August (U.S. Fish and Wildlife Service, 2000, 2003). The main hypothesized functions of SWH under this definition have been to increase primary and secondary productivity and provide larval nursery habitat that was lost to the channelization. In 2009, the USFWS expanded the quantitative definition of SWH to include qualitative characteristics. The expanded definition described dynamic and diverse geomorphic features that should be included in SWH, while still attaining general criteria of 0–1.5 m depth and 0–0.6 m/s current velocity (Olson, 2009).

Although the 2009 qualitative definition may be ecologically defensible, the EA team sought quantitative definitions that could be used in simulation models. The EA team's evaluation of existing pallid sturgeon habitat occupancy data also indicated that adults, juveniles, and age-0 *Scaphirhynchus* spp. were rarely collected in the 0–1.5 m depth and 0–0.6 m/s velocity in the SWH definition (DeLonay and others, 2009; Reuter and others, 2009; Bonnot and others, 2011; Ridenour and others, 2011). Usually sturgeon occupied deeper and somewhat swifter water; in particular, sturgeon are unlikely to be in velocities less than 0.5 m/s. A recent study of catch per unit effort (CPUE) of age-0 sturgeon confirmed that no significant spatial relation exists between CPUE and availability of SWH based on the depth component of the conventional definition (Gemeinhardt and others, 2015). Several factors may be responsible for this lack of relation: (a) processes in areas identified as SWH are not limiting to sturgeon populations, (b) relevant physical and biological habitat conditions are not captured in the conventional definition or if the velocity component of the definition is ignored, or (c) CPUE using conventional sampling techniques is not sufficiently selective to document occupancy of SWH by age-0 sturgeon; moreover, occupancy is not a sufficient criterion for determining value because habitats that are not occupied by a species may, nonetheless, provide food resources or conditions supportive of predators or competitors.

Based on our assessment of the current state of science for habitat affinities of pallid sturgeon, we have defined four specific types of habitat conditions that hypothetically relate to pallid sturgeon functional requirements and working management hypotheses that emerged through the EA process. In defining these new habitat types, our intent is to make the habitat criteria more biologically realistic and relevant to management actions compared to previous definitions. The habitat units are described in detail in the section "Functional Habitat Definitions;" these definitions have varying amounts of empirical support, but all were supported by the expert-driven CEM and hypothesis filtering process (Jacobson and others, 2016). We use preliminary definitions of the functional habitat units in the habitat modeling process; and we theorize that they provide an improved, quantitative, and ecologically defensible basis for assessing pallid sturgeon habitat dynamics. These definitions are always amenable to refinement as more data become available. We emphasize that the functional habitat definitions are an attempt to take a broad, multidimensional, multifaceted concept of habitat and derive quantitative units that are relevant to pallid sturgeon population dynamics and amenable to modeling.

Objectives of Hydrodynamic Modeling

Hydrodynamic modeling of functional habitat units is intended to provide a quantitative basis for assessing effectiveness of combinations of flow regime and channel reconfiguration actions to increase habitat availability for pallid sturgeon. If used in an AM framework that uses hydrodynamic modeling tools to inventory habitat quantity and quality, functional habitat definitions can provide a biologically based bridge between management actions and population dynamics. The objectives of the modeling presented here are the following:

- Assess relative effectiveness of flow regime and channel reconfiguration actions in providing functional habitats.
- Define a modeling framework that can be used to evaluate future management alternatives.
- Define the role of hydrodynamic functional habitat modeling in ongoing AM of pallid sturgeon with an emphasis on linking habitats to population dynamics.

Approach to Hydrodynamic Modeling

Habitats hypothesized to be important to pallid sturgeon growth, survival, and reproduction involve elements of depth and velocity; and may require complex derivatives of depth, velocity, and other variables for complete characterization (Jacobson, Johnson, and Deitrich, 2009). To capture hydraulic processes at a scale and resolution relevant to habitat selection, we elected to use 2D hydrodynamic models as our main tool. The 2D hydrodynamic models provide sufficient realism in hydraulic simulations while lacking the computational and field-verification requirements of complex three-dimensional models. Because of the shortened period of phase 1 of the EA, we were not able to begin any new modeling efforts but were required to select from existing 2D models. Several sources for 2D models at a range of resolutions and reach lengths exist in the Lower Missouri River (fig. 2) and were available for EA team members to run and assess. Similar models have been developed for five reaches on the Lower Yellowstone River and Upper Missouri River (Bowen and others, 2003); although the original model data and solutions were not available for these models, published results have some relevance to functional habitat hypotheses on the upper river.

The models for assessment were selected to satisfy several criteria:

- Model reaches on the Lower Missouri River document a range of flow alteration, representing sites near Gavins Point Dam and sites far downstream from the dam where reservoir releases are less influential.
- Model reaches represent a wide range of channel complexity, from typical channelized, leveed river reaches with minimal rehabilitation to “best-available” reaches with extensively reconfigured channels and secondary channels.
- Model reaches include sufficient length of channel and adjacent flood plain that there are replicates of channel units (bend-crossover units).
- Model domains extend laterally from the channel to low-lying flood plains to assess effects of flood plain-connecting flows on functional habitat availability, especially food-producing habitats.
- Model resolution is sufficient that river-training structures are adequately represented in the computational mesh; and calculated, gridded habitat patches are reliable at 5–10 m cell size.
- Models have been calibrated and validated to provide useful results for relative assessment of habitat availability and dynamics.

Four modeled reaches were selected in the Lower Missouri River (Little Sioux, Iowa; Hamburg, Iowa; Miami, Mo.; and Lisbon-Jameson, Mo.) (table 11; fig. 29) that represent end members of habitat conditions currently available in the lower river. There is substantial variation among the models because they were developed at different times by different teams and optimized to answer different questions. All models are depth-averaged versions of the Navier-Stokes equations for shallow flow, but they vary by type of computational scheme (finite element or finite difference), mesh type (structured or adaptive), and numerical solvers. Two of the 2D hydrodynamic models—Little Sioux, Iowa, and Miami, Mo.—were developed, calibrated, and validated by the USGS as part of studies in 2006 and 2007 to assess the effects of spring rises on pallid sturgeon habitat dynamics (Jacobson, Johnson, and Deitrich, 2009). For application in this report, these two hydrodynamic model domains were extended to include overbank areas, which also required extrapolating results outside of the calibrated range. The Little Sioux and Miami 2D hydrodynamic models represent typical channelized, leveed conditions that existed in 2006 (figs. 30–33). The Little Sioux, Iowa, reach is 139 mi downstream from Gavins Point Dam and has a flow regime that is substantially affected by flow regulation (fig. 27). The Miami, Mo., reach is downstream from the Kansas River, where the flow regime has recovered substantial annual and interannual variability because of tributary inputs (fig. 34). Additional information on calibration, validation, and sensitivity of these 2D hydrodynamic models is available in Jacobson, Johnson, and Deitrich (2009).

Table 11. Characteristics of the two-dimensional hydrodynamic model reaches, Lower Missouri River.

Reach name	River miles	Description
		Big Sioux and Platte Segments
Little Sioux	669–674	Upstream hydrology, channelized. 2006 geometry prior to extensive reconfiguration (Deer Island Project).
Hamburg Bends	550–557	Upstream hydrology, best-available habitat; two side-channel chutes.
		Kansas and Grand Segments
Miami	258–264	Downstream hydrology, channelized. 2006 geometry.
Lisbon-Jameson	210–219	Downstream hydrology, best-available habitat; two side-channel chutes plus widening of the main channel.

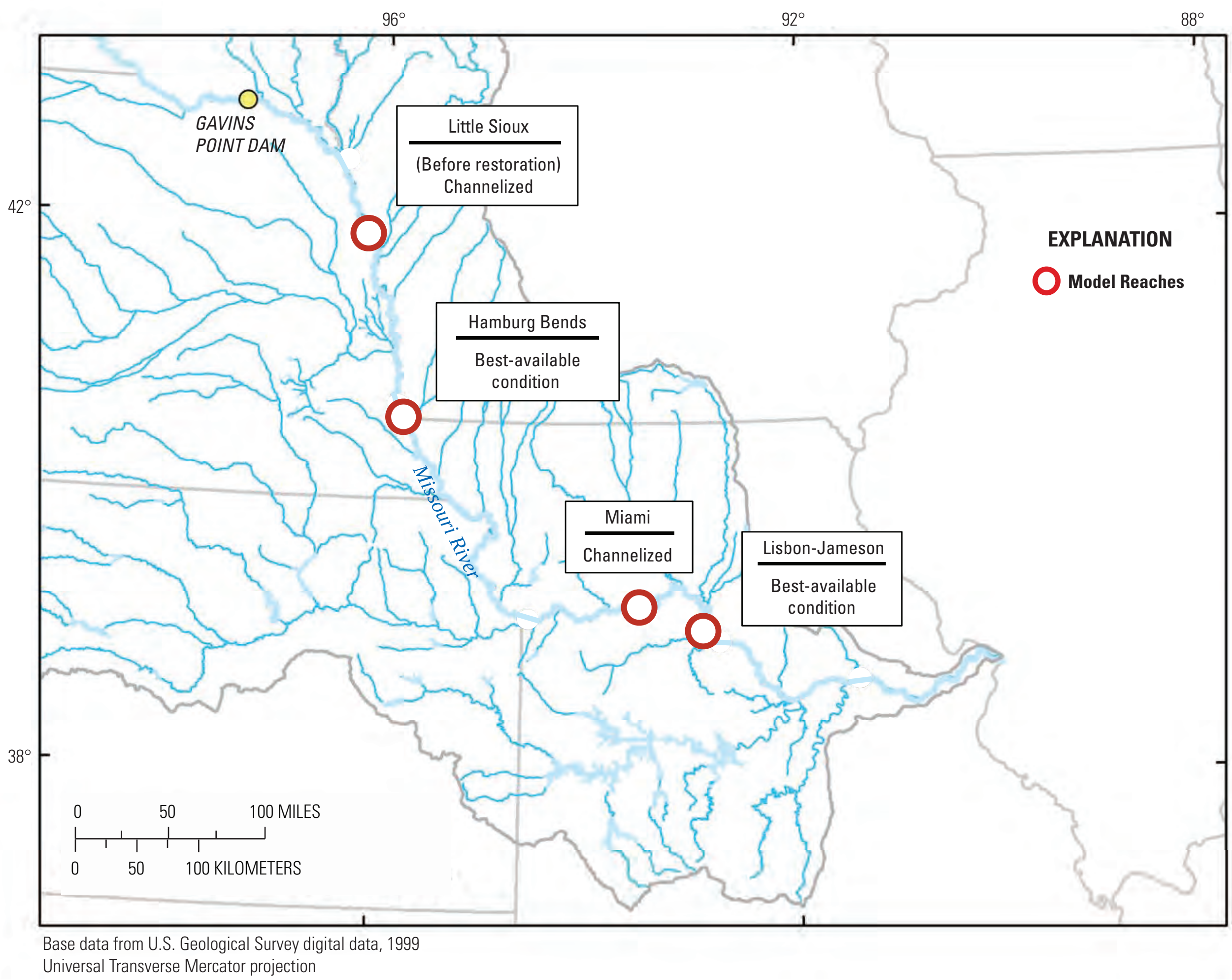


Figure 29. Locations of two-dimensional model habitat inventory reaches, Lower Missouri River.

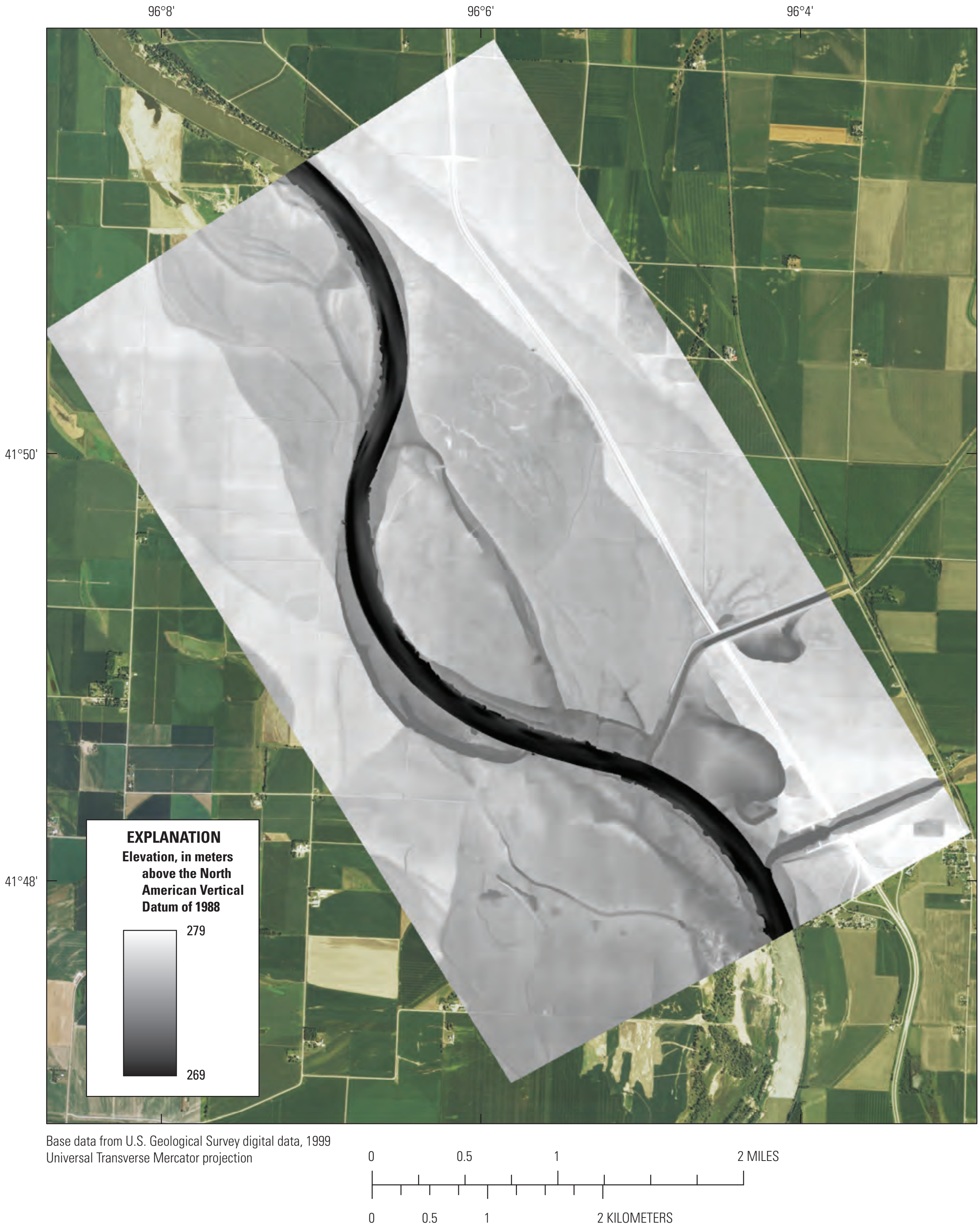


Figure 30. Little Sioux, Iowa, two-dimensional hydrodynamic model reach, representing an upstream, channelized condition.

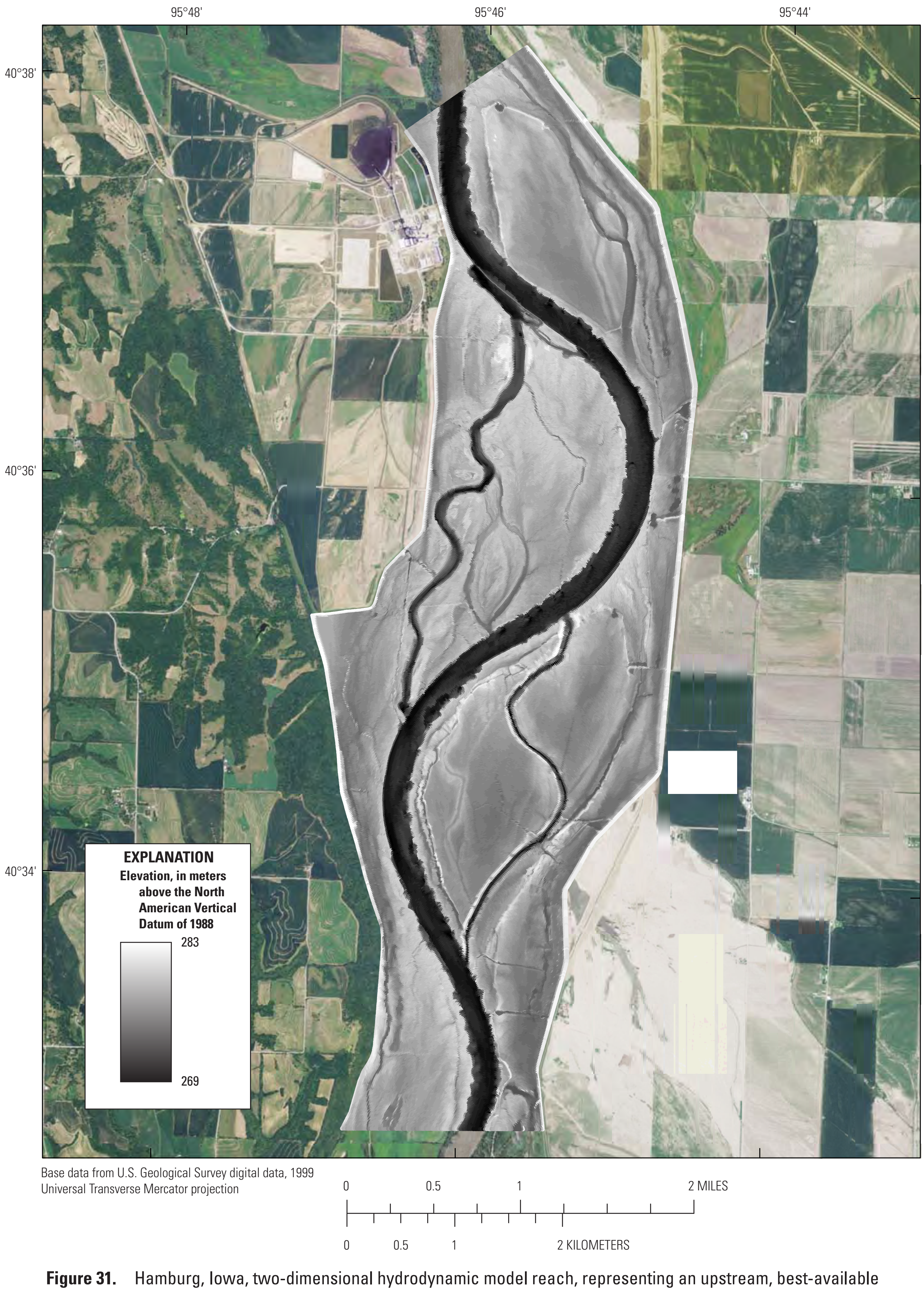


Figure 31. Hamburg, Iowa, two-dimensional hydrodynamic model reach, representing an upstream, best-available habitat condition.

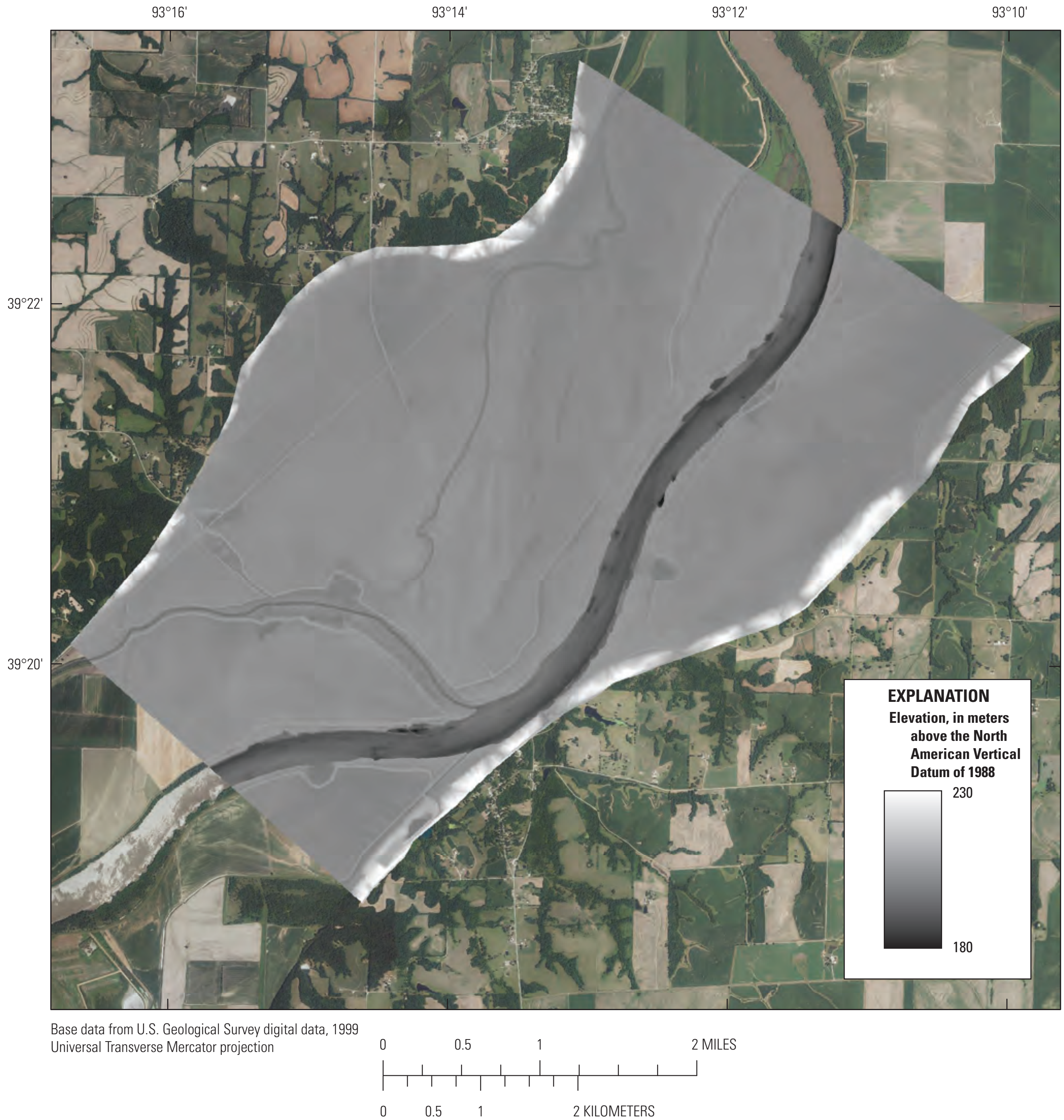


Figure 32. Miami, Missouri, two-dimensional hydrodynamic model reach, representing a downstream, channelized condition.

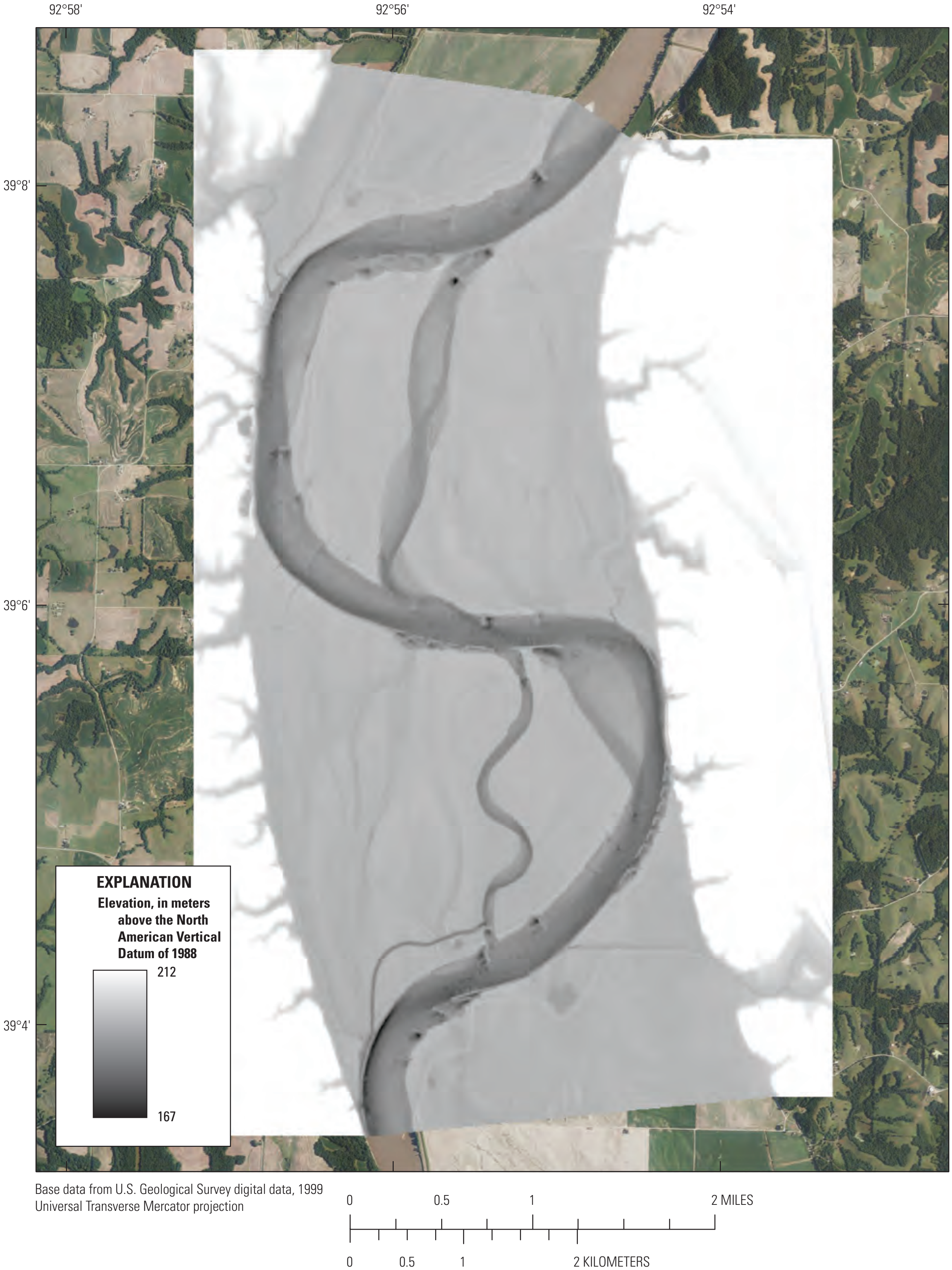


Figure 33. Lisbon-Jameson, Missouri, two-dimensional hydrodynamic model reach, representing a downstream, best-available habitat condition.

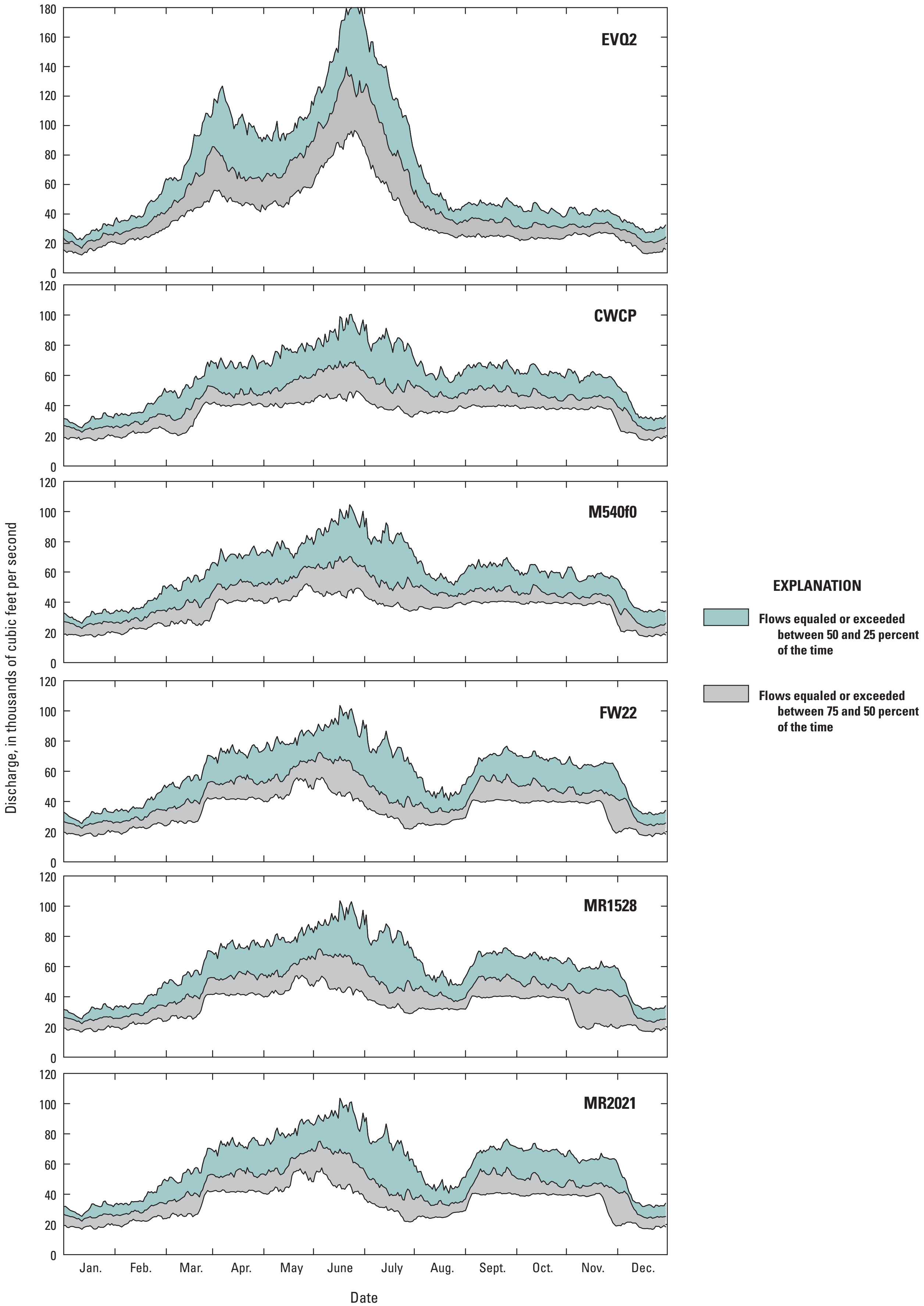


Figure 34. Flow-duration hydrographs for Kansas City, Missouri, for the six flow scenarios used for comparisons. Data are calculated from Daily Routing Model time series, 1898–1997 (U.S. Army Corps of Engineers, 1998).

The Hamburg Bend, Iowa, 2D hydrodynamic model (figs. 29 and 31) was developed by the USACE to include the upper and lower Hamburg Bends rehabilitation areas as they existed in 2013. Details of development, calibration, and validation of the Hamburg Bends hydrodynamic model are available in Fischenich and others (2014). We use the Hamburg Bends hydrodynamic model as the best-available habitat example for the upper, Lower Missouri River (table 11); although, with its location downstream from the Platte River confluence, it is less influenced by Gavins Point Dam flow regime compared to the Little Sioux, Iowa, reach.

The Lisbon-Jameson, Mo., 2D hydrodynamic model (figs. 29 and 33) represents the best-available habitat with minimal influence of Gavins Point Dam flow regime. The hydrodynamic model was constructed by the USGS specifically to evaluate habitat dynamics and free-embryo drift dynamics in a very complex river reach. Bathymetric data were collected in spring 2014, and calibration data (water-surface elevations, discharges, and velocity distributions) were collected throughout summer and fall 2014. The hydrodynamic model was developed in the Aquaveo (Surface-water Modeling System) interface and uses the TUFLOW (2D Unsteady FLOW) hydrodynamic code (Aquaveo, Inc., Provo, Utah). The present mesh has a 10-m spacing.

Modeled, steady discharges for all four hydrodynamic modeling reaches extend from about 0.3 times median discharge to 3–4 times median discharge by increments, where possible, of 3,500–7,000 cubic feet per second (ft^3/s). Solution data were exported as point data, gridded to 5-m geographic information system raster coverages, and used to derive habitat polygons and areas according to the definitions discussed in the “Functional Habitat Model Uncertainties” section. Discharges (normalized by median discharge) and areas of functional habitat units (normalized by channel length, in acres per mile because these units have been used customarily for habitat availability in regulatory decisions and engineering designs) were used to construct discharge-habitat rating curves. Effects of varying flow regime were assessed using the time series of discharges at the most relevant gage with output from the DRM (table 7). The time series was filtered for relevant time of year; for example, on the lower river, food producing and foraging habitats for age-0 pallid sturgeon were considered most relevant May through August, so 4 months of daily data for 100 years were used to evaluate the effects of varying flow. Habitat availability was calculated by interpolation of points in the discharge-habitat rating curves, and distributions during time series of low regimes were summarized graphically as boxplots.

Functional Habitat Model Uncertainties

Analyses of multidimensional model errors and sensitivities reported by Jacobson, Johnson, and Deitrich (2009) provide guidance on expectations for model accuracy. Hydrodynamic model errors may arise from uncertainties in hydraulic parameter estimation (typically a hydraulic roughness parameter and an eddy viscosity parameter), poor spatial representation of the channel and flood plain geometry, roughness conditions that change with discharge (for example, through bed fining or changing bedforms), and failure of a stationary bed assumption. The calibrated models used by Jacobson, Johnson, and Deitrich (2009) attained root mean square errors of 0.05 m in water-surface elevations compared to measurements. Model performances were validated by comparison to measured current velocities, which exhibited good concordance compared to ensemble averages measured with acoustic Doppler current profilers. By systematically varying hydraulic roughness and eddy viscosity, the authors evaluated propagation of error to habitat classes, indicating habitat unit patch areas were insensitive to eddy viscosity errors, but that a 10-percent change in drag coefficient could change the computed area of slow SWHs by as much as 16 percent. Faster habitat classes (for example, spawning habitat) were as much as plus or minus (±) 5 percent, whereas more integrative measures (for example, Simpkins diversity index applied to habitats) were as much as ±2.5 percent. By constructing models for 2 separate years and comparing model results, the authors documented remarkable stability of total habitat availability by classes despite documented spatial redistribution of the habitat patches. This result implies that physical habitats are in a type of dynamic equilibrium, a condition that would not necessarily apply to newly created channel reconfigurations. The 16-percent uncertainty that might be expected for slow SWHs indicates that models may not be useful in discriminating among channel reconfigurations that change total habitat availability less than 16 percent. The uncertainties in biological responses to channel reconfigurations are unknown but certainly much greater. Additional information on calibration, validation, and sensitivity of these models is available in Jacobson, Johnson, and Deitrich (2009).

Present modeling efforts should be evaluated by reference to ±16 percent habitat area. In future modeling, it may be useful to treat that error as a stochastically varying quantity in assessments of time series of habitat availability. Hydraulic uncertainties should be evaluated also in the context of the biological uncertainties involved with definition of the habitat units. Although 2D hydrodynamic models can provide useful information about the distribution of habitat patches with useful levels of uncertainty, the habitat definitions and their biological realism remain hypothetical. As discussed in the following section on definitions, the functional habitat definitions have varying levels of theoretical and empirical support, but robust linkages between these habitats and pallid sturgeon demographic rates are presently lacking.

Functional Habitat Definitions

Functional habitat definitions attempt to quantify the broad continuum of habitat conditions experienced by pallid sturgeon into relatively few habitat classes that relate to important biological and population responses. Definitions of spawning and interception habitats are based on new assessments (see appendixes) and should be considered especially tentative. Habitat areas can be easily recalculated from existing 2D hydrodynamic model solutions as definitions are refined.

Spawning habitat.—Although pallid sturgeon spawning has been documented in the Lower Missouri River, it is not clear that spawning has been successful if evaluated in terms of successful fertilization, incubation, and hatch of free embryos. For successful hatch to take place, hydraulics and substrate must be conducive first to attraction and aggregation of reproductive adults, followed by egg and milt release, fertilization, and deposition of eggs in a protected environment. Habitats quantified at spawning sites on the lower river indicate that females release their eggs in the deepest, fastest, and most turbulent parts of the channel, typically on revetment on outside bends. In previous habitat-modeling studies these habitats were identified based on hydraulic criteria of convergent flow as cells with unit discharge (discharge per unit width) that were greater than the mean plus 1.5 standard deviation (Jacobson, Johnson, and Deitrich, 2009); these criteria successfully mapped fast, highly turbulent areas of the thalweg.

Adhesive eggs are generally associated with spawning over coarse, hard substrate, which is present at the documented spawning sites, but it is unknown whether fertilized eggs end up in interstices of the substrate or on the surface. In addition, it is unknown whether fertilized eggs are at risk of scour or burial by transporting sand. Hydraulic conditions at confirmed spawning sites on the Yellowstone River, which serve as a natural reference condition, have recently been documented and may serve to improve these definitions (appendix 1). Spawning sites on the Yellowstone River are shallower than the Lower Missouri River (fig. 2) (mean of 3.3 m compared to 6.6 m) and slower (mean current velocity 1.1 m/s compared to 1.4 m/s).

Interception habitat.—A prominent hypothesis for recruitment failure posits that newly hatched free embryos are not able to exit the thalweg (navigation channel) to transition to first feeding in sufficient numbers before they starve. This is because the river lacks hydraulic conditions that would transport them into supportive channel-margin habitats with food and protection that are required on first feeding. This hypothesis recognizes that channelization of the Missouri River has created an extremely efficient system for downstream advection compared to the natural system (Jacobson and Galat, 2006). The so-called interception habitats are presently hypothetical, and concepts have been developed at the bend scale from geographic information system associations (appendix 2). In contrast to many conventional habitat definitions that ascribe attributes to a polygon or water volume, the interception habitat is hypothesized to be a hydraulic condition related to channel geometry and not necessarily represented as a space or volume. Presently, available information points to a combination of flow expansion and available channel width that creates secondary flow cells with sufficient velocity to advect free embryos out of the navigation channel and into channel-margin areas. The analysis uses multidecadal sandbar persistence as a metric for physical conditions that would support interception and deposition of particles being transported in the thalweg. A statistical model at the bend scale indicates channel width and the standard deviation of constricted width are dominant explanatory variables for location and size of sandbars. The most direct biological dependent variable available—CPUE of age-0 *Scaphirhynchus* spp. from the PSPAP—does not correlate well with the longitudinal distribution of these physical variables, and the variables used to explain the distribution of sand do a poor job of predicting CPUE (appendix 2). Within the context of uncertainties about CPUE as a reliable metric, the longitudinal distribution of CPUE suggests that physical conditions, measured as channel width and contraction/expansion of flow, may be necessary to intercept drifting free embryos but not sufficient. The distribution may be strongly controlled by the origin, rate of drift, and rate of development of the free embryos, superimposed on the physical conditions promoting interception and retention. Predictive modeling of interception habitats may require the ability to inventory secondary currents and recirculation along the river and evaluate how interception conditions vary with discharge.

Food-producing habitat.—Another hypothesis for recruitment failure is that free embryos cannot find proper food items when they need to transition to exogenous feeding. This hypothesis gains importance if interception habitat is not limiting. Ongoing diet and fitness studies of age-0 sturgeon may provide support for whether or not food-producing habitat is limiting, but results will not be available for several years (Todd Gemeinhardt, U.S. Army Corps of Engineers, written commun.). Presently available data document that age-0 pallid sturgeon larvae diets are dominated by Chironomidae larvae (Sechler and others, 2012; Harrison and others, 2014), and Chironomidae are preferentially associated with stable, fine sediment in low-velocity habitats (Poulton and others, 2003). In a detailed study of age-0 *Scaphirhynchus* diets on the Mississippi River, six Chironomidae taxa made up 74 percent of the fish diets, and all were characterized as sand-dwelling, burrowing species. Using a simple entrainment criterion for fine sand, we estimate that food-producing habitats are characterized by velocities less than 0.08 m/s.

Foraging habitat.—Foraging habitat is conceptualized as the hydraulic conditions conducive to foraging for food items (that is, where velocities are sufficient to bring drifting invertebrates from food-producing source areas to the age-0 pallid sturgeon but where velocities are not so high as to require too much energy expenditure). Conceptually, this describes a zone on the channel margin between low-velocity adjacent to the banks and thalweg (navigation channel) where drifting food is concentrated. Empirical data indicate that age-0 pallid sturgeon are collected in about 0.5–0.7 m/s velocity and 1–3 m depth (Ridenour and others, 2011). These foraging areas are distinct from the SWH definition because they do not extend to zero in either depth or velocity.

Interception-rearing complexes.—Interception, food-producing, and foraging habitats for age-0 pallid sturgeon are interrelated because it is the combination of habitats that would result in retention of young fish in supportive habitats. To represent this combination, we define interception-rearing complexes (IRCs) as complex areas that include hydraulics to intercept drifting free embryos combined with food-producing habitats and foraging habitats. Any of these three habitat types could be limiting to growth and survival, and a limiting role could shift with time as proportions of the habitats change.

Management actions involving IRCs involve at least two scales of design. At a broad scale, the reproductive range of the pallid sturgeon should determine geographic distributions of IRCs along the river. Within IRCs, a finer scale of design would determine proportions and spatial structure of habitats.

Because pallid sturgeon migrate upstream to spawn, and their progeny disperse downstream as free embryos and larvae, the IRCs should be located downstream from spawning locations. Presumably, free-embryo drift is an adaptive trait and indicative that drift during the free-embryo stage contributes to survival. Premature ending of drift may be maladaptive because the relatively immobile free embryos may be susceptible to predation. Settling from the drift and retention in supportive habitats would happen within a range of time (and locations) defined by when the yolk sac is consumed and when the individual is susceptible to starvation. The advection/dispersion models discussed in the section of this report on drift and dispersal modeling can be used to calculate zones of likely settling downstream from likely spawning sites and in a range of steady flow exceedances, including assumptions of immediate drift or interstitial residency.

Once locations of IRCs are determined, finer scale design tasks may include manipulation of channel configuration to do the following:

- create complex hydraulic conditions with secondary currents to advect free embryos from the thalweg into channel-marginal areas;
- create areas of sufficiently slow current velocity to encourage deposition of fine sand and organic material supportive of burrowing Chironomidae; and
- create areas with combinations of depth, velocity, and sedimentary bedforms (ripples or dunes) so exogenously feeding larvae can forage for Chironomidae larvae without undue expenditure of energy.

Moreover, habitat availability within IRCs and efficiency of interception hydraulics will vary with discharge; hence, flow manipulation at Gavins Point Dam may have a substantive effect on IRC functions, depending on IRC location.

Results of Hydrodynamic Modeling

The following results discuss the discharge-habitat rating curves, or discharge functions, for each of the functional habitat types. Because spawning and interception habitat definitions are speculative at this time (appendixes 1 and 2), we present surrogate measures.

Spawning Habitats

The deep, fast, and turbulent sites selected for spawning on outside revetted bends of the Lower Missouri River (fig. 2) may be attractive to reproductive pallid sturgeon adults in the absence of optimal habitat. Documentation of spawning habitats on a more natural reach in the Lower Yellowstone River indicates that spawning adults selected shallower depths, somewhat lower velocities, and a patchy hydraulic structure composed of sand dunes interspersed with gravel, compared to the lower river. Selection of these habitat characteristics within a reach that provides a wide range of other habitat types (including abundant gravel and cobble substrate) is taken as an indication of habitat preference (appendix 1).

The convergent flow definition for spawning habitats predicts discontinuous spawning patches on the outside of bends with minor patches in cross overs (Jacobson, Johnson, and Deitrich, 2009). Because spawning patches mapped by this definition are in the thalweg, they are relatively insensitive to discharge, especially during common spring discharges and availability scales with channel size, increasing downstream (fig. 35).

Interception Habitat

We currently lack a quantitative definition of interception habitat to accompany the conceptual definition. Ongoing analysis of CPUE of age-0 sturgeon suggests a combination of channel width and a measure of channel constriction/expansion may explain where drifting free embryos are intercepted and retained. As an interim indicator of complex interception hydraulics, we propose to use modeled residence time per unit length of channel (the inverse of mean velocity). This metric does not resolve the geometry of flow vectors that might be important to advection of free embryos but does relate to their overall rate of advection through a reach.

Patches of low velocity and high residence time exist in hydraulically sheltered sites marginal to the main channel. At discharges that do not overtop wing dikes, they may exist downstream from spur and L-head dikes but are also pronounced in backwaters at tributary and side-channel junctions. The nearly identical residence time functions at Miami and Lisbon-Jameson, Mo., 2D hydrodynamic model reach (fig. 36) results from the hydraulic efficiency of the channel. Patches of low velocity in the Miami, Mo., reach exist in tributary backwaters and old levee scours, creating longer residence times than the Lisbon-Jameson reach in most of the range of discharges. Residence times do not increase with overbank flows in Little Sioux, Iowa; Miami, Mo.; and Lisbon, Mo. reaches, indicating the overwhelming effect of conveyance in the main channel. Residence times do increase with overbank flows at the Hamburg, Iowa, reach at about 1.7 to 2 times median discharge, a condition indicative of increased susceptibility to overbank flooding at this site.

Food-Producing Habitat

Food-producing habitats are calculated based on a simple velocity criterion: velocity less than or equal to 0.08 m/s. Food-producing habitats mapped with this criterion are in deep or shallow slow water. Patches exist behind wing dikes at low discharges and in connected areas on low-lying lands and flood plains at higher discharges. At low discharges, food-producing areas scale with channel size, with greater area in the larger downstream channel, and greater area in the Lisbon-Jameson, Mo., rehabilitated channel at discharges as much as about 2.0 times median annual discharge (fig. 37). Food-producing habitats may increase rapidly as overbank areas are connected unless channel degradation or levees disconnect the channel from the flood plain. The increase in food-producing habitats at the Hamburg, Iowa, reach at 1.7–2.0 times the median discharge is notable and associated with increased susceptibility to overbank flows at this site where the channel has been aggrading recently (Jacobson and others, 2011).

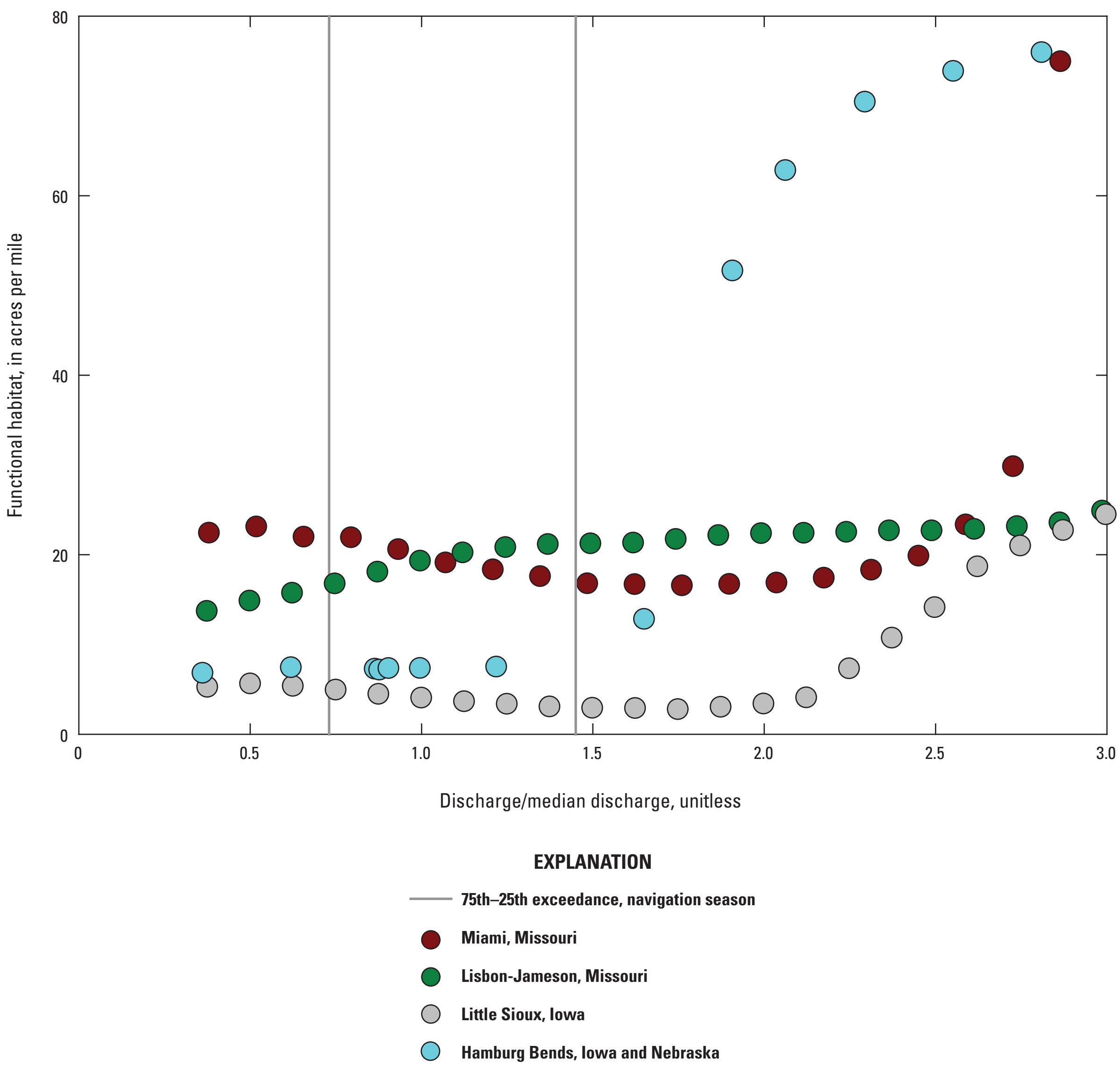


Figure 35. Discharge-functional habitat curves for interim definitions of spawning habitat in hydrodynamic model reaches.

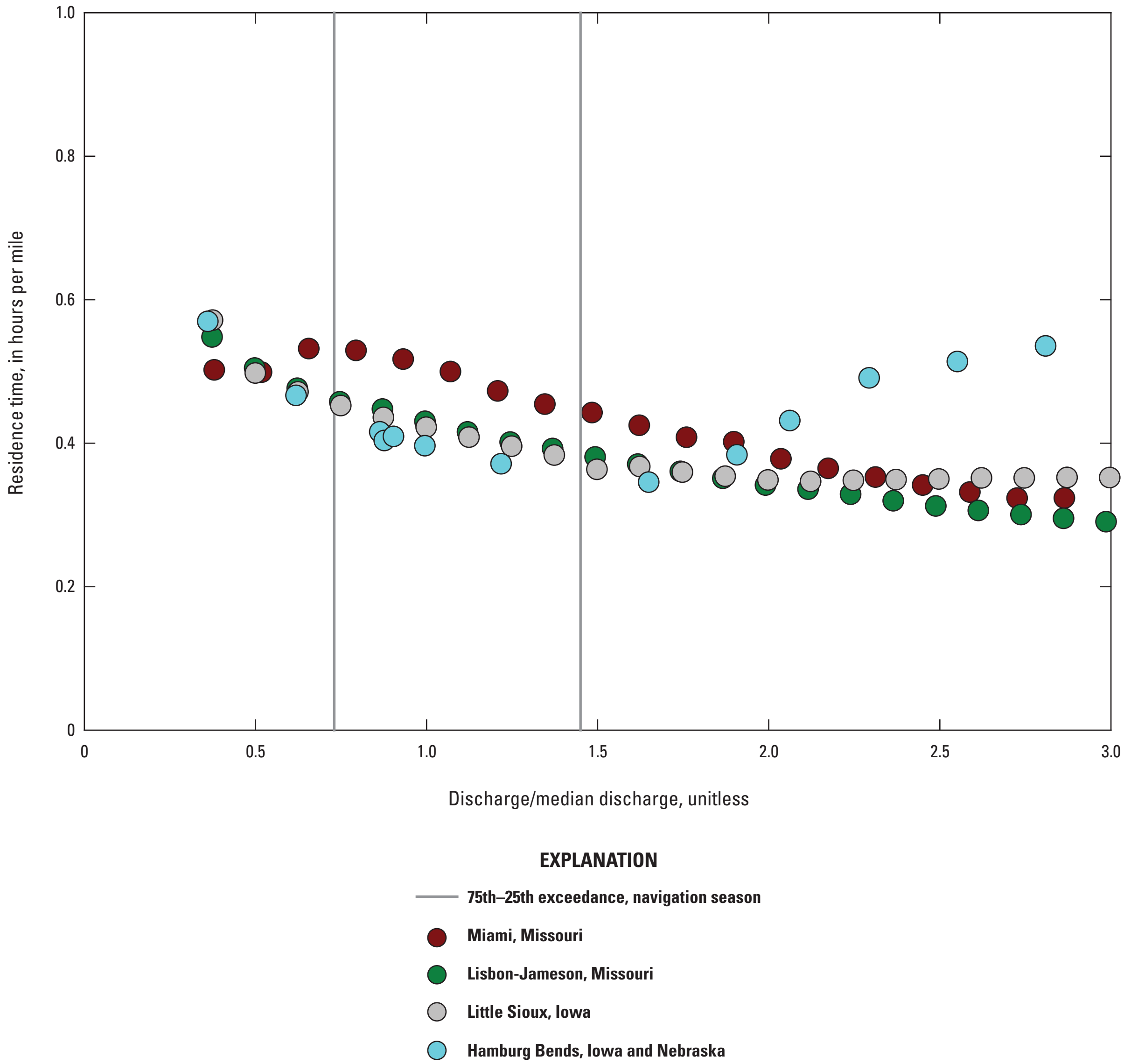


Figure 36. Discharge-functional habitat curves for mean residence time as an indicator for complex interception hydraulics in two-dimensional hydrodynamic model reaches.

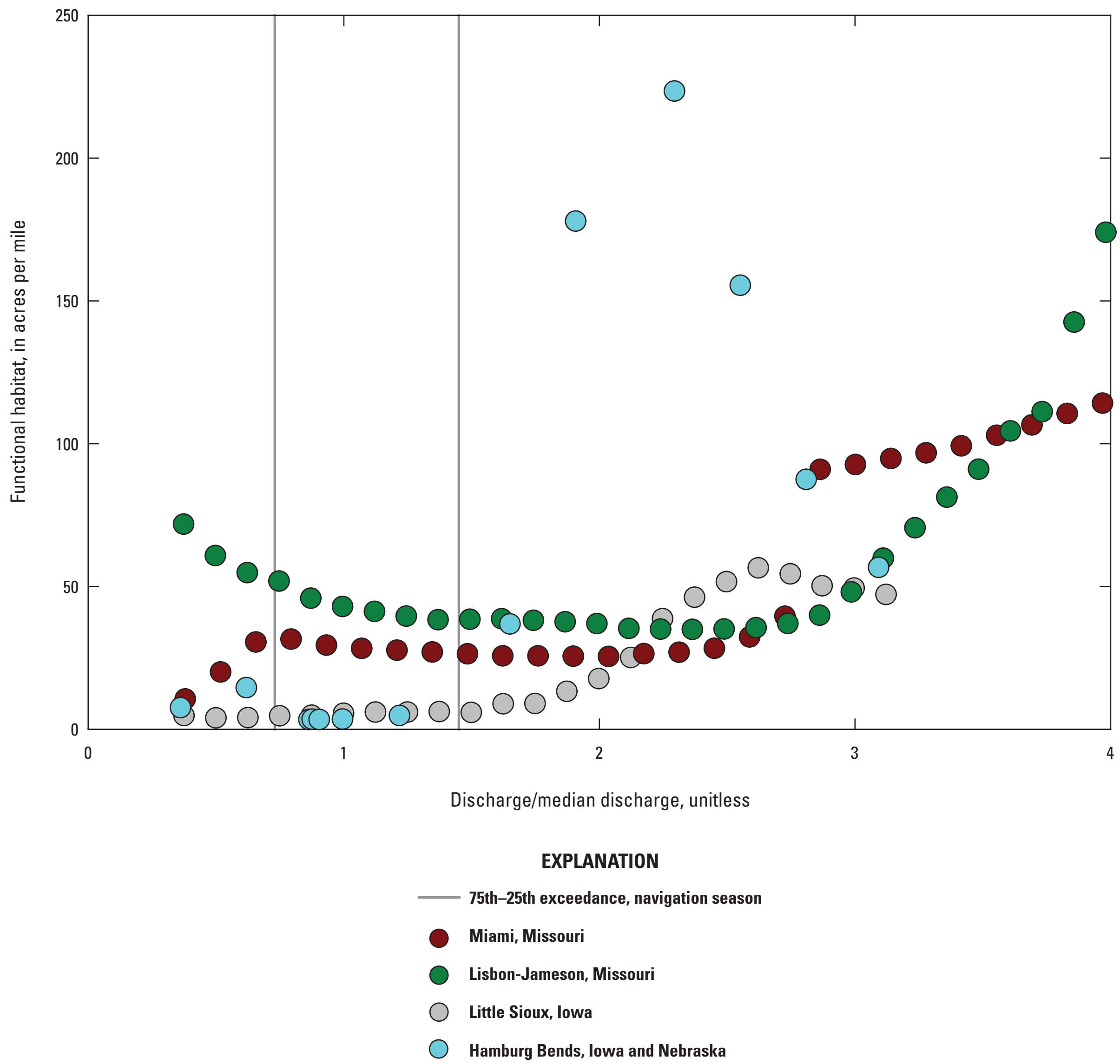


Figure 37. Discharge-functional habitat curves for interim definitions of food-producing habitat in hydrodynamic model reaches.

Foraging Habitat

Foraging habitat is presently calculated as areas that have velocities (0.5–0.7 m/s) and depths of about 1–3 m (Ridenour and others, 2011). Foraging habitats typically exist as bands on inside bends, following the contours of point bars or on larger sandbars associated with wing dikes. In channelized reaches, foraging habitat is most abundant at low discharges and decreases with increasing discharge (fig. 38). Foraging habitats mapped by these criteria increase some as water connects to low-lying lands and flood plains. The Lisbon-Jameson, Mo., best-available, 2D hydrodynamic model reach site presents substantially more foraging sandbar habitat compared to the channelized reaches (Little Sioux Iowa; Miami, Mo.), mostly because of the foraging habitats associated with large point bar complexes in the main channel and chutes but also associated with a large mid-channel bar in the Lisbon-Jameson, Mo., chute. Foraging habitat increases substantially above 2.0 times median discharge at the Hamburg, Iowa, reach, largely because of areas of concentrated flow that satisfy the criteria in overbank areas adjacent to levees and the valley wall.

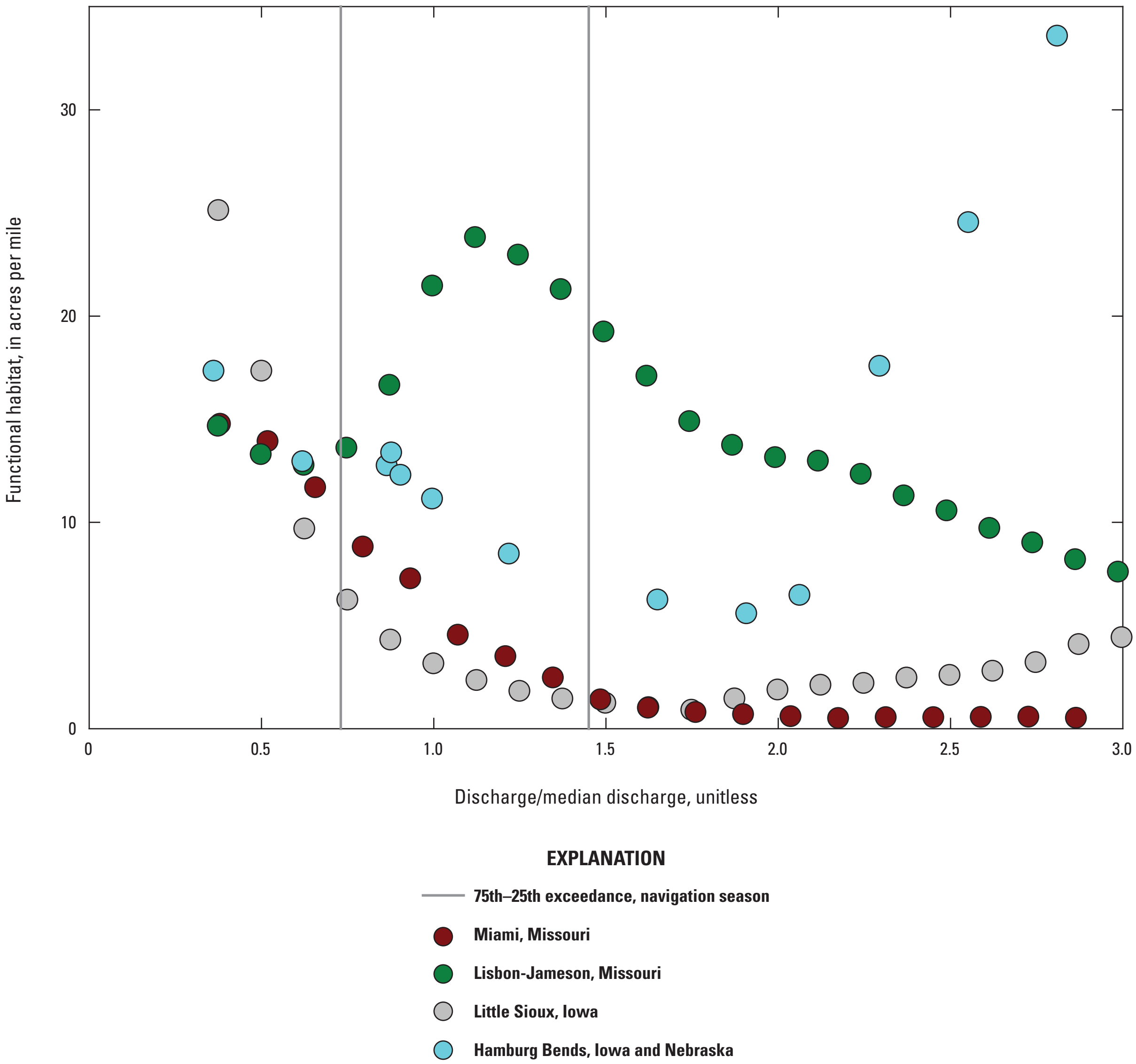


Figure 38. Discharge-functional habitat curves for interim definitions of foraging habitat in two-dimensional hydrodynamic model reaches.

Discussion

These functional habitat definitions and the 2D hydrodynamic models provide a basis for assessing the interaction of flow regime and channel configurations in availability of physical habitat patches. Spawning habitats, as defined here, scale with the size of the main channel, increasing in the downstream direction. Because documented spawning in the Lower Missouri River (fig. 2*B*) has all been in the main channel, this result is consistent with greater area of high velocity, depth, and turbulence in the larger channel. Spawning habitat availability is relatively insensitive to flow regime as the locations and extent of spawning patches (under this definition) stay in the same locations and at similar size in flows in the 75th–25th percent flow exceedance during navigation season. Although large areas satisfying these criteria exist on the Lower Missouri River, especially downstream from the Kansas River, the criteria do not resolve whether or not the patches provide attraction, stability, and water-quality conditions that may be necessary for successful spawning.

The concept of interception habitat has not yet been incorporated into the hydrodynamic modeling; instead, we rely on residence time as an indirect, reach-average measure. Residence time is remarkably consistent among all four 2D hydrodynamic modeling reaches, decreasing generally from 0.3 to 2.0 times median discharge. Residence time at the Miami, Mo., reach is somewhat higher than the three other reaches, perhaps because of an area of slow water in a small tributary confluence on the left bank. Residence time is generally maximized at lowest discharges, except when flow connects to overbank areas. Average residence time may increase, like at the Hamburg, Iowa, reach, if the overbank flows are a large enough volume compared to channel flows. We expect that more detailed analysis of 2D hydrodynamic model results using particle-tracking techniques will improve ability to quantify interception dynamics.

Availability of food-producing habitat is highly variable among reaches. Upstream reaches have relatively little acreage of food-producing habitat when flows are less than about 1.7 times median discharge; that is, when flows are fully within the banks. At the Miami, Mo., reach, food-producing acreage is especially low at very low flows but increases to a nearly constant level of 30 acres per mile (acres/mi) above 0.7 times median discharge and stays there until about 2.6 times median discharge when flows go overbank and food-producing habitat increases greatly in area. Food-producing acreage is initially low at the Hamburg, Iowa, reach but increases steeply above 1.7 times median discharge as flows go overbank. Food-producing habitat peaks at nearly 250 acres/mi at about 2.1 times median discharge and then decreases sharply to about 40 acres/mi at 3.0 times median discharge. In contrast, food-producing acreage at the Lisbon-Jameson, Mo., reach is initially high, about 70 acres/mi, at low discharge because of connected tributaries in backwaters. Food-producing areas decrease with increasing discharge, level off at about 40 acres/mi when flow is in the main channel, and increase with overbank flows above about 2.9 times median discharge. Food-producing habitats at the Lisbon-Jameson, Mo., reach also achieve greater than 250 acres/mi area, but overbank connection is dominant only above 3.0 times median discharge.

Foraging habitat in channelized reaches is maximized at the lowest discharge and decreases to 0–5 acres/mi at discharges greater than 1.5 times median discharge. In the Hamburg, Iowa, reach, foraging habitat also decreases initially with increasing discharge, but stays somewhat higher than the Little Sioux, Iowa, reach because of areas that satisfy the habitat criteria in the upper and lower chutes. At discharges greater than 2.0 times median discharge, the increase in foraging habitat is attributable to overbank areas that satisfy the depth and velocity criteria. At the Lisbon-Jameson, Mo., reach, foraging areas peak between 75th and 25th percent flow exceedance because of extensive areas in the Lisbon chute that satisfy the criteria.

Variation among these reaches in part follows expected patterns in upstream/downstream and channelized/rehabilitated comparisons. Some of the variation, however, results from conditions that are specific to the channel and flood plain configurations. These idiosyncrasies—for example, inundation of the flood plain at the Hamburg, Iowa, reach at relatively low normalized discharge and high contributions of the foraging habitat in the Lisbon-Jameson, Mo., reach chute—demonstrate the need to establish representative reaches for 2D hydrodynamic models meant to inventory habitat effects of management actions. The present models provide useful information, but systematic evaluation of alternatives should be based on a set of statistically representative reaches that are modeled using consistent data and methodology.

It stands repeating that functional habitat models are intended to evaluate how habitats with hypothesized importance to population dynamics are linked to management actions. There will be a continuing need to update definitions of the functional habitats and develop the functional relations between habitat availability and demographic rates (growth, survival, and reproduction). Establishing importance to population dynamics will require that the habitats and demographic rates are incorporated into models that predict population responses.

Assessment of the Effects of Management Actions

Objectives

In the following sections, we present multiple lines of evidence to assess the strength of effects of 21 working management hypotheses on pallid sturgeon populations. The objective is to provide the best-available scientific information bearing on the hypotheses in full realization that uncertainties concerning the hypotheses are substantial. We present the weight of theoretical and empirical information relating to each hypothesis; and where appropriate, we explore quantitative models that predict indicators of population responses. Our operational goals in the context of uncertainty are to provide an assessment of relative effectiveness of types of management actions and a framework of hypotheses and models that can inform future, management-relevant scientific inquiry under AM.

Approach to the Working Management Hypotheses

For each of the working management hypotheses (table 1), we present a definition of the hypothesis, a discussion of the spatial context and interactions among other management hypotheses, and a discussion of lines of evidence to support the action hypothesis. The lines of evidence include empirical field data, laboratory derived data, and theory. The existence of quantitative models does not confer greater weight unless the models are based on a strong foundation of theory and data. In the section on applicable models, we present conceptual, statistical, and predictive models—as available—and assess their utility in forecasting effects of management actions. Where available, model results are presented to document effectiveness. In many cases, models are available to predict habitat responses as an indicator of population responses, but links to population demographic rates are unknown or so highly uncertain as to make modeling ineffective. In these cases, we provide a discussion of the hypothesized linkages from functional habitat units to survival rates. The following sections for each working management hypothesis describe the uncertainty in the existing models and hypotheses with a focus on identifying critical linkages where additional scientific information is needed. Potential interactions with authorized purposes are also discussed to provide some general context on tradeoffs that might affect implementation of management actions to benefit pallid sturgeon. Finally, the working management hypotheses are discussed in context of the EA team's understanding of uncertainties and risks associated with implementation. This leads to options ranging from full implementation with robust monitoring and assessment, to limited field experimentation, and to research without implementation.

Assessment of Working Management Hypotheses

Upper River

Working Management Hypothesis 1—Naturalized Flows from Fort Peck Dam

Hypothesis 1 asserts that naturalizing flows from Fort Peck Dam in the Upper Missouri River (fig. 2) will increase food availability by connecting the river with low-lying lands and providing flow-related processes that increase river productivity (table 1). Increased food availability will result in increased growth and survival of age-0 pallid sturgeon. The hypothesis assumes that age-0 pallid sturgeon are food limited on the Upper Missouri River or would be if other factors were not limiting.

The concept of naturalization (Rhoads and others, 1999) is related to restoration and rehabilitation in that it involves using an understanding of the natural system to design alterations that will result in recovering elements of the natural system but to a condition that is determined to be socioeconomically achievable. In terms of flow regime, naturalization is used to describe using elements of the natural flow regime (for example, flow pulses and low flows) but shrinking or altering them so that ecological benefits do not create unacceptable socioeconomic costs.

Spatial Context and Interactions

The geographic scope of this hypothesis is the Missouri River from Fort Peck Dam (fig. 2) downstream to the headwaters of Lake Sakakawea. Pallid sturgeon spawning adults and drifting free embryos have been documented near Fort Peck Dam and in the Lower Yellowstone River (Elchelberger and others, 2014) through recent monitoring efforts. Drifting free embryos are presumed to settle in riverine habitat downstream from the confluence of the Missouri and Yellowstone Rivers or in the headwaters of Lake Sakakawea. By naturalizing flows from Fort Peck Dam, the productivity and availability of potential food items would increase from inundation of low-lying areas, resulting in higher growth rates that increases the probability of age-0 survival.

Naturalization of flows from Fort Peck Dam could interact with several other hypotheses by changing flow, temperature, and turbidity regimes downstream. Higher spring discharge associated with flow naturalization could attract spawning fish up the Missouri River and dissuade them from migrating up the Yellowstone River where recruitment potential may be poor depending on performance of passage at Intake Diversion Dam. Changes in flow and temperature will influence the dispersal time and the drift distance needed for embryonic development of free embryos (hypotheses 1, 2, 3, 4, 5, and 10). Higher spring flows associated with flow naturalization could counteract actions implemented to increase dispersal distance or reduce dispersal time, unless spring pulses were coordinated to recede before onset of free-embryo drift. Higher spring flows could provide higher levels of turbidity (hypothesis 6) that may diminish the predatory effectiveness of some fish and invertebrate species.

Lines of Evidence to Support Working Management Hypothesis

The natural, pre-impoundment flow regime of the Upper Missouri River (fig. 2) was characterized by a bimodal flood pulse followed by lower summer flows (Galat and others, 1998). The intent of naturalizing flows in a river is to estimate one or more of the critical flow components that regulate ecological processes: timing, frequency, magnitude, duration, or rate of change (Poff and others, 1997). The natural combination of these components work to organize the physical environment under which native species evolved. The flood-pulse concept proposes that long, predictable pulses in discharge are the primary force controlling biota in river-flood plain systems (Junk and others, 1989). The flood-pulse concept emphasizes the role of a predictable flood regime in mobilizing organic and inorganic material and energy from the flood plain into the main channel with this pulse of material acting as the primary driver of river productivity in flood plain systems (Junk and others, 1989). The pulsing of the river discharge creates a shifting mosaic of aquatic and terrestrial habitats that produces high habitat heterogeneity and productivity that generally characterizes flood plain rivers. Tockner and others (2000) also stressed the ecological significance of expansion-contraction events that happen well below bankfull flooding. These "flow-pulse events" considerably enhance river productivity through increases in temperature, primary productivity, and nutrient processing within the main channel (Tockner and others, 2000). In addition, life cycles of many species are synchronized with the flood pulse. Predictable and long flood-pulse events allow a greater exploitation of available resources by native fishes.

Little information presently exists to assess the effects of pulsed flows as part of a naturalized flow regime on Missouri River productivity; no information exists on the relation between river productivity and survival of age-0 sturgeon. Fish communities were sampled from flood plain habitats inundated by the high Missouri River flows of 2011 by PSPAP crews. High production of YOY fish by some species were in Missouri River flood plains; however, increases in YOY *Scaphirhynchus* spp. were not in flood plain habitats or main-channel habitats after flood plain waters began to recede (Tim

Welker, U.S. Army Corps of Engineers, written commun.). Some evidence exists that adult pallid sturgeon benefited from 2011 flood plain connectivity on the Lower Missouri River by increasing relative weight, presumably because additional food was available on the flood plain (Gerald Mestl, Nebraska Game and Parks Commission, written commun.). The Missouri River flood of 1993 did not directly benefit many of the rare, big river fishes in the Lower Missouri River, such as the pallid sturgeon, *Macrhybopsis meeki* (sicklefin chub), and *Macrhybopsis gelida* (sturgeon chub) (Galat and others, 1998). It has been hypothesized that restoring many components of native biota of the Lower Missouri River necessitates a natural flow regime and segments of unconstrained channels and flood plains to enable high and low flows to create, modify, and connect in- and off-channel habitats (Galat and Lipkin, 2000). Many fish species of the Mississippi River responded positively to the flood plain connectivity provided by a 500-year flood event (Barko and others, 2006); however, there was no indication that obligate river fish species responded positively.

Growth in young fishes has been determined to be regulated by the density of invertebrate prey resources for a variety of species (Fox, 1989). Food limitations at the early juvenile stages have been hypothesized as a potential mechanism for recruitment failure for *Acipenser transmontanus* (white sturgeon) in the Kootenai River system (U.S. Fish and Wildlife Service, 1999). Although no empirical data have been collected or theoretical models developed that examine the relation between river productivity and age-0 pallid sturgeon growth and survival in the Fort Peck Dam reach of the Missouri River, the influence of productivity and food availability on growth of many riverine fishes has been strongly established in other rivers (Gutreuter and others, 1999; Dutterer and others, 2013).

Applicable Models

Currently, no models exist that describe the links from flow to productivity and then to pallid sturgeon population dynamics. Researchers at South Dakota State University are developing a spatially explicit growth model for age-0 pallid sturgeon that may provide part of this sequence of links (Steve Chipps, South Dakota State University, written commun.). It is anticipated that once combined with a foraging model, the model will be used to predict growth and survival of age-0 pallid sturgeon within habitats and reaches of the Missouri River (fig. 2); linking this model to a flow-productivity model would be necessary to evaluate this hypothesis. No simulation models linking river flow and productivity with growth and survival of age-0 pallid sturgeon outside of the Missouri River were identified.

Hydrodynamic models have been published that develop the link between comparative flow regimes on the Yellowstone and Missouri Rivers, with implications for productivity. Based on differences of modeled areas of flood plain inundation, Bowen and others (2003) determined that regulated flows on the Upper Missouri River inundated 3.0–3.5 times less woody flood plain habitat compared to the Yellowstone River, implying that nutrient cycling and productivity would be similarly reduced on the Upper Missouri River. The data and models used in Bowen and others (2003) were not available for the EA team to re-run to match modeling scenarios in this report.

The component CEM (fig. 4) for the age-0 life stage (Jacobson, Parsely, and others, 2015) provides direct hypothesized linkages from primary ecological factors to secondary biotic response (that is, survival). The most likely path for this hypothesis through the CEM is (1) flow regime, (2) aquatic community composition and dynamics (productivity), (3) growth and condition (food availability), and (4) survival. The linkages between these components were judged to be of high importance with moderate uncertainty for the link between growth and condition and survival. The relation between flow regime and river productivity, and food availability/productivity and fish bioenergetics, has been well defined through numerous peer-reviewed studies of other species and rivers (Budy and others, 2011; Petty and others, 2014).

The functional relation between naturalized flows and survival for age-0 pallid sturgeon is hypothesized to be positively related and sigmoidal in shape (fig. 39) As more natural properties of the flow regime are recovered, it is anticipated that survival will increase up to an asymptote.

Uncertainty Assessment

Quantified bioenergetic relations between habitat variables, growth, and survival probably will be available in the near future (Steve Chipps, South Dakota State University, written commun.); however, the links from flow management to those habitat variables and system productivity have not yet been established on the Upper Missouri River (fig. 2*B*). Because of the lack of models and data that can explicitly link flow to survival, we judge the uncertainty for this hypothesis to be high.

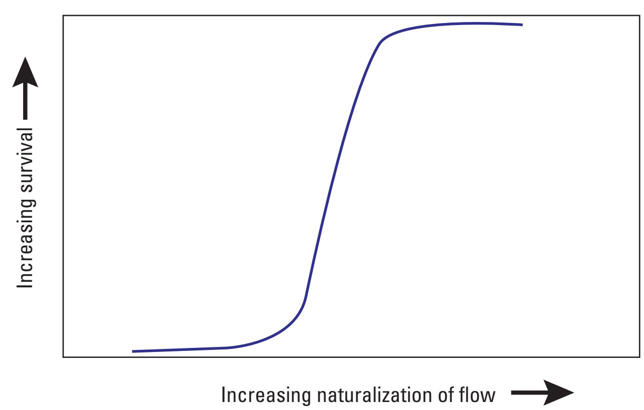


Figure 39. Hypothetical relation between degree of naturalization of flows and survival of age-0 pallid sturgeon.

Potential Interactions with Authorized Purposes

Manipulating flows from Fort Peck Dam (fig. 2) would be linked to system regulation and many of the authorized purposes through potential changes in the management of flows from other storage reservoirs in the system. Downstream target flows, storage capacity, and anticipated runoff would all play a role in the effects of reduced flows from Fort Peck Dam. Interaction of authorized purposes would also depend in part on flows in the Yellowstone River and other tributaries, such as the Milk River. High flows from these tributaries would potentially negate the intended effect of managed flows from Fort Peck Dam. Additionally, if downstream storage capacity is low, rules regarding system regulation may preclude implementing higher spring flows from Fort Peck Dam as a component of naturalized flows.

Implementation of flow changes for pallid sturgeon in the Upper Missouri River may also propagate to affect listed bird species by affecting reservoir shoreline habitats and options for flow management for nesting habitat downstream from Gavins Point Dam. Water used for spring flow pulses would likely decrease reservoir habitat availability or might be accommodated by coordinating with spring pulses from Gavins Point Dam. Spring pulses from Gavins Point Dam could be beneficial as a spawning/aggregation cue (hypothesis 11), and might be useful to transport sand and build sandbars, but could also involve a tradeoff with availability of tern and plover nesting habitat.

Working Management Hypothesis in Adaptive Management Context

With existing information, there is a high level of risk associated with this hypothesis if implemented. The level of response for river productivity, food availability, and survival from naturalized flows in the Upper Missouri River is unknown. This hypothesis assumes that food is limiting in the Upper Missouri River (fig. 2*B*) for age-0 pallid sturgeon; however, this hypothesis is a conjecture. An improved understanding of the potential habitat limitations imposed by current productivity levels and food availability and effects on survival is warranted. This could be achieved, in part, through simulations of a spatially explicit bioenergetics model. Results of the simulations could be used to develop hypotheses that better focus research needed to understand the significance of this hypothesis and the potential productivity has for limiting survival of age-0 pallid sturgeon in the Upper Missouri River.

Working Management Hypothesis 2—Spring Flow Pulses from Fort Peck Dam

Hypothesis 2 asserts that spring flow pulses from Fort Peck Dam (fig. 2*B*) will provide aggregation or spawning cues for reproductive pallid sturgeon, which will increase the chance of spawning success. This will increase the chances that mates will find one another, release their gametes in close proximity to each other, and ultimately result in an increased probability of viable embryos.

Spatial Context and Interactions

Observations of reproductive pallid sturgeon migration patterns in the upper river have indicated that these fish may select between Upper Missouri and Yellowstone River (fig. 2) migrations based on hydrologic cues, such as discharge characteristics (increased flow). It is possible that by increasing flow from Fort Peck Dam during the spawning period (early June) or earlier, reproductively able pallid sturgeon will be cued to migrate to supportive spawning habitat far upstream on the Upper Missouri River, which will increase the chance for successful spawn, fertilization, hatch, and dispersal.

The geographic scope of this hypothesis is the Missouri River from Fort Peck Dam downstream to the headwaters of Lake Sakakawea. The hypothesis also potentially affects pallid sturgeon in the Yellowstone River because reproductive fish may select either the Upper Missouri or Yellowstone Rivers depending on the magnitude or quality of cues from either river.

Because spawning behavior is hypothesized to be influenced by other factors, such as temperature and turbidity, this hypothesis could interact with other hypotheses (hypotheses 1, 3, and 4). Changes in discharge from Fort Peck Dam will affect temperature regimes and sediment mobility downstream. Attracting pallid sturgeon to spawn in the Missouri River could dissuade them from migrating up the Yellowstone River and using a fish passage structure at Intake Diversion Dam, which could diminish recruitment opportunities in the Yellowstone River.

Hypothesis 2 is highly related to hypothesis 1 because naturalization of the flow regime intended to increase productivity would also involve an increase in spring pulse flows. The details of design, however, could vary because of the greater scope of hypothesis 1 and greater specificity of hypothesis 2, which could involve a flow pulse that is not necessarily natural. Hypothesis 2 is also related to hypothesis 3 (decrease of flows to decrease drift distance) although the two hypotheses are in apparent conflict unless the spring pulses are short and happen substantially before free-embryo drift.

Lines of Evidence to Support Working Management Hypothesis

A naturalized flow regime, which includes flow pulses in the spring (“spring rise”), is hypothesized to be necessary to cue sufficient pallid sturgeon spawning behaviors according to the 2000 and 2003 Biological Opinions (U.S. Fish and Wildlife Service, 2000, 2003). Many lotic fishes are adapted to natural variation in water temperature and discharge, and decoupling of water temperature from discharge variation is thought to result in removal of cues for spawning conditions. The role of discharge-related spawning cues is discussed in Goodman and others (2012).

Empirical data collected in the lower river are ambiguous on behavioral responses to flow pulses related to spawning behavior of pallid sturgeon (DeLonay and others, 2009; DeLonay, Chojnacki, Jacobson, Albers, and others, 2016). Reproductive migrations of pallid sturgeon on the Lower

Missouri River (fig. 2) have exhibited little evidence of correlation with natural and manipulated flow pulses. Instead, migrations exhibit evidence of influence of water temperatures; in particular, spawning seems dependent on a temperature threshold of 16–18 degrees Celsius (°C), and weather-related decreases in water temperature have been associated with disrupted spawning migrations. An analysis of shovelnose sturgeon spawning patterns in the Lower Missouri River indicated statistically identifiable clusters of spawning migrations and further identified some patterns that were more likely to be indicative of successful spawning compared to others (Wildhaber, Holan, and others, 2011). This study did not specifically identify the cause for the different patterns but indicated that patterns closer to Gavins Point Dam were less likely to be associated with successful spawning, possibly because of a lack of flow pulses. In summary, lower river data are ambiguous about necessity of spring rise for a spawning cue effect and are insufficient to define what functional relations might look like between pulse characteristics and strength of the spawning behavior response. This conclusion is similar to that of the Missouri River ISAP (Doyle and others, 2011).

In contrast to the lower river, pallid sturgeon telemetry tracking around the Upper Missouri and Yellowstone River confluence provides some evidence to indicate a role for flow pulses (DeLonay and others, 2014). These data document that in most years, most telemetered pallid sturgeon migrate out of the Missouri River and into the Yellowstone River in April–May before the spring pulse from the Yellowstone River, when discharge on the Yellowstone River is higher than that on the Upper Missouri River. This pattern was disrupted in 2011 when a high-flow pulse with warm temperatures and high turbidity was contributed by the Milk River in April, followed by record releases from Fort Peck Dam. During that year, 36–39 percent of the telemetered population migrated up the Upper Missouri River. In addition, smaller but substantive numbers of pallid sturgeon migrated up the Missouri River in preference to the Yellowstone River in 2 years when spring flows in the Missouri River have been greater than those on the Yellowstone River (2004 and 2013), indicating that relative discharge has an effect on selection (Dave Fuller, Montana Fish Wildlife and Parks, written commun.). These observations support the hypothesis that an early spring release from Fort Peck Dam, relative to Yellowstone River flow, may provide an attractant for migration and aggregation.

Applicable Models

Although linkages from flow regime to spawning behavioral responses are conceptually viable and common in the fisheries literature (U.S. Fish and Wildlife Service, 2003), we have not identified any useful, quantitative models linking flow management to production of viable gametes.

The component CEM for reproductive adults (Jacobson, Parsely, and others, 2015) is especially complex in depicting potential linkages from secondary ecological factors to primary biotic responses because of the many ways that reproductive behaviors may be linked to environmental variables. A link from spawning site selection to survival of gametes is apparent based on telemetry information that documents nonsystematic patterns of upstream and downstream migration behavior, suggesting a search for suitable spawning sites with suitable mates (Braaten and others, 2008; DeLonay, Chojnacki, Jacobson, Albers, and others, 2016). Reproductive synchrony, or the period that males and females in the same reproductive condition are at the same location at the same time, is hypothesized to be an important factor related to spawning and fertilization. Flow regime has been shown to be an important factor affecting physical habitat and water-quality dynamics and may lead to synchrony and ultimately production of viable gametes.

The hypothesized linkage from flow regime to aggregation and spawning behavioral response would be captured in the population model as an increase in the probability that mates find each other and successfully spawn, resulting in viable gametes from males and females combining to ultimately form embryos (fig. 6). The functional relation between flow-regime naturalization and ultimately to an increase in viable embryos is unknown but has been hypothesized to be positively related (U.S. Fish and Wildlife Service, 2000). We anticipate that increased magnitude or frequency of a spring pulse would increase the probability of producing viable embryos (fig. 40).

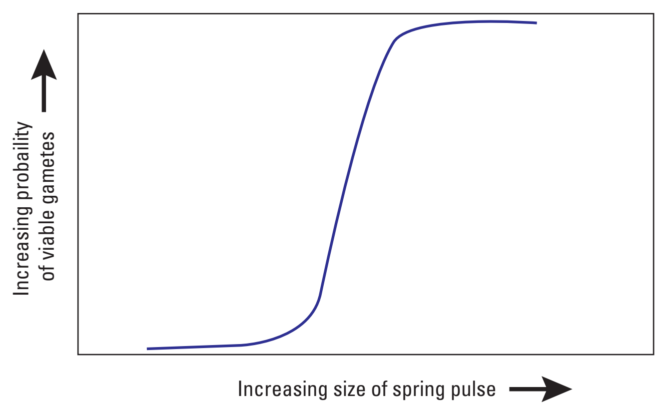


Figure 40. Hypothetical relation between magnitude or frequency of a spring pulse and probability of producing viable gametes.

Uncertainty Assessment

No studies or quantitative models were found that specifically link flow increases as a spawning cue to aggregation and an increase in viable embryos. Therefore, we judge uncertainty to be high.

Potential Interactions with Authorized Purposes

Naturalization of the flow regime from Fort Peck Dam (fig. 2) would be linked through system-wide reservoir operations to nearly all authorized purposes through re-allocation of water during spring pulsed-flow releases. If water storage is too low upstream from Fort Peck Dam or if there is flooding downstream, increased discharge from the reservoir may not be possible. The magnitude of the re-allocation is unknown because of uncertainties in what magnitude and duration would be sufficient to cue a behavioral response. Interaction of authorized purposes would also depend in part on flows in the Yellowstone River. The flow regime in the Yellowstone River is nearly natural and unmanaged, whereas in the Upper Missouri River the flow and temperature regimes are highly managed. If flow is especially high in the Yellowstone River, management rules may preclude increases from Fort Peck Dam that are large enough to be effective in drawing pallid sturgeon up the Missouri River instead of the Yellowstone River.

As with hypothesis 1, implementation of flow changes for spawning cues in the Upper Missouri River may propagate to affect listed bird species by affecting reservoir shoreline habitats and options for flow management for nesting habitat downstream from Gavins Point Dam.

Working Management Hypothesis in Adaptive Management Context

High uncertainty assigned to this hypothesis indicates risk of failure if implemented with currently existing information. If, as data indicate, pallid sturgeon respond to relative (higher) discharges on the Upper Missouri River (fig. 2) compared to those on the Yellowstone River, flow releases may be effective in attracting fish up the Missouri River; however, the hydrologic conditions needed to retain them in the Upper Missouri River and result in successful spawning (magnitude, duration, frequency, timing, and rate of change) are unknown. Implementation of pulsed flows in an AM framework, therefore, would require robust monitoring and assessment of effects on pallid sturgeon behavioral responses and recruitment.

An alternative to implementation would be to continue hypothesis-driven research to increase understanding of physiological and behavioral responses to environmental cues (DeLonay, Chojnacki, Jacobson, Albers, and others, 2016). Research approaches may include controlled studies in laboratory or mesocosm environments and field-based studies of behaviors of telemetry-tagged fish. Field-based research could follow the concept of experimental flow releases (Braaten and Fuller, 2002); or research could be opportunistic, depending on flow events arising from various sources. The current (2016) population of telemetry-tagged pallid sturgeon at the confluence of the Yellowstone and Upper Missouri Rivers provides an ongoing experimental structure to elucidate flow characteristics capable of triggering behavioral responses in adult reproductive pallid sturgeon. Documented fish responses to annual flows from the Yellowstone River, and either experimental releases from Fort Peck Dam or opportunistic flow pulses from tributaries, would decrease uncertainties; reliance on opportunistic flow pulses may require many years to develop sufficient information.

Working Management Hypothesis 3—Decreased Flows in Late June and July from Fort Peck Dam

Hypothesis 3 asserts that reducing flows from Fort Peck Dam (fig. 2*B*) in late June and July will decrease channel velocities, slowing the drift rate of free-embryo pallid sturgeon to increase survival of free embryos; this requires that reproductive adults have been present far enough upstream and that they have successfully spawned. Slowing the drift rate will reduce the distance needed for embryonic development, allowing them to settle into habitats suitable for growth and development upstream from Lake Sakakawea.

Spatial Context and Interactions

The geographic scope of this hypothesis is the Missouri River from Fort Peck Dam (fig. 2) downstream to the headwaters of Lake Sakakawea. Because free embryo development is influenced by other factors, such as temperature and drift duration, this hypothesis could interact with other hypotheses, including actions affecting flow regime (hypotheses 1 and 2). Temperature influences the maturation rate of free embryos (Kynard and others, 2007). Changes in discharge from Fort Peck Dam or implementing other actions that influence river temperatures (hypothesis 5) will affect temperature regimes downstream. Implementing a drawdown of Lake Sakakawea (hypothesis 10) in conjunction with reduced flows from Fort Peck Dam may interact to provide improved drift conditions for developing free embryos more than would happen by implementing either action alone.

Lines of Evidence to Support Working Management Hypothesis

A dominant hypothesis for the absence of pallid sturgeon recruitment in the Upper Missouri River (fig. 2) is that the length of free-flowing river is insufficient for drifting free embryos to complete embryonic development, and this results in free embryos settling into habitats unsuitable for survival (Braaten, Fuller, Lott, Ruggles, and others, 2012; Guy and others, 2015). Water temperature, velocity, and channel form influence pallid sturgeon embryo drift distance and time (Braaten, Fuller, Lott, Ruggles, and others, 2012); spawning location acts as an important determinant for the amount of drift distance required (Fischenich and others, 2014).

Empirical data supporting this hypothesis have been collected in the Missouri River downstream from Fort Peck Dam. In 2011, Montana Fish Wildlife and Parks and the USGS collected wild-produced pallid sturgeon embryos from the main stem Missouri River near Frazer Rapids, Mont., indicating that pallid sturgeon successfully spawned, hatched, and drifted in this river reach (DeLonay and others, 2014). Upper Missouri River models of cumulative drift distance as a function of velocity and temperature suggest that pallid sturgeon drift requirements generally exceed the 189 mi of free-flowing Missouri River downstream from Fort Peck Dam (Braaten, Fuller, Lott, Ruggles, and others, 2012). An absence of recent, natural recruitment to the population supports this assertion.

Braaten, Fuller, Lott, Ruggles, and others (2012) released nearly 600,000 pallid sturgeon free embryos into the Missouri River downstream from Fort Peck Dam as part of a study of drift dynamics. The free embryos ranged in age from 1 to 17 dph. From 2004 to 2010, monitoring programs collected 51 survivors from this study (ranging from 1 to 6 years old), indicating that conditions are suitable for survival of some free embryos if the drift time needed before settling is reduced (Braaten, Fuller, Lott, Ruggles, and others, 2012); therefore, implementing flows from Fort Peck Dam at a rate that allows free embryos to mature and settle before reaching Lake Sakakawea may increase the probability of survival to the next life stage.

Applicable Models

The component CEM for age-0 survival (Jacobson, Parsley, and others, 2015) provides direct hypothesized linkages from primary ecological factors to secondary biotic response (that is, survival). The most likely path for this hypothesis through the CEM is (1) flow regime, (2) hydraulics, (3) habitat suitability, and (4) survival. The linkages between these components are of high importance with high uncertainty for the link between habitat suitability and survival. The strong relation between flow regime, hydraulics, and drift dynamics of free embryos has been quantified through the empirical studies (Kynard and others, 2007; Braaten and others, 2008; Braaten, Fuller, Lott, Ruggles, and others, 2012) and theoretical flow models (Fischenich and others, 2014) described previously. The anoxic conditions in the headwaters of Fort Peck Lake and the potential effects that low dissolved oxygen has on survival of free embryos have been documented by Guy and others (2015) and hypothesized for the headwaters of Lake Sakakawea. In the CEM, the successful first feeding may also be a viable link between hydraulics and survival, but the level of importance was determined to be low.

There are several statistical models that can be used to evaluate how low flows from Fort Peck Dam (fig. 2) will influence the drift dynamics of pallid sturgeon free embryos. Empirical models of drift were developed by Braaten, Fuller, Lott, Ruggles, and others (2012). Their models predicted cumulative drift distance as a function of current velocity and the relation between water temperature and ontogenetic development. Cumulative distance was modeled for mean water velocities of 0.50–0.90 m/s; however, if flow reductions from Fort Peck Dam result in current velocities below 0.50 m/s, this model may be of limited use because the velocities would be outside the range used for model development.

A detailed longitudinal advection/dispersion model of free-embryo drift was recently developed for the Missouri River downstream from Fort Peck Dam (Fischenich and others, 2014). The model predicts the locations that free embryos would settle as they transition to exogenously feeding larvae as a function of distance, drift velocity (a function of water velocity and discharge), and embryonic development (a function of temperature). The model includes a dispersion coefficient, which is based on the hypothesized influences of hydrology and channel morphology in modifying the distribution of drift distances (Erwin and Jacobson, 2014). The inclusion of a dispersion coefficient is supported by the empirical work of Braaten and others (2008) and Braaten, Fuller, Lott, Haddix, and others (2012), where a range of drift rates was observed for free embryos released into the Missouri River. The model uses time and cumulative thermal units to predict yolk-plug expulsion, which signifies the start of exogenous feeding and the point of settling from the drift. The model does not include biologic factors that might retard drift rates below the passive rate; these factors remain as important subjects for research.

Simulations from advection/dispersion models (Fischenich and others,2014) have been used to explore which combinations of distance, flow, and temperature provide the best conditions for retention of free embryos in the riverine habitat above the hypothesized anoxic headwaters of Lake Sakakawea. Initial simulations from the model provide some insight into the potential effectiveness of reduced flows from Fort Peck Dam as a management action. Assuming that spawning happens at or near Fort Peck Dam, 1 to 21 percent of free embryos will settle upstream from Lake Sakakawea during a 10-day drift period at a flow of 3,000 ft^3/s and lake levels between 1856 and 1805 ft above mean sea level (table 8). During an 8-day drift period with the same discharge and pool conditions, 3 to 92 percent of free embryos are predicted to settle in the riverine segment upstream from Lake Sakakawea. Empirical data and models developed by Braaten, Fuller, Lott, Ruggles, and others (2012) indicate that downstream dispersal through drift may persist for 8–14 days depending on water temperature and development. With a 3,000 ft^3/s discharge from Fort Peck Dam and the shortest drift time (that is, 8 days) determined by Braaten, Fuller, Lott, Ruggles, and others (2012), 92, 85, and 60 percent of free embryos would settle in riverine habitats at lake elevations of 1805.0, 1812.6, and 1821.6 ft above mean sea level, respectively.

For some species of sturgeon, newly hatched embryos are known to reside after hatching within the interstitial spaces of river substrates (Du and others, 2011; McAdam, 2011). If pallid sturgeon free embryos spend time in interstitial residency, instead of immediately entering the drift, the distance needed for ontogenetic development would be reduced. Under most model simulations, more than 5 days of interstitial residency would be needed for a high proportion of free embryos to avoid the headwaters of Lake Sakakawea (Fischenich and others, 2014). Other biological-hydraulic interactions could also serve to retard drift rates, but the processes and magnitudes of such interactions are unknown.

Models of the effects of discharge from Fort Peck Dam on survival take into account the time series of discharges (from DRM scenarios), lake level, water temperature, survival functions (table 6), and length of interstitial hiding. To assess the specific hypothesis about flow management, we present the following calculations assuming spawning at the mouth of the Milk River and median historical level of Lake Sakakawea (1,843.2 ft). Survival by number of days of drift is calculated using survival functions from table 6 (fig. 41) and the time series of discharges in June and July from DRM scenarios (table 7). The number of days for yolk-plug expulsion is a function of water temperature (fig. 42). Survival distributions are given by number of days of drift (fig. 43), which will be shortened by any day during which interstitial residency happens.

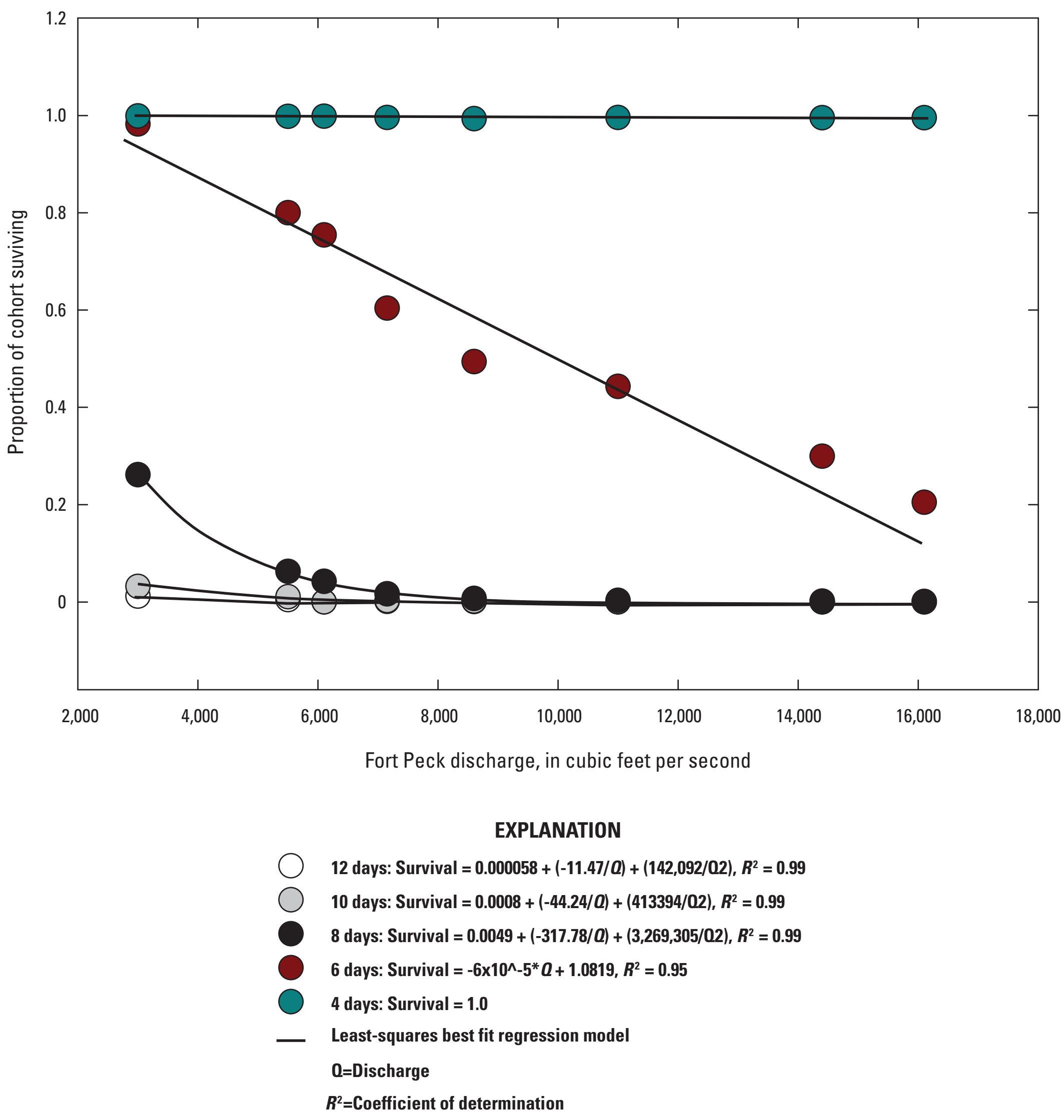


Figure 41. Survival functions by day assuming spawning at Milk River confluence and median historical Lake Sakakawea levels.

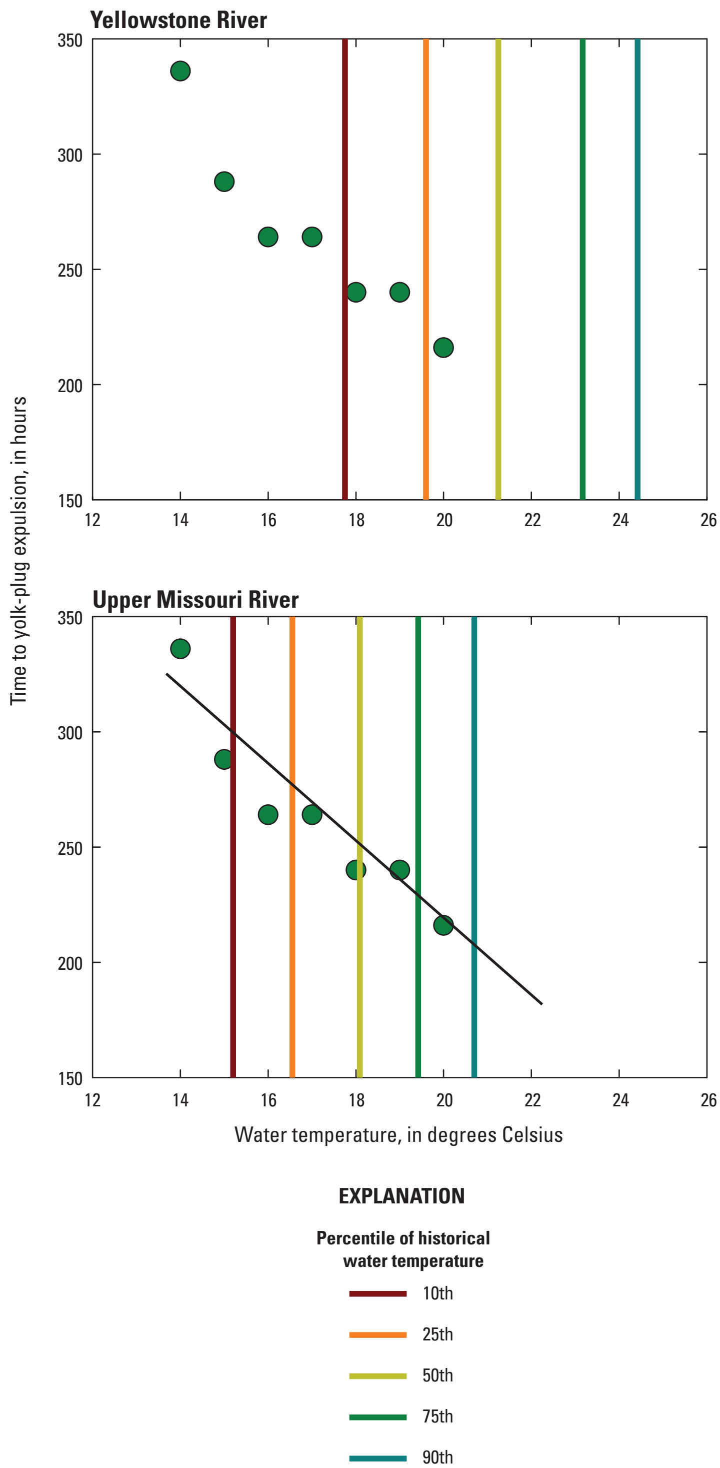


Figure 42. Hours required for 50 percent of individuals to expel yolk plug by water temperature and percentiles of water temperature under historical conditions, Yellowstone and Upper Missouri Rivers.

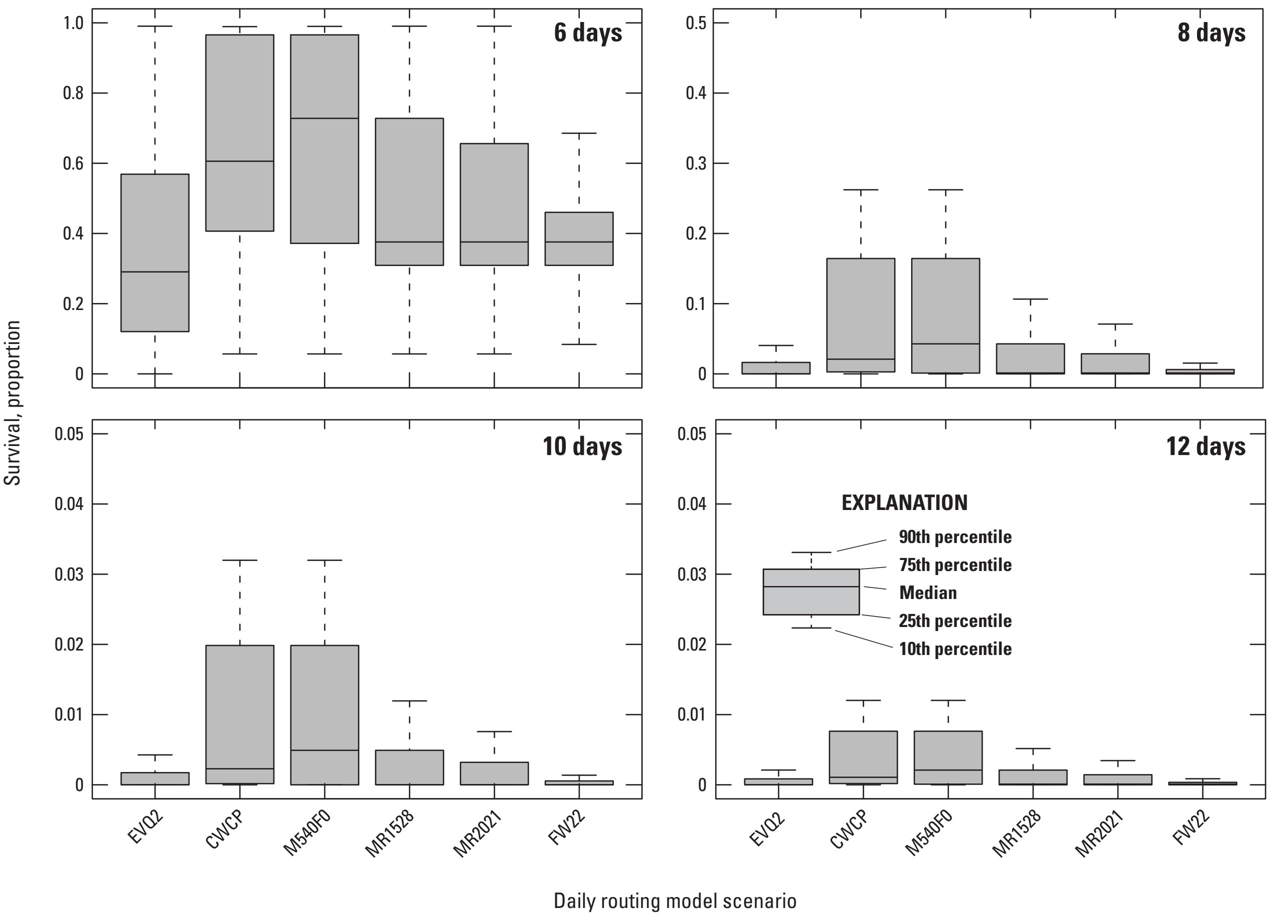


Figure 43. Distributions of survival based on Daily Routing Model scenarios at 6, 8, 10, and 12 days required for drift.

The survival distributions increase with shorter drift, indicating the potential importance of interstitial residency or retarded drift. If free embryos drift for 12 days (immediate drift scenario), median survival is extremely low: less than 0.5 percent for all flow scenarios. The natural flow regime (EVQ2) and the environmental flow alternatives (MR1528, MR2021, FW22) have the lowest survival, whereas the more highly managed flow regimes (CWCP and M540F0) have higher survival. This pattern of relative survival is repeated with lower number of drift days (fig. 43) because the natural and environmental flows have higher flows in June and July, whereas the managed flow alternatives minimize flow and advection velocity at this time of year. Overall, it is clear that flow regime has a substantial effect on relative survival for a given number of drifting days; and under conditions where interstitial residency and water temperature result in 6 days of drift, the models predict that flow regime could make a difference of between 30 and 70 percent survival.

The research of Braaten, Fuller, Lott, Ruggles, and others (2012) indicates that suitable habitat for first feeding larvae exists in the riverine reaches upstream from Lake Sakakawea. The management objective, then, would be to provide the appropriate combination of flow, distance, and temperature to place drifting free embryos into those habitats instead of Lake Sakakawea. The models produced here show that reducing flows from Fort Peck Dam can be effective during some conditions to provide velocities that would allow some part of the free embryos to settle before reaching the lake.

Uncertainty Assessment

The largest uncertainties in this analysis are with the biological unknowns, specifically the assumption that Lake Sakakawea is lethal, the question of interstitial residency, and the potential presence of other factors that may act to retard drift and substantially violate the assumption of passive drift. The predictive capability of these models entirely depends on the assumption of lethality; and if that is incorrect, then the uncertainty is very high. Although hydraulic and temperature uncertainties may be on the order of a fraction of a day in drift time, the interstitial residency question may be ±5 days or more. Considering that the anoxia and interstitial residency questions can be addressed and answered relatively quickly with directed scientific investigations, we judge the uncertainty for this hypothesis to be moderate.

Potential Interactions with Authorized Purposes

Reducing flows from Fort Peck Dam (fig. 2) would be linked to system regulation and many of the authorized purposes through potential changes in the management of flows from other storage reservoirs in the system. Downstream target flows, storage capacity, and anticipated runoff would all play roles in the effects of reduced flows from Fort Peck Dam. Effects may include additional constraints or enhancement of opportunities for reservoir habitats and bird nesting habitat. Interaction of authorized purposes would also depend in part on flows in the Yellowstone River and other tributaries, such as the Milk River. High flows from these tributaries would potentially negate the intended effect of reduced flows from Fort Peck Dam. Additionally, if Fort Peck Dam storage capacity is low, rules regarding system regulation may preclude implementing reduced flows from Fort Peck Dam.

Working Management Hypothesis in Adaptive Management Context

Model simulations indicate a high risk of failure for this hypothesis without very low flows from Fort Peck Dam (fig. 2) in combination with low pool levels for Lake Sakakawea. With certain combinations of low flow, temperature, and lake level, the probability of free embryo survival to the next life stage would likely increase; however, it is also likely that high proportions of free embryos would need to settle above the Lake Sakakawea headwaters before substantial population-level increases would be realized. Interstitial residency could reduce the drift distance and time needed for ontogenetic development and thereby broaden the range of flows and Lake Sakakawea pool levels that would theoretically promote survival.

Implementing low flows in an AM framework would require robust monitoring and assessment of effects on recruitment as well as authorized purposes. It is highly likely that low flows from Fort Peck Dam would need to be implemented with other management actions (for example, with Lake Sakakawea drawdown and temperature manipulations) to provide the drift conditions needed for free-embryo development and recruitment to the next life stage; however, in the absence of interstitial residency for 5 or more days, it is unlikely that low flows from Fort Peck Dam, in isolation or in combination with other management actions, would lead to significant levels of recruitment (Fischenich and others, 2014). Research to confirm anoxia in Lake Sakakawea, determine the degree of interstitial residency, and determine other potential sources of retarded drift are prospective priorities because this information will determine subsequent management decisions (see the following “Discussion” section).

Working Management Hypothesis 4—Increased Temperatures in Late Spring Through Summer from Fort Peck Dam

Hypothesis 4 asserts that increasing temperatures from Fort Peck Dam in the Upper Missouri River (fig. 2) in late spring through summer will increase biological productivity and food availability, resulting in increased growth and survival of age-0 pallid sturgeon. This hypothesis assumes that food is limited in the Upper Missouri River for age-0 pallid sturgeon.

Spatial Context and Interactions

The geographic scope of this hypothesis is the Missouri River from Fort Peck Dam (fig. 2) downstream to the headwaters of Lake Sakakawea. Because pallid sturgeon free embryo development is known to be influenced by temperature, this hypothesis could interact with other hypotheses. Temperature influences the maturation rate of free embryos (Braaten, Fuller, Lott, Ruggles, and others, 2012), and higher river temperatures could lead to higher survival of free embryos by reducing the length of free-flowing river needed for development (hypothesis 5). Shorter drift distances and better growing conditions from higher river temperatures could enhance survival for free embryos and exogenously feeding larvae. Changes in discharge from Fort Peck Dam to manipulate river temperatures could affect flow-related management actions intended to naturalize the hydrograph (hypothesis 1), promote spawning (hypothesis 2), or reduce drift duration of free embryos (hypothesis 3).

Lines of Evidence to Support Action Hypothesis

Depressed river temperatures from hypolimnetic dam releases are well documented in literature (Ligon and others, 1995; Franchi and others, 2014) and for Fort Peck Dam (fig. 2) (DeLonay, Chojnacki, Jacobson, Albers, and others, 2016). Empirical evidence suggests that dam-induced thermal alteration has substantial implications for stream productivity and the growth of organisms (Haxton and Findlay, 2008). Increasing water temperature in some aquatic systems has been positively correlated with rates of primary productivity (Winemiller, 2004) and secondary production of aquatic invertebrates (Plante and Downing, 1989). Growth in young fishes is regulated by the density of invertebrate prey resources for a variety of species (Fox, 1989). Food limitations at the early juvenile stages have been hypothesized as a potential mechanism for recruitment failure for white sturgeon in the Kootenai River system (U.S. Fish and Wildlife Service, 1999).

The effects of hypolimnetic releases are evident 189 mi downstream from Fort Peck Dam as mean (18.3 °C) and maximum water temperatures (25.0 °C) are greater than 1.0 °C cooler than conditions upstream from Fort Peck Lake (Fuller and Braaten, 2012). Kappenman and others (2013) determined that the optimum temperature for pallid sturgeon embryo survival and metabolic processes was 18 °C and slightly warmer at 20 °C for optimum developmental rate. They hypothesized that hypolimnetic releases from Fort Peck Dam might reduce pallid sturgeon recruitment. Spillway releases in the spring from Fort Peck Dam have been proposed to increase river temperatures to provide a spawning cue for pallid sturgeon and improve habitat conditions for native fishes (U.S. Fish and Wildlife Service, 2003). Although no empirical data have been collected or theoretical models developed that examine the relation between river temperature, productivity, and age-0 pallid sturgeon growth and survival in the Fort Peck Dam reach of the Missouri River, the influence of depressed temperatures has been determined to reduce growth, condition, and survival of juvenile shovelnose sturgeon (Kappenman and others, 2009). The authors hypothesized that prolonged depressed temperatures may deplete energy reserves and increase rates of mortality for young shovelnose sturgeon.

Applicable Models

Currently, researchers at South Dakota State University are developing a spatially explicit growth model for age-0 pallid sturgeon (Steve Chipps, South Dakota State University, written commun.). It is anticipated that once combined with a foraging model, the model will be used to predict growth and survival of age-0 pallid sturgeon within habitats and reaches of the Missouri River (fig. 2). No other simulation models linking river temperature with growth and survival of age-0 pallid sturgeon were identified.

A water-quality model for the Fort Peck Dam reach, including temperature effects, is anticipated as part of the EA process, but it is not yet available.

The component CEM for free embryo survival (Jacobson, Parsley, and others, 2015)) provides direct hypothesized linkages from primary ecological factors to secondary biotic response (that is, survival). The most likely path for this hypothesis through the CEM is (1) flow regime, (2) water-quality dynamics (temperature) and aquatic community composition and dynamics (productivity), (3) growth and condition (food availability), and (4) survival. The linkages between these components are thought to be of high importance with moderate uncertainty for the link between growth and condition and survival. The relation between temperature, food availability/productivity, and fish bioenergetics has been validated through numerous peer-reviewed studies of other fish and river systems (Budy and others, 2011; Petty and others, 2014).

The functional relation between temperature (as it influences river productivity and fish growth) and survival for early life stages is thought to be positively related and asymptotic in nature (fig. 44). Productivity, growth rate, and survival would increase with increasing water temperature until an upper threshold is approached.

Uncertainty Assessment

Quantitative data and models that support this hypothesis may be available in the near future; however, published studies that link river temperature with growth, habitat suitability, and survival are currently unavailable; therefore, we judge the uncertainty to be high.

Potential Interactions with Authorized Purposes

Increasing temperatures from Fort Peck Dam (fig. 2*B*) could be implemented through a variety of means, such as temperature-control structures or surface spill of lake water. Any increases in flow from Fort Peck Dam as a part of increasing river temperatures would be linked to system regulation and many of the authorized purposes through potential changes in the management of flows from other storage reservoirs in the system. Downstream target flows, storage capacity, and anticipated runoff would all play roles in the effects of reduced flows from Fort Peck Dam. It is possible that temperature increases could be implemented without increasing flows from Fort Peck Dam.

Working Management Hypothesis in Adaptive Management Context

With existing information, there is a high level of risk associated with implementation of this working management hypothesis. The level of response for river productivity, food availability, and survival from elevated river temperatures is unknown. This hypothesis assumes that food is limiting for age-0 pallid sturgeon in the Upper Missouri River (fig. 2*B*); however, there is no evidence that this is the case, and two lines of evidence support a contrary argument. The first is that age-0 shovelnose sturgeon seem to recruit to age-1 without problem in the Upper Missouri River (Oldenburg and others, 2010), and

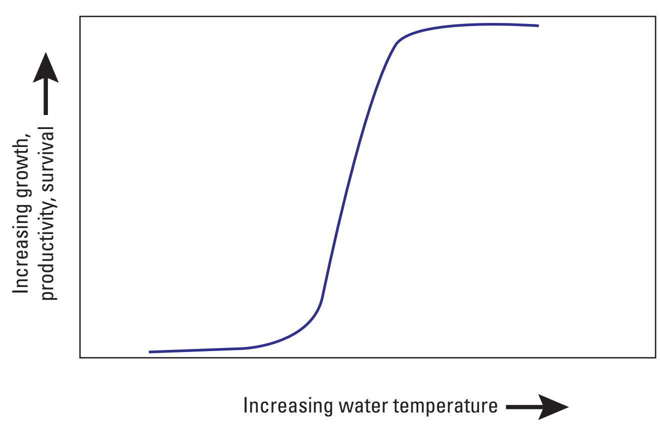


Figure 44. Hypothetical relation between increased water temperature and increased productivity, growth rate, and survival of age-0 pallid sturgeon.

the second is survival and recruitment to the juvenile stage of free-embryo pallid sturgeon that were stocked experimentally into the Upper Missouri River (Braaten, Fuller, Lott, Ruggles, and others, 2012). The potential habitat limitations on recruitment imposed by depressed water temperatures and available food resources remain a substantial unknown. Improved understanding could be achieved through construction and validation of a spatially explicit bioenergetics model and perhaps by comparative field experiments. Results could be used to develop hypotheses that better focus research on the potential temperature and productivity have for limiting survival of age-0 pallid sturgeon in the Upper Missouri River.

Working Management Hypothesis 5—Increased Temperatures in Late June and July from Fort Peck Dam

Hypothesis 5 asserts that increasing temperatures from Fort Peck Dam (fig. 2*B*) in late June and July will increase development rates and survival of drifting pallid sturgeon free embryos. The resulting reduction in drift time will presumably allow free embryos to settle into habitats suitable for growth and development.

Spatial Context and Interactions

The geographic scope of this hypothesis is the Missouri River from Fort Peck Dam (fig. 2) downstream to the headwaters of Lake Sakakawea. Because free-embryo survival is thought to be influenced by other factors, such as flow and current velocity, this hypothesis could interact with other hypotheses. Changes in discharge from Fort Peck Dam (hypothesis 2) will affect the current velocity and, in turn, the drift distance of pallid sturgeon free embryos. Implementing a drawdown of Lake Sakakawea (hypothesis 10) in conjunction with reduced flows (hypothesis 2) and (or) increased temperature from Fort Peck Dam may interact to provide better conditions for developing free embryos than those that would happen by implementing any of the actions in isolation.

Lines of Evidence to Support Action Hypothesis

A dominant hypothesis for the absence of pallid sturgeon recruitment in the Upper Missouri River (fig. 2) is that the length of free-flowing river is insufficient for drifting free embryos to complete embryonic development before settling into unsuitable habitats in Lake Sakakawea (Braaten, Fuller, Lott, Ruggles, and others, 2012). In the Upper Missouri River, depressed water temperature through hypolimnetic discharge from Fort Peck Dam was thought to delay embryo development (Kappenman and others, 2013). Temperature also influences the maturation rate of free embryos; lower temperatures are associated with lengthened embryonic development time and an increased probability of drift into Lake Sakakawea (Braaten, Fuller, Lott, Ruggles, and others, 2012; Kappenman and others, 2013). Depending on where in the Upper Missouri River pallid sturgeon spawn, models suggest that at the current range of temperatures downstream from Fort Peck Dam the drift distance required by free embryos exceeds the available length of free-flowing river (Braaten, Fuller, Lott, Ruggles, and others, 2012).

Empirical data provide some context for this hypothesis. In 2011, Montana Fish Wildlife and Parks and the USGS collected wild-hatched pallid sturgeon free embryos from the main stem Missouri River near Frazer Rapids, Mont., indicating successful spawning, fertilization, hatch, and drift of pallid sturgeon progeny are possible (DeLonay and others, 2014). Upper Missouri River models of cumulative drift distance as a function of velocity and temperature, however, indicate that pallid sturgeon drift requirements typically exceed the 189 mi of free-flowing Missouri River downstream from Fort Peck Dam (Braaten, Fuller, Lott, Ruggles, and others, 2012). Absence of recent, natural recruitment to the population supports this conclusion.

Previous studies have determined that free embryos can survive in the Missouri River downstream from Fort Peck Dam if stocked at 1–17 dph (Braaten and others, 2008; Braaten, Fuller, Lott, Haddix, and others, 2012; see the section on hypothesis 3 for a more detailed description); therefore, increasing the water temperature released from Fort Peck Dam could allow free embryos to mature faster before reaching Lake Sakakawea and may, therefore, increase the probability of survival to the next life stage.

Applicable Models

The component CEM for free embryo survival (Jacobson, Parsley, and others, 2015) provides hypothesized linkages from secondary ecological factors to secondary biotic response (that is, survival). The most likely path for this hypothesis through the CEM is (1) water-quality dynamics, (2) growth and condition, and (3) survival. The linkages between these components are of high importance with moderate uncertainty. Survival is thought to be influenced by anoxic conditions in the headwaters of Lake Sakakawea based on research by Guy and others (2015) where low dissolved oxygen has been implicated in decreased survival of exogenously feeding pallid sturgeon in the headwaters of Fort Peck Lake.

Laboratory studies also provide fundamental data on survival and development of pallid sturgeon (Kappenman and others, 2013). The estimated optimal temperature range for embryo survival was determined to be 17–18 $^{\circ}$C. The thermal niche for pallid sturgeon embryonic development was reported at 12–24 $^{\circ}$C, whereas the lower and upper river lethal temperatures were 8 and 26 $^{\circ}$C, respectively. Although these temperatures were determined for embryos rather than free embryos, they may provide useful estimates for the free-embryo stage. Unpublished data from the USGS (fig. 42) document median time to yolk-plug expulsion for free embryos increases as a decreasing function of water temperature.

There are a few models that can be used to evaluate how changes in water temperature released from Fort Peck Dam (fig. 2) could influence the survival of pallid sturgeon free embryos. Empirical models of temperature were developed by

Braaten, Fuller, Lott, Haddix, and others (2012). Their models predicted cumulative drift distance as a function of temperature and the relation between water velocity and ontogenetic development. The minimum required drift distance for a free embryo decreased from 192 mi at 14 °C water temperature to 184 mi when water temperature was 16 °C at the same water velocity (0.70 m/s). Drift distance would presumably decrease at even higher temperatures because of faster embryonic development time.

Another model recently developed for the Missouri River downstream from Fort Peck Dam (Fischenich and others, 2014) uses the empirical work of Braaten and others (2008; Braaten, Fuller, Lott, Haddix, and others, 2012), more specifically time and cumulative thermal units, that predict yolk-plug expulsion signifying the start of exogenous feeding and the point of settling from the drift. The model by Fischenich and others (2014) is a detailed longitudinal advection/dispersion model of free-embryo drift that predicts where free embryos will settle as they transition to exogenously feeding larvae, as a function of distance, drift velocity (a function of water velocity and discharge), and embryonic development (a function of temperature). Water temperatures driven by alternative releases from Fort Peck Dam are not yet part of the model, but sensitivity can be assessed knowing historical variation.

Simulations from advection/dispersion models (Fischenich and others,2014) have been used to explore which combinations of distance, flow, and temperature provide the best conditions for retention of free embryos in the riverine habitat above the hypothesized anoxic headwaters of Lake Sakakawea. Initial simulations from the model provide some insight into the potential effectiveness of reduced flows from Fort Peck Dam as a management action (see hypothesis 3; figs. 39–41). These results assume fish spawn at or near the mouth of the Milk River. The relation between water temperature and development rate indicates that each degree increase in water temperature results in about 0.71 fewer days of drifting. If combined with favorable combinations of interstitial residency or other drift-retarding processes, spawning location, low discharges, and lake drawdown, temperature manipulation could be effective in increasing survival.

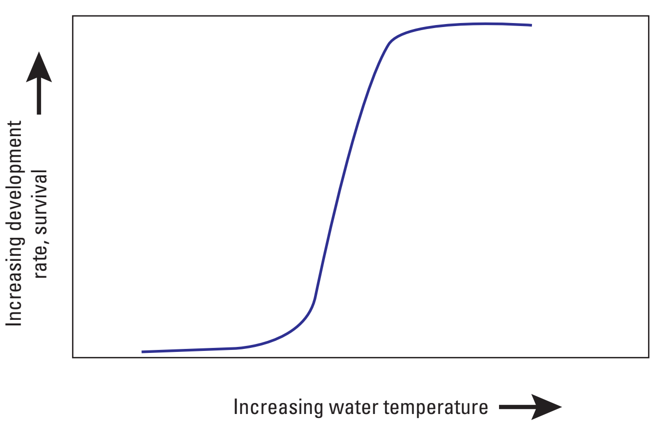


Figure 45. Hypothetical relation between increased water temperature and increased development rate and survival of free-embryos.

The functional relation between water temperature and survival for early life stages is thought to be positively related and asymptotic in shape (fig. 45). The slope of the increasing part of the curve is expected to be steep as it defines a threshold effect when development time is sufficiently short to allow settling before free embryos enter Lake Sakakawea.

Uncertainty Assessment

The largest uncertainties in this analysis are with the biological unknowns, specifically the assumption that Lake Sakakawea is lethal and the question of interstitial residency. The predictive capability of these models is entirely dependent on the assumption of lethality; and if that is incorrect, then drift distance may not be limiting to recruitment, and the uncertainty would be very high. Hydraulic and temperature uncertainties are on the order of a fraction of a day in drift time; however, the interstitial residency question (or other mechanisms of retarded drift) implies uncertainties of ±5 days or more. Some uncertainty exists in developmental rate models for embryos if water temperatures extend above 21 °C where the shape of the curve has not been determined. Considering that the anoxia, interstitial residency, and development rate questions can be addressed and answered relatively quickly with directed scientific inquiries, we judge the uncertainty for this hypothesis to be moderate.

Potential Interactions with Authorized Purposes

The interaction of temperature management with other authorized purposes depends on the engineering approach. If temperatures are managed with a temperature-control structure, there may not be much propagation to downstream flows and other purposes. If increased temperatures requires passing warm water over the spillway, reservoir balancing and releases could be affected.

Working Management Hypothesis in Adaptive Management Context

Model simulations indicate strong dependencies and a risk of failure if temperature manipulations are not coordinated with decreased flows and lake drawdowns. Under certain combinations of low flow, high water temperature, and low lake level, the probability of pallid sturgeon free-embryo survival to the next life stage would likely increase. It is highly likely that low Fort Peck Dam (fig. 2*B*) flows would need to be implemented with other management actions (for example, with Lake Sakakawea drawdown and temperature manipulations) to provide the drift conditions needed for free-embryo development and recruitment to the next life stage; however, in the absence of interstitial residency for 5 or more days, it is unlikely that low flows from Fort Peck Dam in isolation or in combination with other management actions will lead to substantial levels of recruitment (Fischenich and others, 2014). It is also likely that substantial numbers of free embryos would need to settle upstream from the Lake Sakakawea headwaters before significant population-level increases would be realized because other sources of age-0 mortality would continue to exist. Interstitial residency could reduce the drift distance and time needed for ontogenetic development and thereby broaden the range of temperature, flow, and Lake Sakakawea pool levels that could theoretically provide beneficial drift conditions. Implementing higher temperatures in an AM framework would require robust monitoring and assessment of effects on embryonic development and recruitment. It is highly likely that temperature manipulations would need to be implemented with other management actions (for example, lake Sakakawea drawdown and low Fort Peck Dam flows) to provide the drift conditions needed for free-embryo development and recruitment to the next life stage.

Confirmation of anoxia in Lake Sakakawea and determination of the degree of interstitial residency are prospective AM priorities because this information will determine subsequent management decisions (see the following “Discussion” section).

Working Management Hypothesis 6—Increased Turbidity from Sediment Augmentation at Fort Peck Dam

Hypothesis 6 asserts that increased in-stream turbidity by augmenting sediment concentrations out of Fort Peck Lake will decrease predation rates on age-0 pallid sturgeon and thereby increase survival.

Spatial Context and Interactions

This hypothesis potentially affects pallid sturgeon occupying the 189-mi segment downstream from Fort Peck Dam (fig. 2*B*) and upstream from the headwaters of Lake Sakakawea. The spatial context of this hypothesis is limited to free-flowing stream segments because sediment will settle out in the slack water reservoir depositional zone. Sediment deposition in reservoirs acts as a sediment trap; therefore, turbidity downstream from reservoirs is decreased relative to historical levels and water transparencies are increased.

The underlying mechanism for this hypothesis is related to sight-feeding predators preying on pallid sturgeon during vulnerable early life stages, including embryo, free embryo, and exogenously feeding larvae. Predation may also be applicable to age-1 and age-2 juveniles whose sizes do not exceed predator gape limitations.

Within the Missouri River system, channel modifications and impoundment have modified turbidity regimes and fish assemblages relative to historic conditions (French, Graeb, Chipps, and Klumb, 2013). These conditions benefit sight-feeding predators, like *Sander vitreus* (walleye) or *Hiodon alosoides* (goldeye), thereby potentially increasing predation rates on early life-history pallid sturgeon. Olfactory predators (such as catfishes [Siluriformes]) and benthivores (such as suckers [Cypriniformes]), which may have historically been the dominant source of predation, continue to exist in addition to sight-based predation.

Lines of Evidence to Support Working Management Hypothesis

Egg predation is common in fish species. A substantial part of predation can happen at the egg stage after oviposition. Once fertilized, sturgeon eggs are sticky, adhering to substrates and remaining susceptible to predation; for example, Caroffino and others (2010a) determined that lake sturgeon eggs deposited on egg mats were removed at varying rates presumably by predation. In a more controlled study, Caroffino and others (2010b) determined that some of this predatory loss could be attributed to crayfish (Decapoda). Egg predation has not been documented as a significant factor in pallid sturgeon recruitment failure, nor has lack of turbidity been implicated; turbidity-related egg predation remains a hypothesis because of the difficulty in documenting predation of eggs in spawning environments.

Pallid sturgeon are also susceptible to predation during larval stages; however, predation levels vary by predator. *Acipenser oxyrinchus* (Atlantic sturgeon) predation was documented by Flowers and others (2011). Predation of larval white sturgeon by varying predators (including walleye, *Ptychocheilus oregonensis* [northern pikeminnow], *Ictalurus punctatus* [channel catfish], and *Cottus asper* [prickly sculpins]) has been documented, and likelihood of predation decreased with increasing sturgeon size (Gadomski and Parsley, 2005b). In a follow up study to investigate the effect of turbidity on predation rates, Gadomski and Parsley (2005a) determined that decreased light availability, through a combination of increased turbidity, light levels, and cover, reduced predation of the smallest white sturgeon exposed to predators.

Recent experimental predation studied by French, Graeb, Chipps, and Klumb (2013) tested if vulnerability to predation was altered by turbidity for common larval pallid sturgeon predators. Although turbidity has been shown to reduce predation rates of some fishes (Hecht and Lingen, 1992), this study determined no effect of turbidity on larval predation for larvae 40–100 mm fork length. In fact, the study determined that predators avoided pallid sturgeon when alternative prey was available. Although these results indicate that the evidence that turbidity limits predation of exogenously feeding larvae and larger age-0 life stages is marginal, they do not address potential predation on embryos and free embryos or if predation rates could be increased with lower turbidity.

A specific case of age-0 pallid sturgeon predation by a *Pylodictis olivaris (*flathead catfish) was documented by Steffensen and others (2015) on the Lower Missouri River (fig. 2*B*), providing evidence that predation can occur. In this case, a single specimen out of 232 flathead catfish sampled had 14 age-0 pallid sturgeon in its stomach; the rest of the catfish did not have recognizable pallid sturgeon. The authors attributed the incident to high availability of freshly stocked age-0 pallid sturgeon, rather than selection of the prey, and indicated their belief that predation of age-0 pallid sturgeon was uncommon.

Applicable Models

There are no applicable models that can be used in the Missouri River system to predict the effect of turbidity on pallid sturgeon predation rates. No physical models exist to simulate turbidity as a function of sediment bypass or other sediment re-introduction process. As a hypothesis, the functional relation would likely take a sigmoidal form with maximum predation rates (minimum survival rates) of pallid sturgeon early life stages at the lowest levels of turbidity and minimum predation rates (maximum survival) with increasing turbidity (fig. 46).

Uncertainty Assessment

Empirical research on other species provides some support for this hypotheses; however, experimental data on exogenously feeding larvae and age-0 pallid sturgeon indicate there is little effect. Predation of embryos and free embryos has not been directly evaluated. In terms of system-specific evidentiary support, there still exists a high degree of uncertainty in the hypothesis and ways to evaluate the hypothesis.

Potential Interactions with Authorized Purposes

Increased turbidity may interact with current water-quality criteria as well as flow regulation for multiple uses. If sediment augmentation can be achieved independent of flows out of Fort Peck Dam (fig. 2*B*), then there may be limited interaction with authorized purposes.

Working Management Hypothesis in Adaptive Management Context

There is a high degree of uncertainty in this hypothesis and, therefore, high potential for learning but also high risk from implementation. In addition to engineering challenges, the biological challenge of implementing this hypothesis will be determining how to monitor the affected life-history stages; for example, the effectiveness of egg mats as a tool for monitoring egg deposition and predation at a scale sufficient to be informative may not provide reliable feedback. Similarly, costs of quantifying and monitoring larval pallid sturgeon abundances and predation rates may be prohibitive. As fish sampling technology advances, the monitoring constraints may be alleviated. This hypothesis would likely be addressed initially as laboratory-based experimental studies.

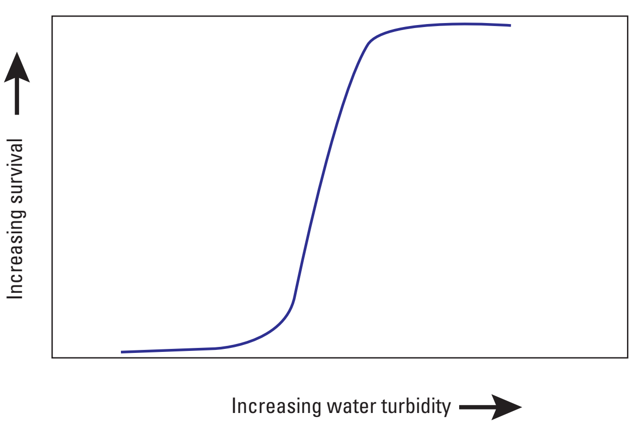


Figure 46. Hypothetical relation between turbidity and survival of embryos, free embryos, and larvae.

Working Management Hypothesis 7—Increased Fish Passage at Intake Diversion Dam on the Yellowstone River

Hypothesis 7 asserts that improving fish passage at Intake Diversion Dam on the Yellowstone River (fig. 2) will increase potential dispersal distance, resulting in increased survival of pallid sturgeon free embryos.

Spatial Context and Interactions

The geographic scope of this hypothesis is the Yellowstone River from Cartersville Diversion Dam (fig. 25) downstream to its confluence with the Missouri River, the Missouri River from the confluence downstream to the headwaters of Lake Sakakawea, and tributaries to the Yellowstone River to an unknown degree (fig. 2). Spawning of pallid sturgeon adults and drifting free embryos have been documented near Fairview, Mont. (about 7 mi above the confluence with the Missouri River), for multiple years through recent monitoring efforts (Elchelberger and others, 2014). By increasing passage at Intake Diversion Dam, potential spawning habitats above the dam will be made more available to spawning adults. Access to the habitats above the dam increases the probability of free-embryo survival by providing additional drift distances for embryonic development that allows free embryos to settle into suitable habitat upstream from Lake Sakakawea.

Because free-embryo development is influenced by factors, such as temperature and drift duration, this hypothesis could interact with other hypotheses. Temperature influences the maturation rate of free embryos (Braaten, Fuller, Lott, Ruggles, and others, 2012). Changes in discharge from Fort Peck Dam (hypotheses 1, 2, 3) or implementing other actions that influence river temperatures (hypothesis 5) will affect temperature regimes downstream. Implementing a drawdown of Lake Sakakawea (hypothesis 10) and (or) reduced flows from Fort Peck Dam (hypothesis 3) in conjunction with improved passage at Intake Diversion Dam may interact to provide better drift conditions for developing free embryos than those that would happen by implementing any of the actions alone.

Lines of Evidence to Support Working Management Hypothesis

A dominant hypothesis for the absence of pallid sturgeon recruitment in the Upper Missouri River (fig. 2) is that the length of free-flowing river is insufficient for drifting free embryos to complete embryonic development. This condition results in free embryos settling into habitats in the headwaters of Lake Sakakawea that are hypothesized to be unsuitable for survival (Braaten, Fuller, Lott, Ruggles, and others, 2012). Water temperature, velocity, and channel form influence pallid sturgeon free-embryo drift distance and time (Braaten, Fuller, Lott, Ruggles, and others, 2012) with spawning location acting as an important determinant for the amount of drift distance available. Improving access to river reaches (and potential spawning habitat) above Intake Diversion Dam would provide additional distance for development of drifting free embryos and promote settling into suitable habitats upstream from Lake Sakakawea.

Successful spawning by pallid sturgeon has been documented in the Yellowstone River (Elchelberger and others, 2014). Drifting free-embryo pallid sturgeon have been collected downstream from these spawning areas indicating that, at least in the Yellowstone River near Fairview, Mont., spawning and hatch are successful. Tracking indicates that some adult pallid sturgeon migrate past the Fairview, Mont., area to Intake Diversion Dam during the spawning period (Fuller and others, 2008). In 2014, a single female and several male pallid sturgeon successfully passed Intake Diversion Dam, migrated upstream, and presumably spawned in the Powder River (Yellowstone River RM 149) (DeLonay, Chojnacki, Jacobson, Braaten, and others, 2016). Sampling downstream from the Powder River spawning site on the Yellowstone River yielded 139 Acipenseriformes free embryos, but genetic identifications indicated that they were all shovelnose sturgeon (DeLonay, Chojnacki, Jacobson, Braaten, and others, 2016).

The research of Braaten, Fuller, Lott, Haddix, and others (2012) indicates that suitable habitat for settling free-embryo and exogenously feeding larvae exists in the Missouri River downstream from the Yellowstone River confluence and upstream from Lake Sakakawea. Increasing the longitudinal connectivity of the Yellowstone River would provide greater potential drift distance for free embryos, which would increase the probability of settling into hypothesized suitable habitat before reaching Lake Sakakawea.

Applicable Models

A detailed longitudinal advection/dispersion model of free-embryo drift, similar to the model developed from Fort Peck Dam (fig. 2) to the headwaters of Lake Sakakawea, has been developed for the Yellowstone River from Miles City, Mont. (184 RM upstream from the confluence), to the confluence of the Missouri River (Fischenich and others, 2014). Earlier, simple calculations of drift on the Yellowstone River were presented in a review report of the Intake Diversion Dam study (Anders and others, 2009). Initial simulations from advection/dispersion models (Fischenich and others, 2014) provide a basis for evaluating conditions under which free-embryo drift from selected spawning locations would likely end with retention in riverine sections upstream from the hypothesized anoxic headwaters of Lake Sakakawea.

The component CEM for free embryo survival (Jacobson, Parsley, and others, 2015) provides direct hypothesized linkages from primary ecological factors to secondary biotic response (that is, survival). The most likely path for this hypothesis through the CEM is (1) longitudinal connectivity, (2), hydraulics, (3) successful first feeding (retention), and (4) survival. The linkages between these components are of high importance with high uncertainty for the links between hydraulics, successful first feeding, and survival. The strong relation between flow, hydraulics, and drift dynamics of free embryos has been quantified through the empirical studies (Kynard and others, 2007; Braaten and others, 2008; Braaten, Fuller, Lott, Ruggles, and others, 2012) and advection/dispersion models (Fischenich and others, 2014) described previously. The anoxic conditions in the headwaters of Fort Peck Lake and the potential effects that low dissolved oxygen has on survival of exogenously feeding pallid sturgeon have been described by Guy and others (2015), and similar conditions have been hypothesized to apply to the headwaters of Lake Sakakawea.

The functional relation between dispersal distance and survival for early life stages is hypothesized to be sigmoidal in nature (fig. 47). If a hard limit on upstream migration does not apply, probability of survival and transition to exogenously feeding larvae will increase with dispersal distance.

Uncertainty Assessment

Numerous uncertainties exist for this hypothesis. With present understanding, it is apparent that only with extremely low flows would free embryos spawned at Yellowstone River RM 184 (Miles City, Mont.) be retained in the Yellowstone River (fig. 2). Models at all flow exceedances indicate that most free embryos from this upstream-most historically observed pallid sturgeon location would exit the Yellowstone River in 5 days or less and, therefore, would be likely retained in Lake Sakakawea. These models predict retention of free embryos in the Yellowstone River or Upper Missouri River upstream from Lake Sakakawea only under conditions of 5 or more days of interstitial hiding or if processes retard drift much more than anticipated in the advection/dispersion models; moreover, it is also unknown if reproductive pallid

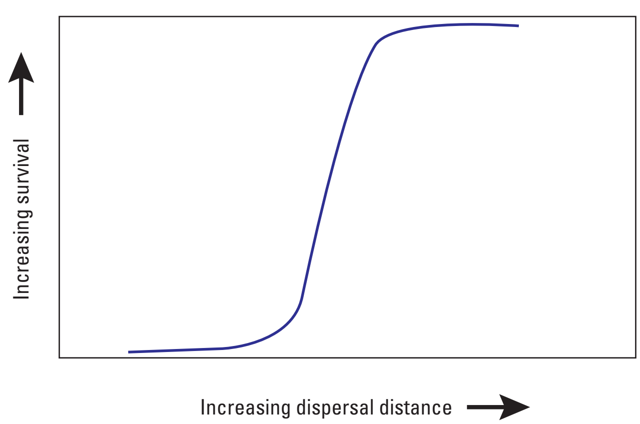


Figure 47. Hypothetical relation between available dispersal distance and probability of survival of pallid sturgeon larvae.

sturgeon will migrate upstream in sufficient numbers to spawn if passage at Intake Diversion Dam is improved and if there are spawning habitats of sufficient quantity and quality upstream from the dam to supply the drift distance needed for embryonic development. An Independent Science Review Panel (PBS&J, 2009, p. 14) reviewed the available habitat data (Jaeger and others, 2009) for potential pallid sturgeon spawning areas above Intake Diversion Dam and determined that:

> "…most of the bluff pool habitats expected to provide suitable spawning conditions for pallid sturgeon are downstream of the confluence of Tongue and Yellowstone rivers (Jaeger, 2005). This might reduce the benefit of the proposed gain of 165 miles of larval drift distance downstream from the Cartersville Diversion as many of the potential spawning locations were far down river from Cartersville and none were reported near Cartersville."

The Cartersville Diversion Dam is at Yellowstone River RM 238.6. The Powder River site of 2014 (upstream from the confluence at Yellowstone River RM 149) is the only documented spawning area upstream from Intake Diversion Dam.

Considering the factors detailed above, we judge the uncertainty for this hypothesis to be high.

Potential Interactions with Authorized Purposes

Providing passage at Intake Diversion Dam would interact very little with authorized purposes on the Missouri River; however, management of Fort Peck Dam may interact with fish use of the Yellowstone River (fig. 2). High spring flows from Fort Peck Dam as a part of managing the system for downstream target flows, for example, could potentially negate the intended effect of improved passage at Intake Diversion Dam by drawing spawning pallid sturgeon adults up the Missouri River and away from the Yellowstone River.

Working Management Hypothesis in Adaptive Management Context

Improving passage at Intake Diversion Dam (fig. 2) has potential to increase the probability of free embryo survival to the next life stage as adult fish would have greater access to upstream spawning areas that provide greater drift distance for free embryos; however, substantial uncertainties exist with this hypothesis, and these uncertainties have a substantial bearing on benefits of alternative management decisions on the Upper Missouri River. It is likely that large numbers of adults would need to pass Intake Diversion Dam and migrate far upstream and spawn before a population-level effect could be realized. To date (2016), only a small proportion of the pallid sturgeon that are monitored during spring spawning have approached Intake Diversion Dam; even fewer individuals have passed the dam to spawn. A higher proportion have remained far downstream from the dam to spawn in the Fairview, Mont., area of the Yellowstone River. Advection/dispersion drift models for the Yellowstone River predict that most free embryos that are spawned as far upstream as Miles City, Mont. (RM 185), will drift into Lake Sakakawea even under conditions of low flow and low lake levels (Fischenich and others, 2014). This indicates that even if passage is provided at Intake Diversion Dam, the probability that this action will lead to significant levels of recruitment is low unless interstitial residency or other factors retard or delay drift by 5 or more days.

High risk is associated with improving fish passage at Intake Diversion Dam; therefore, in addition to modeling drift dynamics of free embryos, several research studies could be implemented to further reduce the uncertainties associated with this hypothesis:

- *Drift dynamics.*—The relations among river length, drift rates, and cumulative drift distance relative to the hydraulic conditions of the Yellowstone River are unknown and will not be fully understood without empirical research to calibrate and validate advection/dispersion modeling. Of particular importance is the extent that complex hydraulics could result in retarded drift. Implementing empirical studies of drift dynamics of pallid sturgeon free embryos from Cartersville Dam to Lake Sakakawea would quantify drift rates and cumulative drift distance in relation to locations of suitable spawning substrate upstream from Intake Diversion Dam and provide valuable insight for this hypothesis and potential management actions.

- *Spawning habitat distribution.*—Suitable, functional spawning habitat has not been documented upstream from Intake Diversion Dam. A systematic, field-based habitat survey would provide the information to improve understanding of the locations and characteristics of potential suitable spawning habitat. Characteristics of known spawning habitats near Fairview, Mont. (appendix 1), could provide a template for identification.

- *Translocation experiment.*—An experiment in which known reproductive male and female pallid sturgeon are translocated upstream from Intake Diversion Dam and tracked would provide strong evidence for whether or not passage past the dam will be sufficient to achieve spawning, hatch, and sufficient drift distance.

Providing passage at Intake Diversion Dam in an AM framework would require robust monitoring and assessment of effects on recruitment. It is highly likely that even under conditions of delayed drift, passage would need to be implemented in coordination with other management actions (for example, Lake Sakakawea drawdown and Fort Peck Dam flow and temperature manipulations) to optimize conditions needed for free-embryo development and recruitment to the next life stage.

Working Management Hypothesis 8—Improved Stocking Strategies by Optimizing Stocked Size Classes

Hypothesis 8 asserts that determining the ideal size to stock hatchery fish will increase survival during the critical first years of life (age-0 to age-1) of hatchery-origin pallid sturgeon. This will allow the stocked sturgeon to obtain an ideal condition factor and a more stable life stage in a controlled hatchery system setting before experiencing the stresses of the Upper Missouri River (fig. 2*B*). The hypothesis is contingent on a continued need to stock fish to attain targeted population size or targeted genetic variation. The USFWS and states share authority and responsibility for stocking decisions through the pallid sturgeon recovery team and recovery workgroups; therefore, the MRRP implementation of management actions to address this hypothesis would require coordination with those groups.

Spatial Context and Interactions

This hypothesis includes the Missouri River from Fort Peck Dam (fig. 2) downstream to the headwaters of Lake Sakakawea, plus accessible parts of the Yellowstone River. Suitable habitats must be available in the Upper Missouri River to support the stocked hatchery-origin fish once released into the wild. Such supportive habitats may be provided, enhanced, or both by other hypothesized actions. Altered flow (hypothesis 1) and temperature profiles (hypothesis 3) from Fort Peck Dam may provide additional opportunities for food and growth while reducing energy demands. Increased turbidity may provide protection from predation (hypothesis 5). Stocking size optimization may interact with management actions intended to increase genetic variation in the population (hypothesis 9).

Lines of Evidence to Support Working Management Hypothesis

Research completed on hatchery propagation programs for recreational and conservation stocking indicates that survival rates are directly linked to stocking size. Lorenzen (2000) investigated seven stocking and augmentation programs and determined that stocking size was the primary factor in survival of three species of sport fish. A review of supplemental white sturgeon stocking and augmentation on the Kootenai River determined a significant increase in the estimated survival of juvenile year classes when stocked at a larger size than years when juveniles were stocked at a smaller size (Ireland and others, 2002; Beamesderfer and others, 2014). Steffensen and others (2012) determined pallid sturgeon juveniles stocked in the Lower Missouri River had higher survival rates when stocking sizes were larger. Hadley and Rotella (2009) determined a similar trend in pallid sturgeon stocked in the Upper Missouri River.

These studies suggest that increased size at stocking provides a higher chance for survival; however, additional time in the hatchery, which may be needed to attain a larger size, may also create factors detrimental to pallid sturgeon stocking and augmentation goals. These factors include hatchery imprinting, disease, physiological stress responses, and altered behaviors, which may affect the fitness of the stocked fish (Kurobe and others, 2011; Oldenburg and others, 2011; Nelson and Small, 2014; Webb and others, 2007; Hadley and Rotella, 2009). These potentially harmful factors would be weighed against the advantages associated with increased size at stocking.

Actions related to propagation and stocking are recognized as short-term actions that will increase numbers of adults and ensure genetic variability. Stocking and augmentation in isolation from other actions are not considered to be sufficient to recover the species or avoid jeopardy (U.S. Fish and Wildlife Service, 2000, 2003, 2014); moreover, success of stocking and augmentation strategies depends on other factors like the carrying capacity of the river segment (Braaten and others, 2009).

Applicable Models

In the CEM developed by Jacobson, Parsley, and others (2015), stocking and augmentation input are accounted for in the exogenously feeding larvae and juvenile stages. Fitness of these stocked fish has been hypothesized to be related to size at stocking as well as other possible inputs, including disease and maternal contaminant load. Stocking at optimal size would increase positive primary biotic responses (condition and growth), which could contribute to survival of the stocked fish while limiting negative primary biotic responses that would contribute to direct mortality (disease and predation). Wildhaber and others (2007) detail stocking and augmentation variables in their population-level CEM (fig. 3), which provides insight into stocking and broodstock considerations and their role in population dynamics. Stocking survival estimates for white sturgeon (Ireland and others, 2002; Beamesderfer and others, 2014) and Missouri River pallid sturgeon (Hadley and Rotella, 2009; Steffensen and others, 2010) provided a modeling framework for size optimization. Although population models like the one presented in this report are capable of modeling the effects of size at stocking on survival on population dynamics, the utility of such a model would depend on capturing the causal mechanisms for differential mortality.

A potentially important aspect of modeling to optimize size distributions is an economic analysis that would address optimum hatchery size and throughput to achieve maximum survival in the field. Such a model would consider the benefits and risks of building facilities to hold captive brood stock, raise fish to larger size classes, or explore novel ideas like streamside rearing.

The assumed functional relation between size and survival is asymptotic but with a fairly gentle rate of increase (fig. 48).

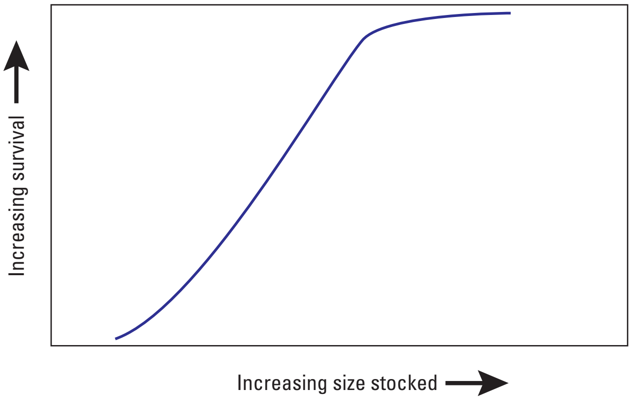


Figure 48. Hypothetical relation between size at stocking and survival of pallid sturgeon.

Uncertainty Assessment

Uncertainties for this hypothesis are thought to be relatively low considering size and survival. Extending models to the optimization of rearing techniques to achieve desired size classes includes substantially more uncertainty. Numerous studies for sport and conservation stocking have determined the importance of stocking size to survival of fish in general (Lorenzen, 2000; Ireland and others, 2002; Hadley and Rotella, 2009; Beamesderfer and others, 2014), and empirical data from the Missouri River (fig. 2) pallid sturgeon stocking and augmentation program are available to help develop guidelines for stocking-size optimization (Hadley and Rotella, 2009; Steffensen and others, 2010). Re-evaluation and optimization of current hatchery protocols to enhance stocking fitness through increased size and removal of hatchery stressors may be achieved with limited perceived risk.

Potential Interactions with Authorized Purposes

This hypothesis presumably does not interact with authorized purposes.

Working Management Hypothesis in Adaptive Management Context

As supplemental stocking and augmentation are already being performed, changes in current hatchery protocols that increase stocking size and limit hatchery stressors would allow implementation of this hypothesis with minimal risk. Empirical data from records of pallid sturgeon stocking could provide an initial strategy to optimize stocking size. Additional factors that may contribute to overall pallid sturgeon fitness and survival could also be investigated, including carrying capacity of river segments, broodstock contaminant levels, and genetics (Braaten and others, 2009; Buckler, 2011; Saltzgiver and others, 2012). Continued monitoring of survival of stocked fish through field sampling and hatchery evaluation will be needed to ensure adequate assessment of this hypothesis.

Working Management Hypothesis 9—Improved Stocking Strategies by Optimizing Genetic Diversity

Hypothesis 9 asserts that selection of genetically diverse broodstock in population augmentation will increase population viability; that is, the ability of the population to sustain itself demographically (Hallerman, 2003). Managing for genetic variation that approximates that of the natural population will result in greater fitness of the upper river population as a whole. The USFWS and states share authority and responsibility for stocking decisions through the pallid sturgeon recovery team and recovery workgroups; therefore, the MRRP implementation of management actions to address this hypothesis would require coordination with those groups.

Spatial Context and Interactions

This hypothesis includes the Missouri River from Fort Peck Dam (fig. 2) downstream to the headwaters of Lake Sakakawea, plus accessible parts of the Yellowstone River. Suitable habitats and productivity must be available in the Upper Missouri River to support the stocked hatchery-origin pallid sturgeon once released into the wild. Such supportive habitats may be provided, enhanced by other hypotheses, or both. Altered flow and temperature profiles from Fort Peck Dam (hypotheses 1 and 3) may provide additional opportunities for food and growth while reducing energy demands and potentially increasing the probability of survival. Size optimization (hypotheses 8) may interact with parentage decisions because stocking of broodstock at larger size may increase contribution of particular genotypes to the population.

Lines of Evidence to Support Working Management Hypothesis

The advent of new genetic techniques allows hatcheries to increase support for stocking and augmentation efforts. To ensure healthy and fit hatchery-origin fish, biologists manage against inbreeding, outbreeding, and domestication (Schrey and Heist, 2007; Heist and others, 2013). Extensive genetic sampling as part of pallid sturgeon recovery efforts suggests genetically distinct populations of pallid sturgeon are in the Upper Missouri, Lower Missouri, and Mississippi Rivers (fig. 2) (Campton and others, 2000; Tranah and others, 2001; Schrey and others, 2006). This has resulted in a spatial distribution of pallid sturgeon with phenotypic differences between distinct genetic groups. Upper Missouri River pallid sturgeon are larger and morphologically distinct from the their middle and lower Mississippi and Atchafalaya River counterparts (U.S. Fish and Wildlife Service, 1993, 2014). Such distinctions between genetic groups are thought to be adaptations to ecological differences. Heist and others (2013) suggest a loss of offspring fitness if progeny from a broodstock MU is not stocked to the parental river reach. This is illustrated by Philipp and Claussen (1995), who reciprocally translocated *Micropterus salmoides* (largemouth bass) stocks from northern and southern Illinois and determined they had significantly reduced growth rates when compared to locally translocated stocks, whereas both groups had similar growth rates in central Illinois. Selecting broodstock families from only the Great Plains MU could be of particular importance because pallid sturgeon inhabit a broad geographic range in which ecological differences are evident (Heist and others, 2013).

In conservation stocking for small populations, strategies to limit inbreeding and domestication are also recommended. Inbreeding not only limits fitness of offspring (reproductive impairments, reduced survival and growth, and physical abnormalities) but limits genetic diversity (Heist and others, 2013). Research suggests current populations of Great Plains MU broodstocks (wild and captive) are sufficiently large to limit the effects of inbreeding, but inbreeding could be a factor in future generations. Domestication can happen when a family that is genetically adapted to hatchery conditions survives and is stocked in higher numbers than families that are poorly adapted to hatchery conditions; this can result in reduced fitness in the wild and is considered detrimental to augmentation programs (Schrey and Heist, 2007; Saltzgiver and others, 2012; Heist and others, 2013). Domestication of various Alaskan salmon species, for example, has resulted in reduced survival and growth, increased reproductive impairments, and decreased predator avoidance (Grant, 2012). Christe and others (2012) observed domestication of *Oncorhynchus mykiss* (steelhead trout) in one generation; progeny of hatchery-reared fish outperformed their wild counterparts in the hatchery, with a reverse trend seen in the wild. Genetic optimization may benefit survival through selection against inbreeding, outbreeding, and domestication.

Actions related to propagation and stocking are recognized as short-term actions that will increase numbers of adults and ensure genetic integrity. Stocking and augmentation in isolation from other actions are not considered to be sufficient to recover the species or avoid jeopardy (U.S. Fish and Wildlife Service, 2000, 2003, 2014); moreover, success of stocking and augmentation strategies depends on other factors like the carrying capacity of the river segment (Braaten and others, 2009).

Applicable Models

In the CEM developed by Jacobson, Parsley, and others (2015), stocking input is accounted for in the exogenously feeding larvae and juvenile stages. Fitness of these stocked fish are related to size at stocking as well as other possible inputs, including disease and maternal contaminant load. It is theorized that this hypothesis would increase positive primary biotic responses (condition and growth), which could contribute to survival of the stocked fish, while limiting negative primary biotic responses, which would contribute to direct mortality (disease and predation). Wildhaber and others (2007) detail stocking and augmentation variables in their population-level CEM (fig. 3), which provides insight into stocking and broodstock considerations and their role in population dynamics.

More quantitative models to explore results of parentage strategies have not been developed for pallid sturgeon in the Missouri River (fig. 2) like they have for white sturgeon (Jager and others, 2001). Such models might provide insights into risks and benefits associated with alternative genetics management strategies.

Uncertainty Assessment

Uncertainties for this hypothesis are thought to be relatively low because present plans limit stocking to local fish (by MU) that are presumably adapted to local river conditions; presently available genetic tools identify parentage sufficiently to support the family crossing decisions.

Potential Interactions with Authorized Purposes

This hypothesis presumably does not interact with authorized purposes. As augmentation stocking is currently ongoing, it is thought that present activities and river use will not be affected by the proposed hypothesis.

Working Management Hypothesis in Adaptive Management Context

Population modeling results indicate that stocking will be needed to contribute to recovery of the pallid sturgeon population in the Missouri River (fig. 2) until other recruitment bottlenecks are identified and eliminated (figs. 17–22). Ongoing assessment of survival of stocked fish, carrying capacity of the river system, changes to effective population size, and genetic variation represented within the population will contribute to informed management decisions about propagation. The advancement of genetic techniques and their use in stocking optimization may act to limit problems associated with conservation breeding programs (inbreeding, outbreeding, and domestication). Practices, such as the cryopreservation of milt from the Great Plains MU and increased family crosses, would help to ensure increased genetic diversity and limit the effects of inbreeding (Heist and others, 2013; U.S. Fish and Wildlife Service, 2014).

Working Management Hypothesis 10—Drawdown of Lake Sakakawea

Hypothesis 10 asserts that drawdown of Lake Sakakawea will provide additional dispersal distance for free embryos in a riverine environment, thereby increasing survival of age-0 pallid sturgeon because free embryos will not be transported into nonsupporting habitats.

Spatial Context and Interactions

Drawdown of Lake Sakakawea has the potential to increase dispersal distance in a riverine environment, but this hypothesis is highly interactive with other factors. Free embryos from pallid sturgeon that spawn in either the Upper Missouri or Yellowstone River (fig. 2) have the potential to drift into the segment of the Upper Missouri River between the Yellowstone River confluence and headwaters of Lake Sakakawea. The effectiveness of drawdowns to increase dispersal distance, however, depends on how far upstream the fish spawns, prevailing discharge and velocity, channel hydraulics, and water temperature.

On the Yellowstone River, drawdown will presumably be effective for fish that spawn within a range of distances upstream from the Yellowstone River confluence. If they spawn too far downstream on the river, no combination of interstitial residency, retarded drift, temperature, or discharge will be effective to keep free embryos from ending up in the headwaters of Lake Sakakawea. At some distance upstream, combinations of these factors may result in settling of free embryos in riverine sections before reaching the headwaters of Lake Sakakawea. At intermediate spawning distances upstream on the Yellowstone River, drawdown of Lake Sakakawea may provide an increase in dispersal distance that would allow for settling in riverine conditions.

Reproductive adults are also free to migrate up the Upper Missouri River to spawn. Whether they select the Upper Missouri or the Yellowstone River may depend on characteristics of flow-related cues emanating from both rivers (hypothesis 2). In the event that adults migrate and spawn in the Upper Missouri River, drawdown of Lake Sakakawea may provide needed additional dispersal distance, depending on a combination of discharge, velocity, temperature (hypotheses 3 and 5), and degree of interstitial residency and retarded drift.

Lines of Evidence to Support Working Management Hypothesis

Newly hatched pallid sturgeon develop pelvic fin buds after about 5 dph, but pelvic fin development is not complete until the fish grows to at least 80 mm (Snyder, 2002). During this time, the free embryo has limited ability to control its movement in the river and, if released into the current, will drift more or less passively downstream. Drift may be immediate or instead may be delayed by several days if the free embryo can hide in substrate interstices (interstitial residency hypothesis) or other factors retard drift. Whether or not pallid sturgeon free embryos reside in interstices for any length of time is a substantive source of uncertainty to understanding drift and required drift distance (DeLonay, Chojnacki, Jacobson, Albers, and others, 2016), although some experimental evidence now supports immediate drift of free embryos (DeLonay and others, 2015). Total downstream dispersal distance is a function of discharge, water temperature (which affects development rate), and channel hydraulic conditions that may be more or less conducive to retaining drifting particles. When the free embryo has used up its yolk sac, it must begin feeding on an alternative source of food or it will starve. The transition to first feeding, or “settling,” is a critical life-stage transition hypothesized to be associated with low survival in other sturgeon species (Gisbert and Doroshov, 2003). If food is present, other factors must also support survival through this stage, including low predation rates and sufficient water quality.

Field studies completed in a Missouri River side channel during 2004 (Braaten and others, 2008) and the main stem Missouri River (fig. 2) in 2007 (Braaten and others, 2012b) provided empirical data on free-embryo drift and dispersal dynamics, including information that free embryos drift and disperse downstream at a rate slightly less than mean water-column velocity; and they drift and disperse during day and night. Total required drift distances extrapolated in these studies assumed drift started immediately after hatch, an assumption supported by the lack of recruitment in the Upper Missouri River and by a few catches of free embryos with estimated ages of 0–1 dph in 2011, 2012, and 2013 (DeLonay and others, 2014; DeLonay, Chojnacki, Jacobson, Albers, and others, 2016). The interstitial hiding hypothesis is supported by inference from white sturgeon and laboratory experiments (Kynard and others, 2010, 2012); in some white sturgeon studies, free embryos selected interstitial space and delayed drift by as much as 15 days (McAdam, 2011).

Applicable Models

The CEMs (Jacobson, Parsley, and others, 2015) capture the drawdown management action as a reservoir action (releases from Garrison Dam to draw down Lake Sakakawea plus curtailed releases from Fort Peck Dam [fig. 2]) that dominantly affects longitudinal connectivity (distance of available riverine sections), channel hydraulics, and habitat suitability. Under the prevailing assumption that Lake Sakakawea headwaters are lethal to free embryos, the increased drift distance will allow for increased survival.

The hypothesis that Lake Sakakawea headwaters are anoxic and lethal provides a mechanism to link habitat to survival and population dynamics. Quantitative predictions of numbers of free embryos remaining in riverine reaches under various combinations of management actions, including drawdown of Lake Sakakawea, could then be used directly in a population model as a parameterization of survival from free embryo to exogenously feeding larvae, or as a contribution to total survival of age-0 pallid sturgeon.

Advection/dispersion models of drawdown scenarios indicate that drawdowns could add a maximum of about 60 mi of riverine habitat, comparing maximum to minimum historical lake levels (Fischenich and others, 2014). On the Upper Missouri River, scenarios based on maximum upstream spawning at the mouth of the Milk River indicate that free embryos that drift for 2–4 days before settling would have nearly 100 percent survival for discharges ranging from 90 to 10 percent exceedance (fig. 49), independent of drawdown. For the same spawning and discharge conditions, free embryos that drift 10–12 days (or more) before settling would have 0 percent survival, independent of drawdown. In comparison, survival rates of free embryos that drift 6–8 days before settling would be affected by discharge exceedance and lake level. In particular, lake levels in this range can determine 0–100 percent survival of 6-day drifting free embryos at median discharges, and 0–90 percent survival at 10 percent flow exceedance. For 90 percent exceedance flows (low flow conditions) as much as 14 percent survival is predicted even at the highest pool level. At 90 percent exceedance flows, 8-day drifting free embryos are predicted to have 50 percent survival at lowest lake levels, decreasing to about 12 percent

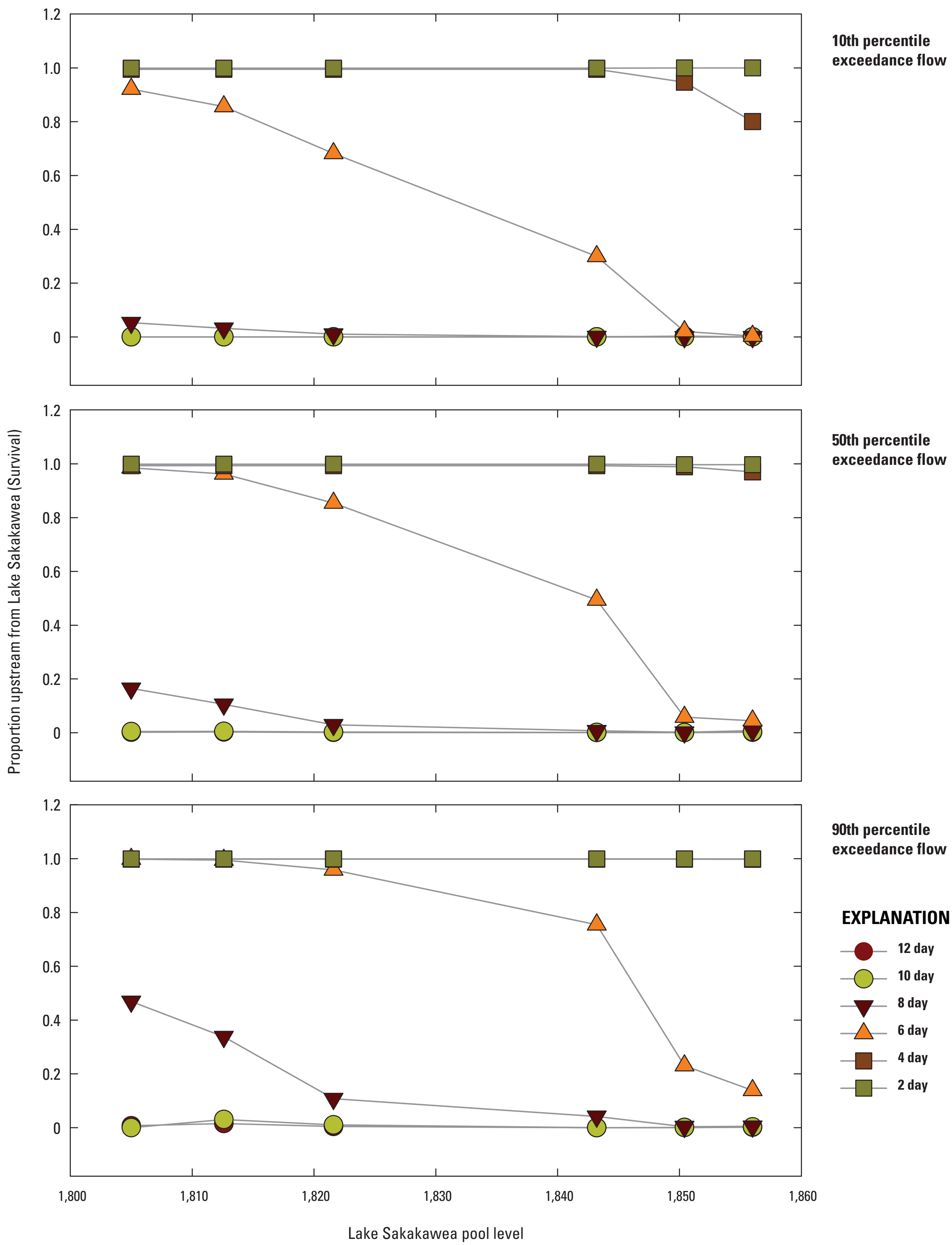


Figure 49. Graphs of proportional survival of free embryos assuming spawn at the Milk River confluence using quantiles of historical flows from Fort Peck Dam.

at 90 percent exceedance lake level. These calculations show that drawdown can be effective in some drift and spawning scenarios, although the calculations are subject to physical and biological uncertainties. Similar calculations apply to the Yellowstone River; however, there is considerably more uncertainty about locations where spawning and drift initiation would happen.

The number of days required for drift and dispersal, to yolk-sac plug expulsion and beginning of first feeding, varies with temperature (fig. 42) and length of interstitial residency, if any. Developmental rates indicate a decrease of 0.71 drift days for each degree increase in water temperature. Historical water temperature data for the Upper Missouri River in June–July indicate a decile range (from 90 to 10 percent exceedance) from 15.2 to 20.7 °C, which would equate to a decile range of required drift days of 12 to 8.6, assuming immediate drift. Because developmental-rate data presently do not extend to the higher temperatures of the Yellowstone River, it is not possible to make the same calculation for that river.

If interstitial residency happens, drift time would be decreased proportionately. Interstitial residency remains a highly speculative hypothesis but one with substantial importance for strategies to mitigate recruitment failure on the upper river (DeLonay, Chojnacki, Jacobson, Albers, and others, 2016). If residency is as long as 5 days, the decile range of drift days could be 7 to 3.6, a range for which drawdown of Lake Sakakawea could substantially affect survival.

Uncertainty Assessment

Multiple levels of uncertainty apply to drift and dispersal models. The greatest sources of uncertainty are in structural components of the models and biological assumptions. Chief among these is the assumption that the headwaters of Lake Sakakawea are lethal to free embryos because of anoxic water-quality or other conditions. This assumption is based on transfer of results from the headwaters of Fort Peck Dam (fig. 2) (Guy and others, 2015), and although it is probable that the same conditions exist in the headwaters of Lake Sakakawea, it is uncertain if they have the same lethality; moreover, their spatial distribution and temporal persistence (for example, after a lake drawdown) are unknown. A second substantive source of uncertainty is the issue of interstitial residency. The uncertainty associated with a maximum interstitial hiding of 5 days is 70–138 percent of the decile range of drift days, which means that even the longest interval to first feeding of 12 days would result in 7 days of drift and survival predictions ranging from 0 to nearly 85 percent (fig. 49). A third source of uncertainty is if other hydraulic factors could contribute to retarded drift such that existing advection/dispersion models overestimate downstream drift rates.

An additional level of uncertainty is associated with selection of spawning sites. The advection/dispersion model results presented for the Upper Missouri River assume spawning near Fort Peck Dam at the mouth of the Milk River. Although spawning seems to have happened near here in 2011, it is not clear that there is fidelity to that spawning site, and spawning downstream would mean less available drift distance. On the Yellowstone River side it is unknown if reproductive fish will bypass Intake Diversion Dam and migrate sufficiently far upstream to provide for effective drift distance. In addition, to have an effect on population, sufficient numbers of fish will need to make such a migration, spawn, hatch, and survive.

Uncertainties are also added with errors associated with development rates and the advection/dispersion model. Uncertainties in the development rates are difficult to estimate because there is only one set of data for comparison, but we think they are small compared to other uncertainties. We estimate errors associated with the underlying advection/dispersion model to be ± fractions of a drift day for passive particles.

Potential Interactions with Authorized Purposes

Drawdown of Lake Sakakawea could involve decreases in lake recreation, increases in riverine recreation and fisheries, decreases in power generation, increases in flood storage, increases in reservoir shoreline habitat for terns and plovers, and increases in risk to downstream water supplies. These changes would propagate through the Missouri River main stem reservoir system and could require accommodation by changes in other components of the reservoir system.

Action Hypothesis in Adaptive Management Context

The uncertainties around implementation of a drawdown of Lake Sakakawea to increase survival of free embryos are substantial. The pervasive uncertainties suggest a decision tree approach may be appropriate to provide a pathway to reduce uncertainties and structure the learning needed to support management decisions (see the following “Discussion” section). Present uncertainties indicate that implementation of drawdowns would incur considerable risk without additional information and that a systematic approach to reducing uncertainties through directed research should be considered.

Lower River

Working Management Hypothesis 11—Spring Flow Pulses in May from Gavins Point Dam

Hypothesis 11 asserts that spring flow pulses in May from Gavins Point Dam (fig. 2*B*) will provide aggregation and spawning cues for reproductive pallid sturgeon, increasing the chance that mates will find one another, release their gametes in close proximity to each other, and ultimately result in an increase of fertilized embryos.

Spatial Context and Interactions

The geographic scope of this hypothesis is the Missouri River from Gavins Point Dam downstream to the Mississippi River, with some potential for hydrologic effects downstream in the Middle Mississippi River (fig. 2). The hypothesis also potentially affects pallid sturgeon in several tributaries downstream from Gavins Point Dam because reproductive pallid sturgeon adults may select the main stem Missouri River rather than a tributary depending on the magnitude or quality of cues from other locations.

Because spawning behavior is hypothesized to be influenced by other factors, such as temperature, turbidity, or suitable spawning habitat, this hypothesis could interact with other hypotheses. Changes in discharge from Gavins Point Dam will affect temperature regimes and sediment mobility downstream. Attracting fish to spawn in the Missouri River could dissuade them from using tributaries in the lower river. Because of the large watershed area of the Missouri River below Gavins Point Dam, runoff because of precipitation events will interact with intentional pulses. Increased flow pulses from Gavins Point Dam could potentially attract fish to specific spawning locations, which relates to the hypothesis that the probability of mates finding one another is diminished by overprovision of hard, coarse substrate in bank revetment and channel-training structures (DeLonay, Chojnacki, Jacobson, Albers, and others, 2016).

Lines of Evidence to Support Working Management Hypothesis

A naturalized flow regime, which includes flow pulses in the spring (“spring rise”), has been hypothesized to be necessary to cue pallid sturgeon spawning behavior according to the 2000 and 2003 Biological Opinions (U.S. Fish and Wildlife Service, 2000, 2003). Many lotic fishes are adapted to natural variation in water temperature and discharge, and it is thought that decoupling of water temperature from discharge variation can result in removal of cues for spawning. Evidence for the role of discharge cues in spawning of shovelnose sturgeon and other species is presented in Goodman and others (2012).

Empirical data are ambiguous on behavioral responses of reproductive pallid sturgeon to flow pulses (DeLonay and others, 2009; DeLonay, Chojnacki, Jacobson, Albers, and others, 2016). Reproductive migrations of pallid sturgeon on the Lower Missouri River (fig. 2) have exhibited little evidence of correlation with natural and manipulated flow pulses; however, reproductive migrations of pallid sturgeon on the upper river indicate that fish may select between the Upper Missouri and Yellowstone Rivers based on hydrologic cues (discharge characteristics, temperature, turbidity, or a combination of the three). Taken together, existing information documents flow pulses that have not been sufficient to elicit a reproductive response and some hydrologic conditions that may be sufficient. Available information is not adequate to define flow pulses or hydrologic conditions that are necessary for a reproductive response, nor what functional relations might look like between pulse characteristics and strength of the spawning behavior response.

Pallid sturgeon tracking near the Upper Missouri and Yellowstone River confluence exhibited that, in most years, most telemetered pallid sturgeon migrated out of the Missouri River and into the Yellowstone River in April–May when discharges on the Yellowstone River were greater than those on the Upper Missouri River. Notably, this typically happened before the beginning of the spring/summer snowmelt pulse (DeLonay and others, 2014). This pattern was disrupted in 2011 when a high-flow pulse (presumably with warm temperatures and high turbidity) was contributed by the Milk River in April, followed by record releases from Fort Peck Dam. The April flow pulse on the Upper Missouri River was 30,000 ft^3/s compared to less than 10,000 ft^3/s in the Yellowstone River (DeLonay and others, 2014). During that year, 36–39 percent of the telemetered pallid sturgeon population migrated up the Upper Missouri River. The pattern was disrupted again in 2013 when late-April–May discharges in the Upper Missouri River were greater than 10,000 ft^3/s, whereas those in the Yellowstone River were less than 5,000 ft^3/s (DeLonay, Jacobson, and others, 2016). During this period in 2013, as much as 45 percent of the telemetered pallid sturgeon population migrated some distance up the Upper Missouri River (Dave Fuller, Montana Fish Wildlife, and Parks, written commun.). These observations support the hypothesis that sufficiently large flow pulses, or flow pulses relative to antecedent or adjacent flow, may trigger migration and aggregation.

The Missouri River ISAP considered the available information on the efficacy of flow pulses in relation to pallid sturgeon spawning and concluded “the spring pulse management action, as currently designed, is unnecessary to serve as a cue for spawning in pallid sturgeon” (Doyle and others, 2011, p. 1–2). The design pulses refer to technical criteria adopted in the Missouri River annual operating plans and implemented in 2006, 2008, and 2009. The largest of the three implemented pulses was in May 2006, an increase of about 11,000 ft^3/s above antecedent flow of 14,000 ft^3/s. In attempting to reconcile Missouri River ISAP conclusions about the Lower Missouri River and observations from the Upper Missouri River, fundamental questions arise about whether a behavioral response to a hydrologic event would relate to absolute discharge (or associated characteristics) or discharge relative to antecedent flows.

An analysis of shovelnose sturgeon spawning patterns in the Lower Missouri River indicated statistically identifiable clusters of spawning migration patterns and further identified some patterns that were more likely to be indicative of successful spawning compared to others (Wildhaber, Holan, and others, 2011). This study did not specifically identify the cause for the different patterns but indicated that patterns closer to Gavins Point Dam were less likely to be associated with successful spawning, possibly because of some aspect of altered hydrology or water quality.

Applicable Models

Although linkages from flow regime to spawning behavioral responses are conceptually viable and common in the fisheries literature (U.S. Fish and Wildlife Service, 2003), the empirical evidence from sturgeon in the Missouri River (fig. 2) is ambiguous; moreover, we have not identified any useful, quantitative models linking design of flow components (magnitude, duration, timing, sequence, rate of change) to production of viable gametes.

The component CEM for reproductive adults (Jacobson, Parsley, and others, 2015) is especially complex in depicting potential linkages from secondary ecological factors to primary biotic responses because of the many ways that reproductive behaviors may be linked to environmental variables. A link from spawning site selection to survival of gametes is apparent based on telemetry information that documents nonsystematic patterns of upstream and downstream migration behavior, suggesting a search for suitable spawning sites with suitable mates (Fuller and others, 2008; DeLonay, Chojnacki, Jacobson, Albers, and others, 2016). Reproductive synchrony, or the period that males and females in the same reproductive condition are at the same location, is fundamental to success of spawning and fertilization. Flow regime is shown in the CEM as an important factor affecting physical habitat and water-quality dynamics that leads to synchrony and ultimately production of viable gametes.

The hypothesized linkage from flow regime to aggregation and spawning behavioral response would be captured in the population model as an increase in the probability that mates find each other and spawn successfully, resulting in viable gametes from males and females combining to ultimately form embryos (fig. 6). The functional relation between flow-regime naturalization, and ultimately to an increase in viable embryos, is unknown, but these factors are hypothesized to be positively related and asymptotic (fig. 50).

Uncertainty Assessment

Quantitative data to support the CEM are lacking as are published studies specifically linking flow increases as a spawning cue to aggregation and an ultimate increase in viable embryos. The uncertainties associated with this hypothesis are, therefore, high.

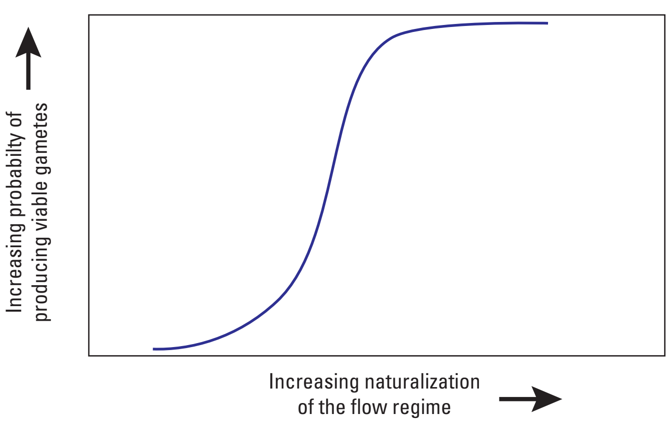


Figure 50. Hypothetical relation between degree of naturalization of the flow regime and probability of producing viable pallid sturgeon gametes.

Potential Interactions with Authorized Purposes

Naturalization of the flow regime from Gavins Point Dam (fig. 2) would be linked through system-wide reservoir operations to nearly all authorized purposes through re-allocation of water during spring pulsed-flow releases. If water storage is too low upstream from Gavins Point Dam or if there is flooding downstream, increased discharge from the reservoir may compete with other authorized purposes. The magnitude of the re-allocation is unknown because of uncertainties in what magnitude and duration would be sufficient to cue a behavioral response. Interaction of authorized purposes would also depend in part on flows in the Missouri River watershed downstream from the dam because runoff from precipitation events in the watershed downstream is largely unmanaged. If runoff is especially high in the watershed, management rules may preclude increases from Gavins Point Dam that are large enough to be effective in drawing fish up to specific locations within the Missouri River.

Spring pulses from Gavins Point Dam have the potential to interact negatively with nesting of least terns and piping plovers. The natural timing of the second spring pulse—late May through early July—may threaten to flood nests if birds do not select sufficiently high bar elevations (Jacobson and Galat, 2008; Jorgensen, 2009; Catlin and others, 2010). On the other hand, spring-pulse flows may be compatible among these species if pulses are distributed among years such that pulses designed to build high sandbars for tern and plover nesting habitat and cue sturgeon aggregation happen with relatively low frequency (for example, every third year). In 2 out of 3 years, in this hypothetical case, flows could be maintained at low levels to ensure successful nesting; moreover, in years with high spring pulses, flows could be designed to build sandbars to high elevations that would be available for nesting in other years, thereby providing greater opportunity for birds to nest at elevations that would minimize flooding.

Working Management Hypothesis in Adaptive Management Context

High uncertainty assigned to this hypothesis indicates considerable risk of failure if implemented with currently existing information. As documented in the lower river, the size of pulsed-flow releases that have been accepted because of their minimal effect on authorized purposes have not been determined to elicit spawning responses (Jacobson and Galat, 2008; Doyle and others, 2011); increases in magnitude and duration of pulsed releases beyond those implemented in the spring rise technical criteria (U.S. Army Corps of Engineers, 2006) would, therefore, be necessary. Implementation of pulsed flows in an AM framework would require robust monitoring and assessment of effects on pallid sturgeon behavioral responses and recruitment, as well as effects on authorized purposes.

An alternative to implementation would be to continue hypothesis-driven research to increase understanding of physiological and behavioral responses to environmental cues (DeLonay, Chojnacki, Jacobson, Albers, and others, 2016). Research approaches may include controlled studies in laboratory or mesocosm environments and field-based studies of behaviors of telemetry-tagged fish. Field-based research could follow the concept of experimental releases or research could be opportunistic, depending on flow events arising from various sources. The current (2016) population of telemetry-tagged pallid sturgeon in the Lower Missouri River (fig. 2) can be considered existing experimental capital that can be used to quantify flow characteristics capable of triggering behavioral responses in adult reproductive pallid sturgeon. Increased documentation of fish responses to annual flows from the Missouri River, and either experimental releases from Gavins Point Dam or opportunistic flow pulses from tributaries, would decrease uncertainties about this action. Reliance on opportunistic flow pulses may require substantially more time to develop sufficient information compared to controlled experimental releases.

Working Management Hypothesis 12—Naturalized Flows from Gavins Point Dam

Hypothesis 12 asserts that naturalized flows from Gavins Point Dam (fig. 2*B*) will increase food availability and overall productivity of the Lower Missouri River by resulting in increased connectivity with low-lying lands and flood plains during the spring and increased temperatures and residence times during the summer and fall. In turn, increased productivity will increase growth and survival of age-0 pallid sturgeon.

Spatial Context and Interactions

The effects of system flow management, culminating with releases from Gavins Point Dam (fig. 2), are realized throughout the 811 mi of the Lower Missouri River, although to a decreasing extent as unregulated tributaries are added in the downstream direction. As a result, the area affected most by flow management will be upstream from the Platte River, with effects decreasing downstream, especially for high flow pulses. The effects of increased summer and fall navigation flows (relative to natural flows) are presently (2016) notable throughout the Lower Missouri River (Galat and Lipkin, 2000; Pegg and others, 2003; Jacobson and Galat, 2008). Flow management is strongly interactive with channel configuration because the two together determine habitat dynamics. Flow management would also interact with temperature management (hypothesis 15) and velocity distributions (affecting bioenergetic demands, hypothesis 13). In addition to flow naturalization effects, productivity would be affected by nutrient loading, flood plain vegetation communities, and fish communities.

Lines of Evidence to Support Working Management Hypothesis

The relation of natural flow regimes and riverine ecosystem productivity has strong theoretical roots, especially with the hypothesis that seasonal flood pulses provide episodes of connectivity, nutrient exchange with the flood plain, and flushing of organic matter to the main stem (Junk and others, 1989; Poff and others, 1997; Sparks and others, 1998). Empirical evidence to support the hypothesis includes substantial weight gains of pallid sturgeon after the 2011 flood (DeLonay, Chojnacki, Jacobson, Albers, and others, 2016) and indirect evidence of effects on pallid sturgeon, such as increased growth of some fish species after the 1993 flood on the Mississippi River (fig. 2) (Gutreuter and others, 1999); however, specific linkages from hydrology and connectivity to age-0 pallid sturgeon diet, growth, and survival have not been documented. Counter arguments include the fact that age-0 shovelnose sturgeon survive, grow, and recruit in the Lower Missouri River, suggesting that productivity and food may not be a limiting factor (Oldenburg and others, 2010).

Applicable Models

The CEMs (Jacobson, Parsley, and others, 2015) illustrate the general hypothesis that flow regime and channel morphology interact to provide increased productivity, which may then cascade to increased food items for free embryos and exogenously feeding pallid sturgeon. The role of flow regime in food production can be assessed through hydrodynamic modeling of food-producing habitats as an indicator. Flow regime scenarios and the food-producing habitat discharge function for the Little Sioux, Iowa (upstream), and Miami, Mo. (downstream), channelized reaches indicate that flow regime alone has the potential to affect variability in food production. The difference in variation is evident in the natural hydrograph, upstream channelized condition (fig. 51*A*). Notably, the medians of the upstream channelized (Little Sioux, Iowa) distributions are statistically different from one another (Wilcoxon rank sum test, p less than [<] 0.001). The medians of the downstream channelized (Miami, Mo.) distributions are statistically different except for M540f0 compared to the natural hydrograph and CWCP and FW22 compared to MR2021 (Wilcoxon rank sum test, $p<0.001$), indicating somewhat increased variation and decreased sensitivity to Gavins Point Dam (fig. 2*B*) releases downstream.

Based on these analyses and the assumptions that food-producing habitats are limiting to pallid sturgeon growth and survival, the models show that statistically significant variation attributable to flow-regime management can happen for upstream, channelized reaches. Notwithstanding the statistical significance, the amount of change is small compared within flow regime scenarios and is much smaller than changes related to upstream or downstream locations (fig. 51*A*).

Comparisons of food-producing habitats between channelized and best-available reaches (Little Sioux, Iowa, and Hamburg, Iowa) indicates that flow-regime management can be more effective in altering distributions of these habitats when the channel has been reconfigured. All the Hamburg, Iowa, reach analyses indicate greater variation in food-producing habitats; and the EVQ2, MR1528, MR2021, and FW22 show substantial increases in medians (fig. 51*B*).

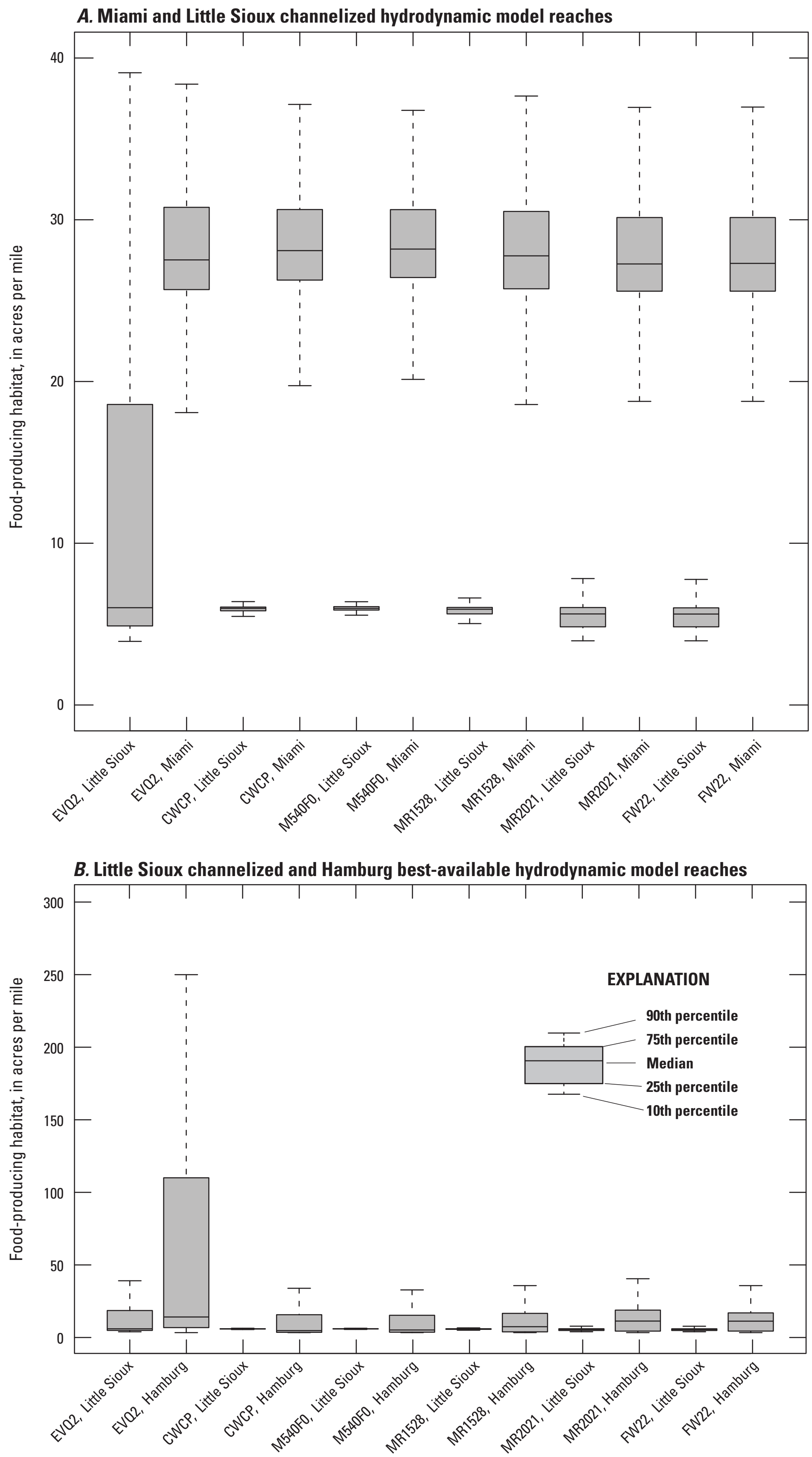


Figure 51. Boxplots of distributions of food-producing habitat area by flow-regime scenarios for *A*, the Miami and Little Sioux channelized hydrodynamic model reaches of the Missouri River and *B*, the Little Sioux channelized and Hamburg best-available hydrodynamic model reaches of the Missouri river.

The functional relation between availability of food-producing habitat and proportional contribution to survival of age-0 pallid sturgeon is likely to be represented as an increasing, asymptotic curve (fig. 52). Presumably, survival would increase with food availability up to a point where food is no longer limiting. Presently, we do not know where the population is on this curve or if food is limiting.

Uncertainty Assessment

A large source of variability in the functional habitat models is the input hydrologic time series. The time series is partially filtered hydraulically through the hydrodynamic models, but hydroclimatically driven variability persists as a dominant source of uncertainty or "noise" in comparing flow regimes or channel reconfigurations, or both. Probably a greater source of uncertainty existing at this point, however, is the uncertainty of whether or not food production is limiting to age-0 pallid sturgeon and if slow-velocity hydraulic definitions are adequate to describe Chironomidae-producing habitats. Both of these uncertainties can be cast as hypotheses and addressed in research, monitoring, and evaluation.

Potential Interactions with Authorized Purposes

Any changes to flow regime will affect system operations and most authorized purposes. The increases in food-producing habitats with the natural flow regime and environmental-flow scenarios (MR2021, FW22) are small in the Sioux-Platte River segment, so it would take much larger changes in flow regime—or combined effects of channel reconfigurations—to have substantive effect in these upstream areas. Such changes would likely create greater interactions with system regulation and authorized purposes.

Naturalized flows from Gavins Point Dam (fig. 2*B*) for the purpose of increasing productivity would mostly be high flows that would connect with low-lying land and the flood plain to increase nutrient exchange, although low summer flows could also achieve higher temperatures, lower velocities, and increased water clarity that could increase in-channel primary productivity. Interactions of high spring flows with tern and plover nesting was discussed with hypothesis 11. Summer low flows to increase productivity would presumably be consistent with maximizing bird nesting success because low flows would minimize flooding risk.

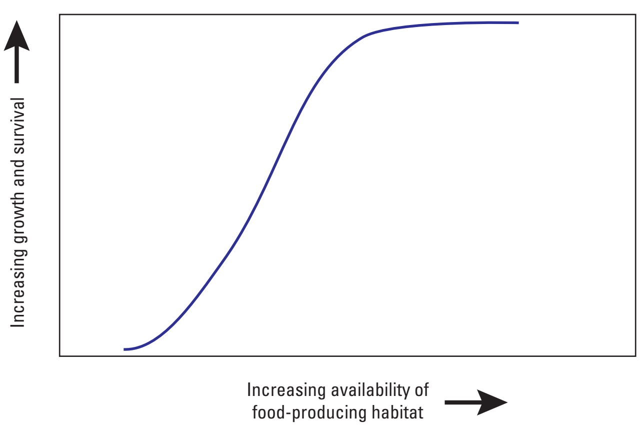


Figure 52. Hypothetical relation between availability of food-producing habitat and growth and survival of age-0 pallid sturgeon.

Working Management Hypothesis in Adaptive Management Context

The physical models linking flow regime alone to food-production potential indicate relatively small effects, but the importance to pallid sturgeon recruitment is unknown. Implementation of changes in flow regime alone to achieve greater food production (similar to the extremes of the natural flow regime at the Little Sioux, Iowa, hydrodynamic modeling reach; fig. 43*A*) would entail high risk and uncertain benefits. Uncertainties in this hypothesis may be addressed effectively by hypothesis-driven field research to resolve the questions of whether or not food is limiting to age-0 pallid sturgeon survival and, if so, validating or refining the definition of food-producing functional habitat based on improved understanding of invertebrate habitat affinities. Opportunistic studies of production, growth, and year-class strength associated with flood events and by comparison between channelized and best-available sites may also provide useful information.

Working Management Hypothesis 13—Naturalized Flows from Gavins Point Dam

Hypothesis 13 asserts that naturalized flows from Gavins Point Dam (fig. 2*B*) will decrease velocities or shift conditions in selected habitats to decrease energetic demands on age-0 pallid sturgeon. The effect of velocities may be direct on foraging energy expenditures of age-0 pallid sturgeon, or it may be indirect in how it alters drift dynamics of food items.

Spatial Context and Interactions

System flow management, culminating with releases at Gavins Point Dam (fig. 2), affect the 811 mi of the Lower Missouri River, although to a decreasing extent as unregulated tributaries are added in the downstream direction. As a result, the area affected most by flow management will be upstream from the Platte River, with effects decreasing downstream, especially for high-flow pulses. The effects of increased summer and fall navigation flows are presently (2014) notable throughout the Lower Missouri River (Galat and Lipkin, 2000; Pegg and others, 2003; Jacobson and Galat, 2008). The potential effect of summer-fall navigation flows on energetic demands is expected to be highest in upstream segments (Sioux and Platte Rivers) where channel complexity is less compared to downstream segments (Grand and Osage Rivers). Flow management is strongly interactive with channel configuration, as the two together determine habitat dynamics and velocity distributions. Flow management would also interact with temperature management (hypothesis 15) and food production (affecting growth rates, hypothesis 12).

Lines of Evidence to Support Working Management Hypothesis

Water temperature, diet, and water velocity are common parameters in bioenergetic models for fish growth, as they have been applied to growth of pallid sturgeon juveniles (Chipps and others, 2008). The theoretical assumption is that energetic demands increase as water velocities increase in areas where fish need to forage for food items. The functional relations between water velocity and energetic demand have not been documented for age-0 pallid sturgeon; moreover, as a benthically oriented fish, the pallid sturgeon forages in the boundary layer with complex flow fields related to flow obstructions and dune or ripple fields. Actual bioenergetic demands on age-0 pallid sturgeon are, therefore, likely to be complex and nonlinearly related to mean velocities or depth-averaged velocities; nevertheless, this hypothesis reflects the broad understanding that lower velocities create lower bioenergetic demands.

The relation between discharge and depth-averaged velocities can be assessed with hydrodynamic models if the assumption is accepted that habitat units defined using depth-average velocities are indicative of bioenergetic demands. On a reach-average basis, water residence time in hours per mile of channel length (the reciprocal of mean velocity in miles per hour) is a broad indicator (fig. 36), that mean velocities generally increase with discharge. Hydrodynamic model results can be used to explore the sensitivity of foraging habitat availability to discharge to assess how that functional habitat unit is affected by flow regime (fig. 38).

Applicable Models

The CEMs (Jacobson, Parsley, and others, 2015) illustrate the general hypothesis that flow regime and channel morphology interact to affect habitat quality and quantity, which may then cascade to changes in velocity fields and bioenergetic demands. Flow-regime scenarios and foraging habitat availability for the Little Sioux, Iowa (upstream), and Miami, Mo. (downstream), channelized reaches indicate that flow regime has the potential to affect variability in amounts of foraging habitat and energetic requirements. The difference in variation is evident in the upstream channelized condition (fig. 53*A*). Notably, medians of the upstream FW22 and MR2021 are significantly higher than the other flow-regime scenarios (Wilcoxon rank sum test, $p<0.001$). The medians of all downstream channelized (Miami, Mo.) distributions also differ statistically (Wilcoxon rank sum test, $p<0.001$), except for MR2021 and FW22 scenarios. Comparisons by flow-regime scenario and degree of channel reconfiguration indicate that the best-available reconfigured channel has greater amounts of foraging habitats, as well as greater variability (fig. 53*B*).

The boxplots of habitat availability (fig. 53*A*, *B*) illustrate that there are generally greater variation and greater amounts of foraging habitat in the downstream sections of the river and in reconfigured channels. The more natural flow regimes (EVQ2, MR2021, and FW22) have substantially greater amounts of foraging habitat at the Little Sioux, Iowa, reach and somewhat greater habitat at the Miami, Mo., reach. The same is seen in the comparison between the Little Sioux, Iowa, and Hamburg, Iowa, reaches, except that the Hamburg, Iowa, reach provides substantially more foraging habitat than either the Little Sioux, Iowa, or Miami, Mo., reaches across all flow regimes. The increased amounts of foraging habitat under the EVQ2, MR2021, and FW22 flow regimes is due to inclusion of summer low flows that substantially increase foraging habitat area in channelized sections (fig. 38). Medians and 75th percentiles of foraging habitat availability at downstream reach (Miami, Mo.) are greater than the upstream reach except for the EVQ2 flow regime where the median Miami, Mo., reach availability is slightly less than the median Little Sioux, Iowa, reach availability.

Links from foraging habitat availability to pallid sturgeon population demographic parameters are uncertain, but the form of the relation likely to be represented as an increasing, asymptotic curve (fig. 54). If foraging habitat is limiting, an increase of habitat availability will increase survival until foraging habitat is no longer limiting.

Uncertainty Assessment

A large source of variability in the functional habitat models is the input hydrologic time series. The time series is partially filtered hydraulically through the hydrodynamic models, but hydrologically driven variability persists as a dominant source of uncertainty or "noise" in comparing flow regimes or channel reconfigurations, or both. Probably a greater source of uncertainty existing at this point, however, is the uncertainty of foraging habitat availability is a useful indicator of a bioenergetic benefit to age-0 pallid sturgeon. In particular, laboratory and field studies are lacking to assess dependency of energetic expenditures of young fish on current velocity, and if 2D hydrodynamic models at the scale used resolve relevant velocities. These uncertainties can be cast as hypotheses and addressed in research, monitoring, and evaluation.

Potential Interactions with Authorized Purposes

Any changes to flow regime affect system operations and most authorized purposes. The increases in foraging habitats with the natural flow regime and natural environmental scenarios (MR2021, FW22) are small, although significant, in the upper section of the Lower Missouri River (fig. 2*B*). The shape of the forage habitat functions (fig. 38) indicates that for channelized sections of the river, foraging habitat is maximized at very low flows, generally below acceptable navigation flows; hence, optimization of foraging habitat in channelized sections with minimal rehabilitation of channel complexity would require flow releases that would interact strongly with navigation and possibly water supply. Summer low flows may entail increased recreational benefits from use of sandbars.

Naturalized flows from Gavins Point Dam for the purpose of decreasing energetic expenditures of age-0 pallid sturgeon would entail decreased mid-summer to fall discharges with concomitant decreases in velocities in foraging areas. Summer low flows to decrease velocities would presumably be consistent with maximizing bird nesting success because low flows would minimize flooding risk.

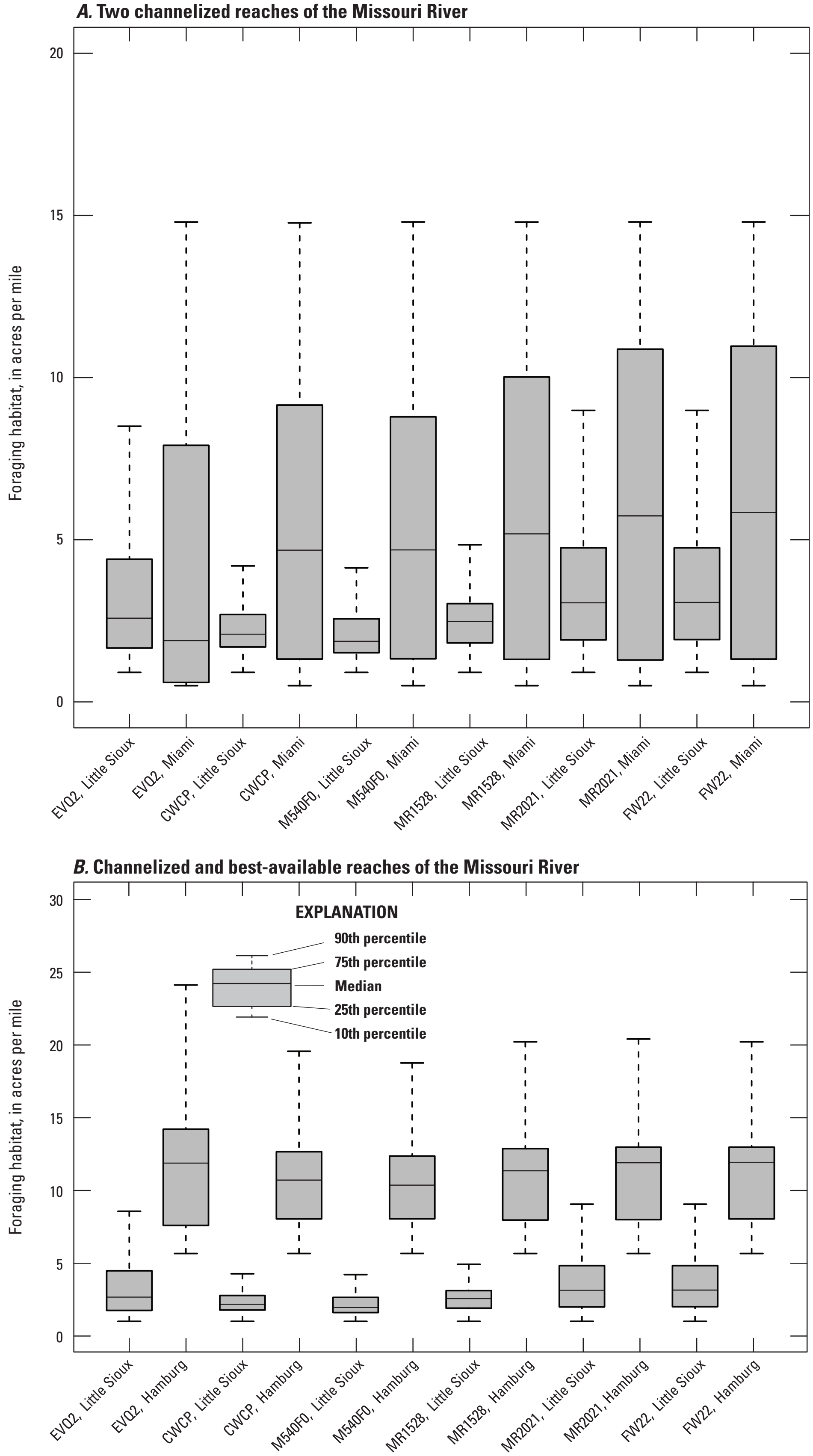


Figure 53. Boxplots of distributions of foraging habitat area by flow-regime scenarios for *A*, the Miami and Little Sioux channelized hydrodynamic model reaches of the Missouri River and *B*, the Little Sioux channelized and Hamburg best-available hydrodynamic model reaches of the Missouri River.

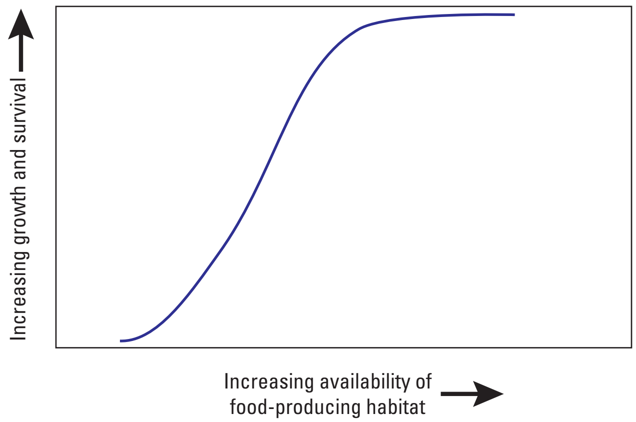


Figure 54. Hypothetical relation between availability of foraging habitat and growth and survival of age-0 pallid sturgeon.

Working Management Hypothesis in Adaptive Management Context

The physical models linking flow regime alone to foraging habitat indicate relatively small effects, but the importance to pallid sturgeon recruitment is unknown. Implementation of changes in flow regime in isolation to achieve greater foraging habitat (similar to the extremes of the natural flow regime at the Little Sioux, Iowa, reach; fig. 51*A*) may entail high risk to navigation and other authorized purposes and uncertain benefits to the pallid sturgeon. Uncertainties in this hypothesis may be addressed effectively by hypothesis-driven field and laboratory research to resolve the questions of biological sensitivity of age-0 energetic demands to velocity fields and the nature of the velocity fields actually occupied by age-0 pallid sturgeon. These investigations would indicate if foraging habitat is limiting and if flow-regime management may be a useful mechanism to provide more energetically favorable habitats.

Working Management Hypothesis 14—Decreased Flows in Late May and June from Gavins Point Dam, Increased Survival of Pallid Sturgeon Free Embryos

Hypothesis 14 asserts that reducing flows from Gavins Point Dam (fig. 2) in late May and June will decrease channel velocities, slowing the drift of free-embryo pallid sturgeon. Slowing the drift rate will reduce the river distance needed for embryonic development and allow free embryos to settle into habitats in the Missouri or Mississippi Rivers hypothesized to promote growth and survival.

Spatial Context and Interactions

The geographic scope of this hypothesis is the Missouri River from Gavins Point Dam downstream to the Mississippi River confluence, with potential for some effect of decreased flow downstream on the Middle Mississippi River (fig. 2). By decreasing flows from Gavins Point Dam during the time pallid sturgeon free embryos would enter the drift, the distance needed for embryonic development before settling into suitable habitat above the Mississippi River confluence would be reduced, potentially increasing the probability of free-embryo survival. The influence of reduced flows on dispersal of drifting free embryos is dependent on spawning occurring at some functional distance from Gavins Point Dam. If spawning occurs too far downstream, the effect of reduced releases from Gavins Point Dam may be negated by downstream tributary flows.

Because free-embryo development is influenced by other factors, such as temperature and drift duration, this hypothesis could interact strongly with other hypotheses. Temperature influences the maturation rate of free embryos (Braaten, Fuller, Lott, Ruggles, and others, 2012), so changes in discharge from Gavins Point Dam, or implementation of other actions that influence river temperatures (hypothesis 15), will affect temperature regimes downstream. Reconfiguration of selected channel sections to provide interception habitat for drifting free embryos (hypothesis 19) in conjunction with reduced flows from Gavins Point Dam may interact to provide better drift conditions for developing free embryos than those that would occur by implementing either action alone. Implementing naturalized flows (hypotheses 12 and 13) from Gavins Point Dam would be generally incompatible with low flows in May and June.

Hypotheses related to drift dynamics relate directly with spawning habitat (hypothesis 16), which determines how and where drift originates from hatching embryos, and interception habitat (hypothesis 19), which relates to the hydraulic conditions that may limit advection of drifting free embryos into supportive, marginal habitats.

Lines of Evidence to Support Working Management Hypothesis

A dominant hypothesis for the absence of pallid sturgeon recruitment in the Missouri River (fig. 2) is that the length of free-flowing river, in combination with channel form and hydrology, is insufficient for drifting free embryos to complete embryonic development; and this results in free embryos settling into habitats that are potentially unsuitable for survival (DeLonay and others, 2009; Braaten, Fuller, Lott, Ruggles, and others, 2012). In the Lower Missouri River, there is no obvious source of downstream mortality (in contrast to Lake Sakakawea in the Upper Missouri River). Instead, this hypothesis on the Lower Missouri River implies that free embryos cannot exit from the highly engineered navigation channel when they need to transition to first feeding or that other unknown characteristics of downstream habitats are not supportive. Water temperature, velocity, and channel form influence pallid sturgeon embryo drift distance and time (DeLonay and others, 2009; Braaten, Fuller, Lott, Ruggles, and others, 2012; Erwin and Jacobson, 2014) with spawning location acting as an important determinant for the amount of drift distance available.

A reduction in flow from Gavins Point Dam has the potential to reduce the drift rate of free embryos by decreasing mean velocities. The greatest influence would be on free embryos that emerge from spawning substrates closer to Gavins Point Dam where the influence of the reservoir releases is high, and lower velocities would have the greatest effect on drift distance. It is also possible that higher flows may contribute to retention of drifting larvae if the flow and channel hydraulics allow larvae to be transported into vegetated riparian zones or other areas of high roughness and low velocity (Coutant, 2004; Leeuw and others, 2006). Erwin and Jacobson (2014) used acoustic Doppler current profiler measures of longitudinal dispersion coefficients to document that dispersion—a measure of hydraulic characteristics that retard and retain particles—may increase with increasing discharge, depending on channel geometry. In this case, dispersion increased as water overtopped wing dikes and sandbars and then decreased as flows continued up to near bank-full. Such flows may have the potential to increase retention of free embryos by inundating low-lying alluvial surfaces within the active channel, secondary channels, and vegetated riparian habitats in the channel. The reduced flow velocities and high roughness values characteristic of these environments increase hydraulic gradients and promote the retention of drifting free embryos.

In contrast to the upper river where there is a reasonable presumption that drift into the headwaters of Lake Sakakawea is lethal to free embryos, there is no evidence to support the hypothesis that excess drift is linked to mortality in the lower river. In the lower river, drift processes serve mainly to determine on what parts of the river rearing habitats should be constructed. Several corollary hypotheses related to negative effects of increased drift exist, but because of a lack of supportive information they remain speculative:

- Locations along the lower river exist where conditions are lethal to free embryos (for example, wing-dike pools with low dissolved oxygen); drift dynamics could be manipulated so free embryos do not settle in such areas.

- Dispersal into the Middle Mississippi River is deleterious to survival because habitat conditions there are not supportive; drift dynamics could be manipulated to minimize transport into the Mississippi River.

- The physical process of drift in the turbulent flow field of the channelized river is damaging and fatal to free embryos; drift dynamics could be manipulated to slow velocities and dampen turbulence to minimize damaging conditions.

- Enhanced downstream dispersal of free embryos increases chances for mixing with formerly isolated genetic subpopulations or congenerics, thereby increasing chances of hybridization; drift dynamics could be manipulated to slow dispersal and maintain age-0 fish upstream.

A final corollary hypothesis was given greater support from expert-opinion surveys (Jacobson and others, 2016). This hypothesis is captured separately in hypothesis 19 (discussed later in this report) and asserts that drifting free embryos are unable to exit the thalweg and move into supporting, channel-marginal habitats and, therefore, starve.

Applicable Models

The component CEM for free embryos this life stage (Jacobson, Parsley, and others, 2015) illustrates direct hypothesized linkages from primary ecological factors to secondary biotic response (that is, survival); although, as indicated above, there is no empirical evidence linking drift with mortality. The most likely path for this hypothesis through the CEM is (1) flow regime, (2) physical habitat dynamics (hydraulics), (3) successful first feeding (retention), and (4) survival. The linkages between these components are hypothesized to be of high importance with high uncertainty but low importance for the link between retention and survival because of the lack of evidence for mortality. The strong relation between flow regime, hydraulics, and drift dynamics of free embryos has been quantified through empirical studies (Kynard and others, 2007; Braaten and others, 2008; Braaten, Fuller, Lott, Ruggles, and others, 2012) and theoretical models (Erwin and Jacobson, 2014; Fischenich and others, 2014).

The CEMs capture the role of current velocity in free-embryo drift by indicating strong and moderately uncertain linkages from flow regime, through habitats, to survival (Jacobson, Parsley, and others, 2015). The 1D and 2D hydrodynamic models provide quantitative insights for the left side of the CEMs, subject to the inability to link drift directly to survival and based on the assumptions that it is reasonable to model drift as passively transported particles. These models use discharges, hydraulic relations, and water temperature to predict the location where free embryos may settle as they transition from free embryos to exogenously feeding larvae.

A 1D longitudinal advection/dispersion model of free embryo drift was recently developed for the Missouri River downstream from Gavins Point Dam (fig. 2) (Erwin and Jacobson, 2014). This model estimated total drift distance and used a longitudinal dispersion coefficient as a metric to quantify the tendency towards dispersion or retention of passively drifting free embryos. The authors modeled the drift of free embryos from two known spawning locations on the Lower Missouri River: RM 218 (near the Grand River) and RM 638 (near the Big Sioux River). Model simulations predicted that at 3 dph, most free embryos spawned at RM 218 would have drifted downstream into the Middle Mississippi River. Modeled drift distances for the spawning event near RM 638 predicted that most drifting free embryos may have been retained in the Missouri River through 9 dph.

An update to the 1D approach has been developed using HEC–RAS as part of the EA (Fischenich and others, 2014). Simulations from the 1D model demonstrate that drift is substantial during the period for embryonic development and is affected by flow magnitude (table 10). Information is lacking, however, to evaluate linkages from fate of free embryos—locations of retention—to survival. Understanding where free embryos are likely to be retained will show where other supportive habitats are needed.

For some species of sturgeon, newly hatched embryos are known to hide within the interstitial spaces of river substrates (Du and others, 2011; McAdam, 2011, 2012). If pallid sturgeon free embryos hide within interstitial spaces instead of immediately entering the drift, the distance needed for ontogenetic development would be reduced. On the Lower Missouri River, interstitial residency would result in substantially shorter drift distances (table 10), which would affect where along the river the free embryos would be when they transition to first feeding. Whether or not pallid sturgeon free embryos reside in interstices for any length of time is a substantive source of uncertainty to understanding drift and required drift distance (DeLonay, Chojnacki, Jacobson, Albers, and others, 2016), although some experimental evidence now supports immediate drift of free embryos (DeLonay and others, 2015). In addition, it is possible that some interactions of fish behavior and hydraulics could result in retarded dispersal rates or early retention in channel-marginal habitats. The velocities and turbulence intensity of the channelized Lower Missouri River are much greater than those explored in laboratory studies where it was demonstrated that late-stage free embryos were unable to maintain position in the current (Kynard and others, 2007), so it is likely that free embryos are limited in their ability to seek supportive habitats in the river. It has also been argued that long drift and dispersal is an adaptive trait that allows free embryos to avoid predators and find food when they transition to first feeding (Kynard and others, 2002; Kynard and others, 2007), indicating risks that may exist if free embryo drift is pre-empted before transition and acquisition of mobility. It is possible that quality and quantity of habitats to support first feeding vary along the river, resulting in differential growth and survival depending on combinations of interstitial residency, current velocity, other hydraulic factors, and water temperature that affect dispersal distance; however, present information does not indicate that habitat quality is a limiting factor for free embryos, or whether it is beneficial or detrimental to have free embryos disperse into the Mississippi River.

An additional perspective can be gained by assessing how mean velocities, or mean residence times, vary with flow regime using the 2D hydrodynamic models used for functional habitats. The mean residence time curves (fig. 36) show small difference among sites, indicating that channel morphology as it presently exists seems to have a small effect on advection of transported constituents, like free embryos. The residence time curves can be used with flow regime time series to calculate distributions of residence times for various flow scenarios (fig. 55). Medians of the distributions at the Little Sioux, Iowa, hydrodynamic modeling reach are all significantly different from one another (Wilcoxon rank sum test, $p<0.001$), indicating the effectiveness of flow regimes in changing residence time; boxplots of the distributions show substantial increases in residence time associated with the environmental flow scenarios with summer low flows (MR2021 and FW22, fig. 55*A*). In the channelized lower section, Miami, Mo., reach, residence times were higher, indicating that (although discharges increase substantially between the two reaches) greater width and hydraulic resistance actually increase residence times of water. Among flow regimes at the Miami, Mo., reach, differences in medians are not significantly different from zero for comparisons CWCP00 to M540F0, and for CWCP00 to MR1528 (Wilcoxon rank sum test, $p<0.001$). Comparing channelized (Little Sioux, Iowa) and best-available (Hamburg, Iowa) reaches in the upper section, the best-available reach has smaller medians than the channelized reach but is characterized by substantially greater variation (fig. 55*B*).

Reducing flows from Gavins Point Dam as a means of increasing survival by shortening the distance needed for embryonic development before settling may be a valid hypothesis if habitats downstream are not supportive. In contrast to the upper river, what constitutes suitable habitat for settling embryos on the lower river has not been clearly defined, and the link between suitable habitat and survival is poorly understood. Reducing velocities would also contribute to increased survival according to the corollary hypothesis that turbulent energy is physically damaging. The functional relation between current velocity and survival for early life stages is hypothesized to be peaked and asymmetrical in shape (fig. 56). This is based on the assumption that velocity is necessary to help disperse free embryos, but as velocity increases, survival decreases because of inability to exit the thalweg or from damaging turbulence. Increased downstream transport may also be deleterious because of increased mixing of formerly distinct genetic subpopulations or with congenerics. Velocities (and discharges) that are too low would not provide the geographic dispersal for which the species is adapted and may promote predation.

Uncertainty Assessment

A large source of variability in the advection/dispersion and functional habitat models is the input hydrologic time series. The time series is partially filtered hydraulically, but hydrologically driven variability persists as a dominant source of uncertainty or "noise" in comparing flow regimes or channel reconfigurations, or combinations thereof. Uncertainties associated with hydrologic and hydraulic modeling components are certainly small compared to the biological uncertainties related to interstitial residency, other biotic-hydraulic interactions that may retard drift, and unknowns about mechanisms of mortality for free embryos. Interstitial residency, in particular, could subtract several days from total dispersal time and distance. The question of whether or not some Lower Missouri River (fig. 2) habitats may be lethal for pallid sturgeon free embryos is being addressed by age-0 sampling on the Lower Missouri River, and the contribution of Missouri River free embryos to larval and juvenile populations

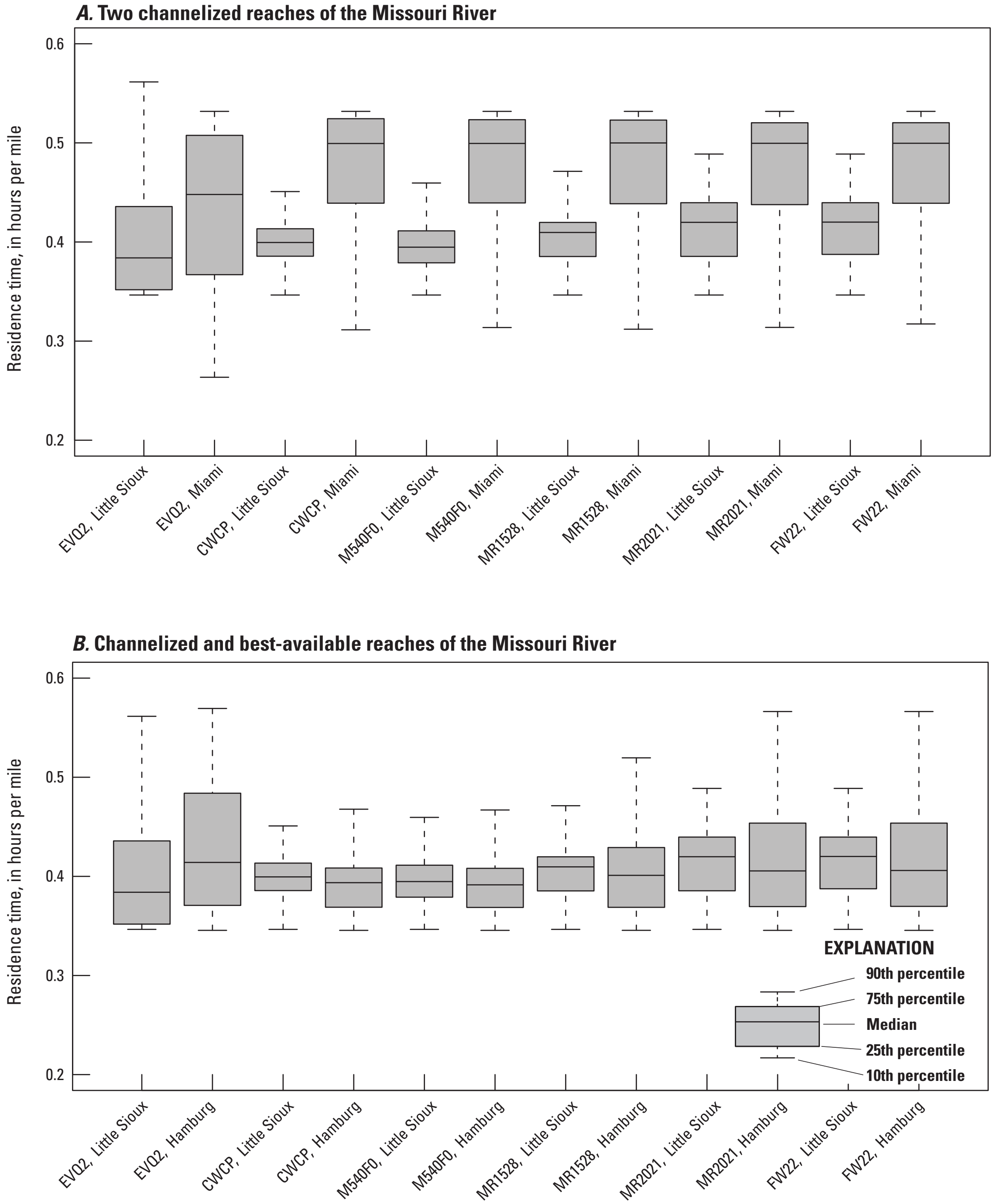


Figure 55. Boxplots of distributions of residence times by flow-regime scenarios for *A*, the Miami and Little Sioux channelized hydrodynamic model reaches of the Lower Missouri River and *B*, the Little Sioux channelized and Hamburg best-available hydrodynamic model reaches of the Lower Missouri River.

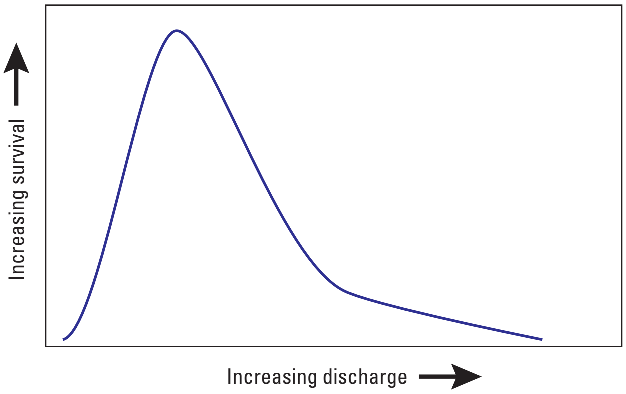


Figure 56. Hypothetical relation between discharge and survival of free embryos.

in the Mississippi River are being addressed by coordinated microchemistry assessments (Todd Gemeinhardt, written commun.). Each of these uncertainties can be cast as hypotheses and addressed in research, monitoring, and evaluation. Considering the multiple unknowns in drift dynamics, we consider uncertainty for this hypothesis to be high.

Potential Interactions with Authorized Purposes

Reducing flows from Gavins Point Dam (fig. 2*B*) would be linked to system regulation and many of the authorized purposes through potential changes in the management of flows from other storage reservoirs in the system. Downstream target flows, storage capacity, and anticipated runoff would all play roles in the effects of reduced flows from Gavins Point Dam. Additionally, if upstream reservoir storage capacity is low, rules regarding system regulation may preclude implementing reduced flows from Gavins Point Dam altogether. The shape of the residence-time functions (fig. 36) indicates that for channelized sections of the river, residence time is maximized at low flows, generally below acceptable navigation levels; hence, optimization of drift distance may require flow releases that would interact strongly with navigation and possibly water supply.

Naturalized flows from Gavins Point Dam for the purpose of decreasing drift would entail decreased mid- to late-summer discharges with concomitant decreases in velocities. Summer low flows to decrease drift rates would presumably be consistent with maximizing bird nesting success because low flows would minimize flooding risk.

Working Management Hypothesis in Adaptive Management Context

Advection/dispersion and mean residence time data indicate that alternative flow regimes at Gavins Point Dam (fig. 2*B*) have measurable, although relatively small, effects on drift distance. Given the considerable biological uncertainty associated with spawning locations, interstitial residency, and if drift distance itself is associated with mortality, implementation of this action would carry a high risk of failure; moreover, success in flow manipulation would probably require implementation in coordination with other actions (such as creation of interception habitat, creation of spawning habitat, or temperature manipulations) to provide the drift conditions and distance needed for free-embryo development and recruitment to the next life stage.

Uncertainties could be addressed through a combination of laboratory and field studies. The uncertainties related to interstitial residency are critical and resolving them would provide a much improved foundation for modeling and decision making; recent evidence supports the converse, immediate drift model (DeLonay and others, 2015). A corollary hypothesis about whether or not velocity and associated turbulence contribute to direct physical mortality is related in that free embryos that grow for a period in interstices may be more physically fit and able to withstand main channel conditions. The details of flow interaction with reconfigured channels, and how they may together contribute to increasing survival of drifting free embryos, can be further explored with hypothesis-driven, high-resolution hydrodynamic models using particle-tracing techniques and perhaps effectively combined with targeted field studies with tracers or live free embryos. Implementation of test low flows in an AM framework would require robust monitoring and assessment of effects on recruitment as well as on authorized purposes.

Working Management Hypothesis 15—Increased Temperatures in May from Gavins Point Dam Aggregation and Spawning Cues

Hypothesis 15 asserts that increasing the temperature of water released from Gavins Point Dam (fig. 2*B*) in May will provide aggregation and spawning cues for reproductive pallid sturgeon increasing the chance that mates will find one another, release their gametes in close proximity to each other, and ultimately result in a larger probability of viable embryos.

Spatial Context and Interactions

The geographic scope of this hypothesis is the Missouri River from Gavins Point Dam downstream to the Mississippi River, although practical implementation might require actions at Fort Randall Dam (fig. 2). The hypothesis also potentially affects pallid sturgeon in one of several tributaries downstream from Gavins Point Dam because reproductive fish may select the main stem Missouri River rather than a tributary depending on the magnitude or quality of cues from other locations.

Observations of reproductive pallid sturgeon migration patterns in the Missouri River provide little support for the idea that these fish initiate spawning migrations based on discharge characteristics (cues), but it is possible that discharge has been ineffective because other associated factors—such as water temperature and turbidity—are not synchronized. By adjusting temperature of water released from Gavins Point Dam or Fort Randall Dam during the spawning period (May) to that hypothesized to be optimal for pallid sturgeon, reproductive fish may be cued to migrate to a similar location and aggregate, which would increase the chance of successful spawning, fertilization, and hatch.

Because spawning behavior is hypothesized to be influenced by other factors (such as flow, turbidity, or suitable spawning substrate), this hypothesis could interact with other hypotheses. Attracting fish to spawn in the Missouri River could dissuade them from using tributaries in the lower river. Because of the large watershed area of the Missouri River downstream from Gavins Point Dam, runoff from precipitation events would frequently interact with intentional temperature changes. Increasing temperature of water released from Gavins Point Dam potentially could attract fish to one or more similar locations for aggregation, which relates to the hypothesis that the probability of mates finding one another is diminished by overprovision of hard, coarse substrate in bank revetment and channel-training structures (Jacobson and others, 2016).

Lines of Evidence to Support Working Management Hypothesis

A naturalized flow regime, which includes changes in temperature and flow pulses in the spring (“spring rise”), has been promoted as necessary to cue pallid sturgeon spawning behavior (U.S. Fish and Wildlife Service, 2000, 2003). Many lotic fishes are adapted to natural variation in water temperature and discharge; decoupling of water temperature from discharge variation can result in removal of cues for spawning conditions (Goodman and others, 2013).

Research based on documentation of spawning migrations by telemetry-tagged, reproductive pallid sturgeon provides insights into the role of temperature in reproductive ecology (DeLonay, Chojnacki, Jacobson, Albers, and others, 2016). This body of work documents temperature thresholds for migration (generally around 10–12 °C) and spawning around 16–18 °C. DeLonay, Chojnacki, Jacobson, Albers, and others (2016) have characterized the relation of spawning to water temperature as a threshold event—a temperature that must be reached but that does not necessarily result in successful release of eggs. An important observation of this work is that episodes of decreased water temperature of 2–4 °C can interrupt upstream migrations and have been associated with reproductive failures of some female fish. The documented temperature anomalies have been caused by spring time cold-weather systems and are not associated with releases from Gavins Point Dam (fig. 2).

Some additional research has been completed regarding temperature-related spawning cues with shovelnose sturgeon. In the Marias River (a tributary to the Upper Missouri River), Goodman and others (2013) determined that shovelnose sturgeon did not spawn when discharge was below a threshold level despite suitable and optimal water temperatures. They suggested that discharge must reach a threshold level and be coupled with suitable water temperature to provide a spawning cue; however, in the Mississippi River, Phelps and others (2010) determined that shovelnose sturgeon spawning was loosely related to temperature and a slight increase in river stage. More importantly, temperature was related to survival of post-hatch embryos.

Applicable Models

The EA is in the process of developing the physical water-quality and flow models that will be useful to address the hydrologic and hydraulic parts of this question, including how much of a water temperature effect is possible given the configuration of dams and reservoirs. Empirical information exists to provide some context.

Although releases from Gavins Point Dam (fig. 2*B*) have been shown to track air temperature and be relatively insensitive to discharges during spring–fall (DeLonay, Chojnacki, Jacobson, Albers, and others, 2016), it is not clear if the release temperatures continue to be lower than natural because of the persistent effects of cold releases from Fort Randall Dam. Subhourly temperature data from multiple channel habitats at four sites in the Fort Randall and Gavins Point Dam segments in 2003–4 illustrate substantial spatial trends (fig. 57). Differences between water temperatures at Fort Randall Dam and just downstream from Gavins Point Dam increase during the spring to mid-summer when, during the day, water temperatures in Gavins Point Dam may be 10 °C warmer than just downstream from Fort Randall Dam. By September 1, the two sources have similar temperatures; moving into the fall, Fort Randall Dam releases are 2–3 °C warmer than Gavins Point Dam. Within these segments, there is also some variation by macrohabitat units. In the Fort Randall Dam segment, water temperatures in a side channel were somewhat warmer on average than the main channel during summer months, whereas in the Gavins Point Dam segment there was less variation among habitats (fig. 58).

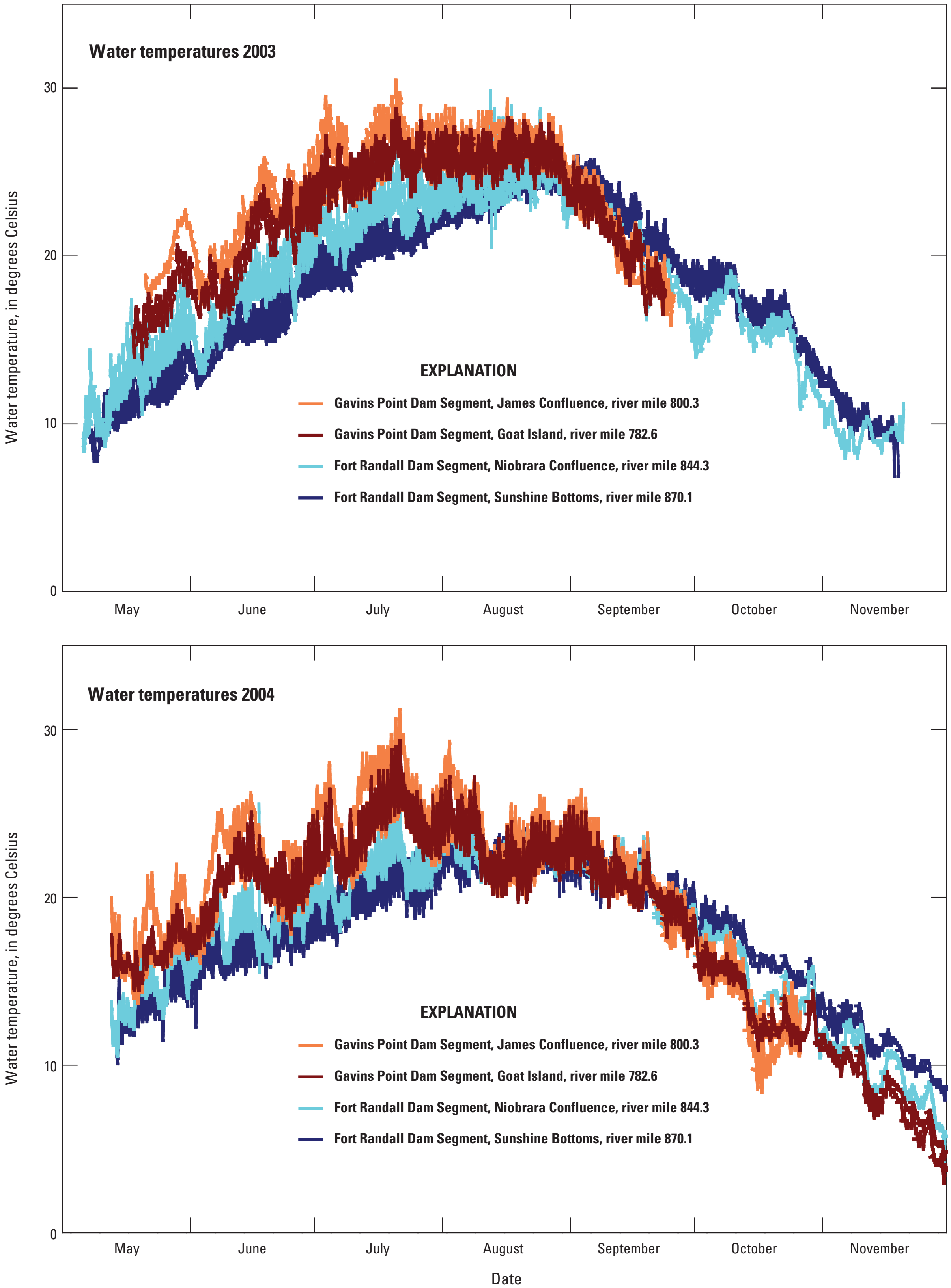


Figure 57. Water temperature records from three macrohabitats at four sites in the Fort Randall and Gavins Point Dam segments, in 2003 and 2004 (R. Klumb, unpub. data).

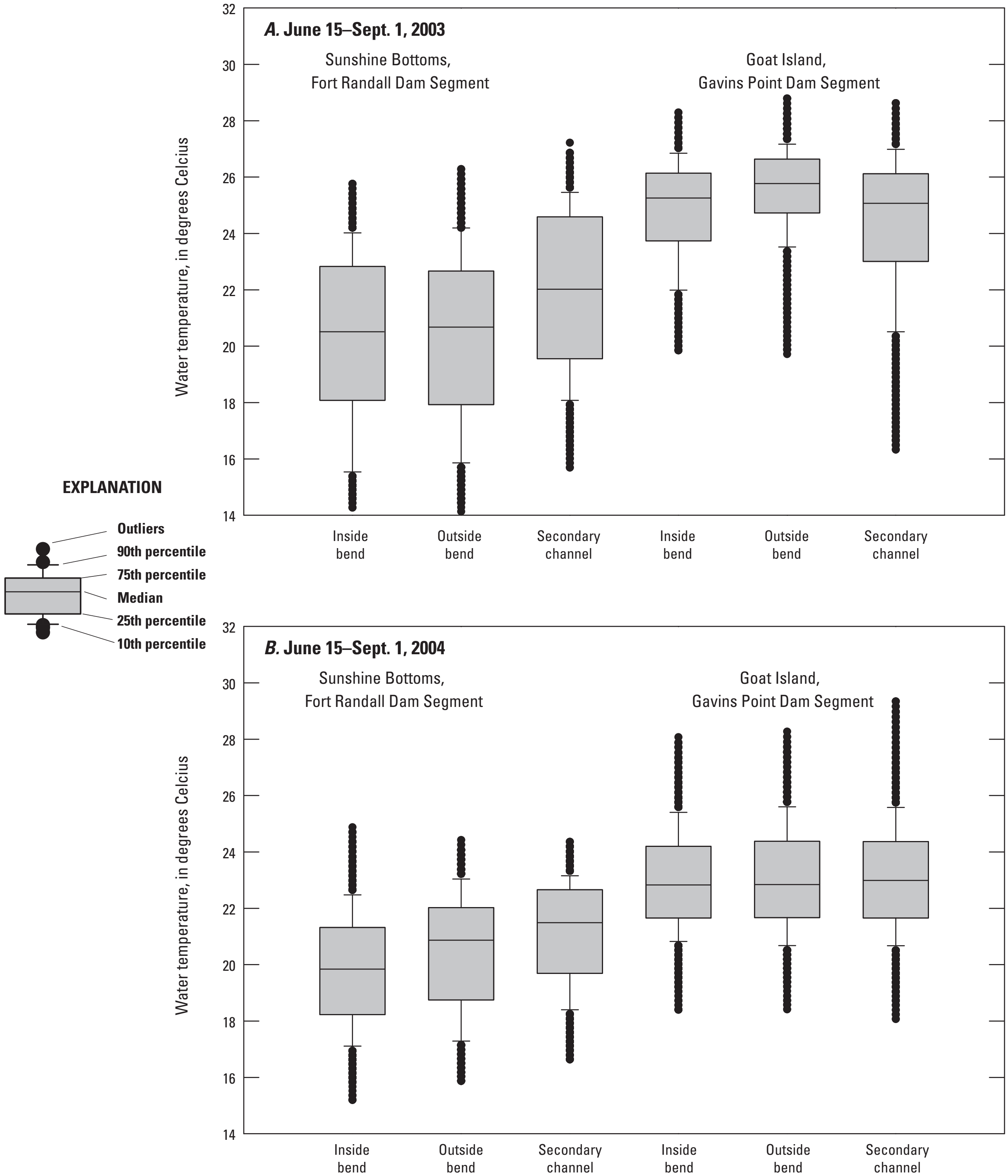


Figure 58. Boxplots of water temperature distributions by macrohabitat unit, June 15 – September 1, Fort Randall Dam and Gavins Point Dam segments in A, 2003 and B, 2004.

Historical data for water temperatures at these sites before main stem dam construction would help document if Gavins Point Dam water temperatures show a persistent effect of lowering from Fort Randall Dam releases. Unfortunately, only poorly described monthly averaged data have been documented for the period before dam construction; and, given the extreme temporal variation inherent in these rivers (fig. 57), the monthly data are not sufficient to develop comparisons. Historical water temperature data from the USGS National Water Information System database are available for Yankton, South Dakota, from 1949 to the present, a period that begins in the middle of main stem dam construction. These data are instantaneous, instead of averaged, but interpretation has some of the same challenges because of differences in time of day; nevertheless, a comparison of temperatures in 1949–56 (before completion of Gavins Point Dam but after completion of Fort Randall Dam), and in 1967–2013 (after stabilization of system operation) shows that water temperatures at Yankton, S. Dak., have increased in association with completion of Gavins Point Dam (fig. 59). These data do not address what temperatures were before main stem dams or if effects of Fort Randall Dam are still felt as a depression of temperatures downstream from Gavins Point Dam, but they do indicate that Gavins Point Dam presently operates to mitigate some of the cold water coming from upstream.

The physical context establishes that Gavins Point Dam temperatures are not as depressed as Fort Randall Dam. Lacking useful predam temperature data, we cannot determine if releases from Gavins Point Dam are significantly depressed relative to natural, but the correlation of water and air temperatures at Yankton, S. Dak., indicates that water temperatures are likely not depressed. The data also do not indicate if temperatures of releases could be increased or if those increases would be biologically effective. Although linkages from temperature to spawning behavioral responses are conceptually viable and common in the fisheries literature (U.S. Fish and Wildlife Service, 2003), we have not identified any useful, quantitative models linking water temperature management to production of viable embryos.

The component CEM for reproductive adults (Jacobson, Parsley, and others, 2015) is especially complex in depicting potential linkages from secondary ecological factors to primary biotic responses because of the many ways that reproductive behaviors may be linked to environmental variables. A link from spawning site selection to survival of gametes is apparent based on telemetry information that documents nonsystematic patterns of upstream and downstream migration behavior, suggesting a search for suitable spawning sites with suitable mates (Fuller and others, 2008; DeLonay, Chojnacki, Jacobson, Albers, and others, 2016). Reproductive synchrony, or the period that males and females in the same reproductive condition are at the same location at the same time, is an important factor related to spawning and fertilization. Temperature regime could be an important factor affecting physical-habitat and water-quality dynamics, leading to synchrony and ultimately production of viable embryos.

The hypothesized linkage from temperature regime to aggregation and spawning behavioral response would be captured in the population model as an increase in the probability that mates find each other and successfully spawn, resulting in viable gametes from males and females combining to ultimately form embryos (fig. 11). The functional relation between flow-regime naturalization and ultimately to an increase in viable embryos is unknown, but they are hypothesized to be positively related (fig. 60).

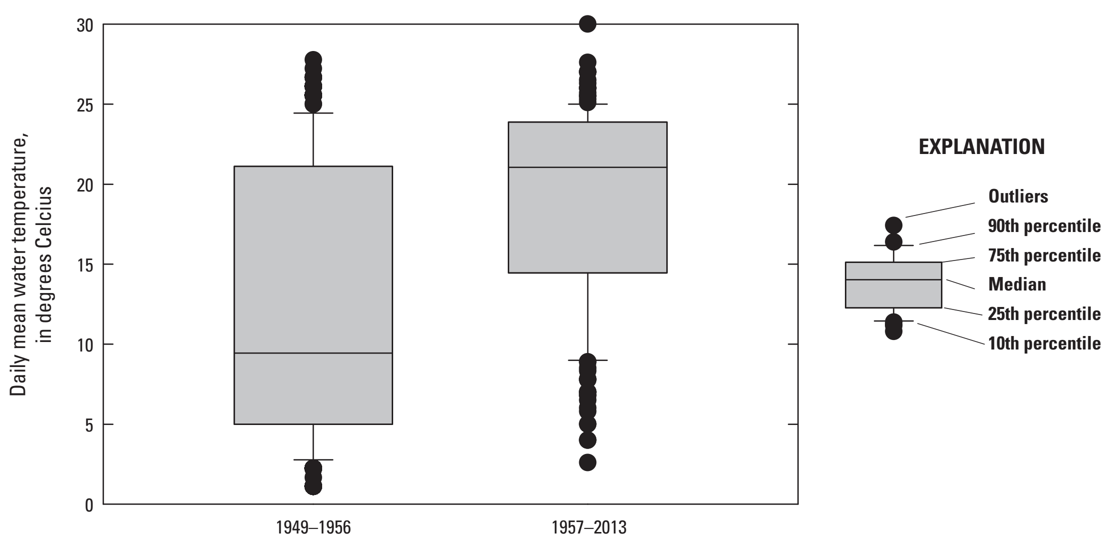


Figure 59. Boxplots of instantaneous water temperature measurements at Yankton, South Dakota, 1949–56 and 1967–2013.

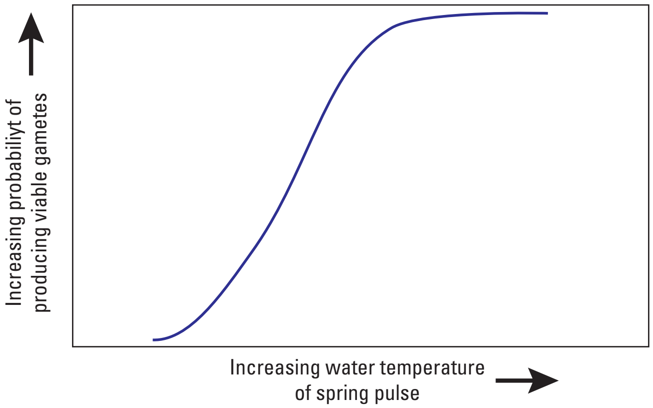


Figure 60. Hypothetical relation between water temperature of spring pulses and probability of producing viable gametes.

Uncertainty Assessment

Quantitative data and models to support this hypothesis are lacking. Published studies specifically linking temperature increases as a spawning cue to aggregation and an ultimate increase in viable embryos do not exist; therefore, we judge uncertainty to be high.

Potential Interactions with Authorized Purposes

Increasing temperature of water released from Gavins Point Dam (fig. 2*B*) would not likely be linked to system regulation or many of the authorized purposes because it would not directly affect management of flows from other storage reservoirs in the system. Downstream target flows, storage capacity, and anticipated runoff would play a minor role in the effects of increased water temperature from Gavins Point Dam.

Working Management Hypothesis in Adaptive Management Context

High uncertainty assigned to this hypothesis indicates considerable risk of failure if implemented with currently existing information. Implementation of temperature regime changes in an AM framework would require robust monitoring and assessment of effects on pallid sturgeon behavioral responses and recruitment, as well as effects on authorized purposes. Because of interactions with flow components (exclusive of temperature), unregulated tributary flows, spawning habitat quality and quantity, and numbers of reproductive fish that could be affected, adaptively managed flow and temperature experiments would have high logistical requirements.

Working Management Hypothesis 16—Channel Reconfiguration to Increase Quality and Availability of Spawning Habitat

Hypothesis 16 asserts that spawning habitats can be improved through reconfiguration of the channel to achieve a combination of conditions that would be more attractive to reproductive pallid sturgeon, hydraulic conditions that are favorable for egg deposition and fertilization, and a hydraulic and sediment-transport regime that allow for successful incubation and hatch.

Spatial Context and Interactions

The general spatial context for this hypothesis is the Lower Missouri River downstream from Gavins Point Dam (fig. 2*B*). Spawning habitat would be best developed where it would be met by migrating reproductive pallid sturgeon at or near the upstream apex of their reproductive migrations. DeLonay, Chojnacki, Jacobson, Albers, and others (2016) documented widely dispersed spawning locations (fig 28), and it is not clear if any of these locations are preferred or functional spawning habitats. Based on documented upstream migrations of reproductive adults and downstream dispersal of free embryos, it is clear that spawning sites should be upstream from areas occupied by later life stages; but it is not clear if any of the documented locations would produce greater chances of hatch and survival. Maps of natural gravel and bedrock deposits may indicate where historical spawning took place before channelization (Laustrup and others, 2007), but because predevelopment spawning cannot be verified, this remains speculative.

Reconfiguration locations and designs for spawning would interact with flow and temperature management for spawning cues, productivity, and drift distance (hypotheses 11–15). Locations would also interact with locations for channel reconfigurations intended to provide interception, food, and foraging habitats (hypotheses 17–19).

Lines of Evidence to Support Working Management Hypothesis

Like most sturgeon species, pallid sturgeon are thought to prefer coarse, hard substrate for spawning; coarse substrate provides stable sites for egg adhesion and may provide interstitial spaces for protection of newly hatched free embryos (Laustrup and others, 2007; DeLonay, Chojnacki, Jacobson, Albers, and others, 2016). Mapping of documented spawning locations on the Lower Missouri River (fig. 2) indicate selection of deep, turbulent, fast water on the outside of bends, typically over bank revetment or bedrock. The focused velocities in these areas, steep banks underlain by angular revetment, and abrupt transition at the base of the bank to actively transporting sand have prompted concern that the selected locations may not have hydraulic or sediment-transport conditions conducive to fertilization, hatch, and incubation (DeLonay, Chojnacki, Jacobson, Albers, and others, 2016).

Hydraulic conditions measured at spawning habitats in the Lower Yellowstone River near Fairview, Mont., are thought to provide a characterization of more natural spawning habitat (appendix 1). Geomorphically, these sites are broad troughs or flat areas within a multibranched reach and bounded by alluvial banks. These areas lack the degree of flow convergence associated with spawning on the Lower Missouri River. They are also characterized by patches of gravel substrate scattered among sand dunes, a condition that creates complex hydraulics and velocity distributions. Acoustic imagery has shown sturgeon aggregating in these gravel patches downstream from sand dunes, perhaps engaged in spawning behaviors. Repeat bathymetric surveys indicate that these patches are subject to transporting sand, which would presumably create a substantial risk of burial and mortality of fertilized embryos but perhaps less risk than in the Lower Missouri River. Although detailed hydroacoustic mapping, sediment sampling, and acoustic imagery at Yellowstone and Lower Missouri River sites provide quantitative assessments at the patch scale, they do not resolve potentially fatal processes operating at the embryo scale.

Applicable Models

The CEMs document spawning habitat hypotheses as several related pathways (Jacobson, Parsley, and others, 2015). Flow regime, channel configuration, and hydraulics are linked to aggregation and spawning site selection for adults and subsequent production of viable embryos. The same physical factors are additionally linked with sediment transport to determine potential for sedimentation or scour and subsequent survival of embryos.

Computational 2D hydraulic models of spawning habitat are based on the criteria developed by Jacobson, Johnson, and Deitrich (2009). These criteria select unit discharges (discharge per unit width) greater than the mean plus 1.5 standard deviations as a measure of convergent flow in spawning locations. The locations and shapes produced by this criterion are broadly consistent with observed spawning locations on the Lower Missouri River (fig. 2). Hydrodynamic models confirm that these conditions exist on nearly every outside bend and in some cross overs at some discharges, making them ubiquitous along the river. This result is consistent with the corollary hypothesis that the present channelized river has too much attractive but low-quality habitat; and, as a result, reproductive fish fail to aggregate sufficiently for mates to find one another.

Consideration of new information from the Yellowstone River shows that more natural spawning patches have similar velocities but shallower depths than the Lower Missouri River. The new datasets were collected in summer 2014 and have not yet been analyzed sufficiently to define new spawning criteria. For now, the flow convergence criteria are being used to compare spawning habitat availability between the Miami, Mo., and Little Sioux, Iowa, channelized sites and the best-available Lisbon-Jameson, Mo., reach. Although the channel reconfigurations at the Lisbon-Jameson, Mo., reach were not designed specifically to improve spawning habitat, the comparison provides a measure of how sensitive spawning habitats may be to general channel reconfigurations (fig. 35). The Little Sioux, Iowa, reach has relatively little spawning habitat available until water goes overbank near three times median flow; because these patches identified at this discharge would not have coarse, hard substrate, it is unlikely they would be suitable spawning habitats. The Miami, Mo., reach has almost twice the spawning habitat availability compared to the Lisbon-Jameson, Mo., reach at discharges less than median but decreases as water deepens and is distributed more broadly across the channel. The Lisbon-Jameson, Mo., reach spawning habitat increases from median to 2.5 times median flow indicative of channel complexity that allows spawning to persist and increase in a wider range of flows.

Analysis of spawning habitat availability at Miami and Lisbon-Jameson, Mo., reaches by flow scenario indicates that spawning habitat is relatively insensitive to channel reconfiguration at the range of discharges likely to be met in May–August (fig. 61); for example, 14 of the 66 possible unique pairwise comparisons had medians that were not significantly different (Wilcoxon rank sum test, $p<0.001$).

Increased quality of spawning habitat may be connected to population models in two ways. The attraction and aggregation of reproductive fish in suitable spawning habitats would be captured in a submodel relating survival ($S1$) to numbers or spatial density of fish, as shown in equation 14. This is envisioned as a sigmoidal function of fish density (fig. 62). The relation between quality of spawning habitat and survival ($S1$) is also expected to have a sigmoidal shape, although we expect it could have a steep slope because of attainment of a threshold of hydraulic or sediment sorting (fig. 63).

Uncertainty Assessment

Two sources of uncertainty are dominant in this hypothesis. The first is that we lack a biologically validated definition of what conditions support functional spawning habitat. Without improved understanding of how adults, gametes, and embryos function in the sequence from egg release through hatch, the definition of spawning habitat remains problematic. Building on that uncertainty, the second source is lack of a well-defined model of channel reconfiguration that specifically addresses that spawning habitat definition. Available information and models provide some limited direction about sensitivities of presumed spawning habitat to flow and channel reconfiguration, and the modeling framework provides structure for addressing future information needs. This information, however, is not sufficient to forecast effects of channel reconfigurations in producing such habitat or for influencing population dynamics. The primary uncertainty in measuring spawning habitat can be addressed through coordinated field and laboratory studies, but field validation of millimeter-scale processes at spawning sites is inherently challenging and likely to take years to develop.

Potential Interactions with Authorized Purposes

Assuming that design criteria could be developed for improving functional spawning habitat, and based on present information that indicates spawning habitat is likely to be in or adjacent to the thalweg, there is potential for spawning habitat to interact with the navigation channel. Depths currently used by spawning pallid sturgeon on the edge of the navigation channel are below the 3 m minimum depth needed

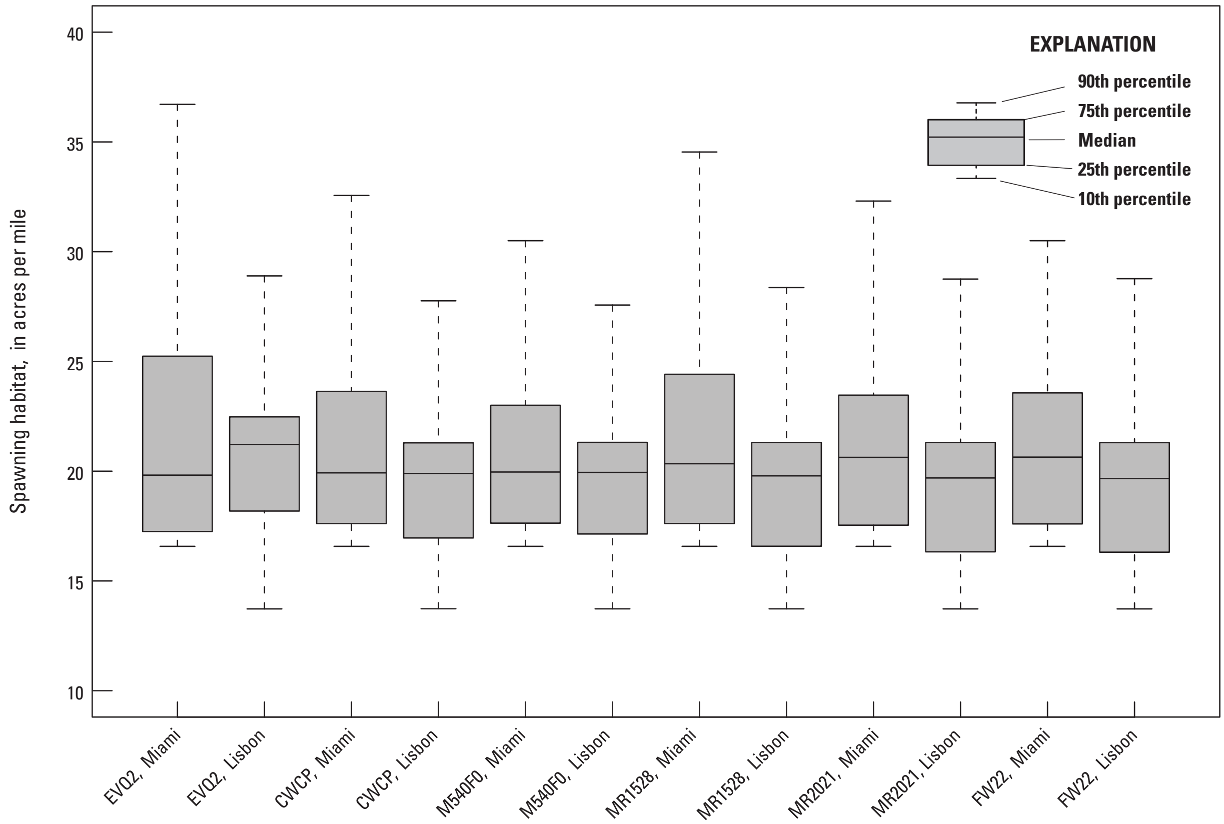


Figure 61. Boxplots showing distributions of spawning habitats, comparing the downstream Miami channelized and Lisbon-Jameson best-available hydrodynamic model reaches by flow scenario.

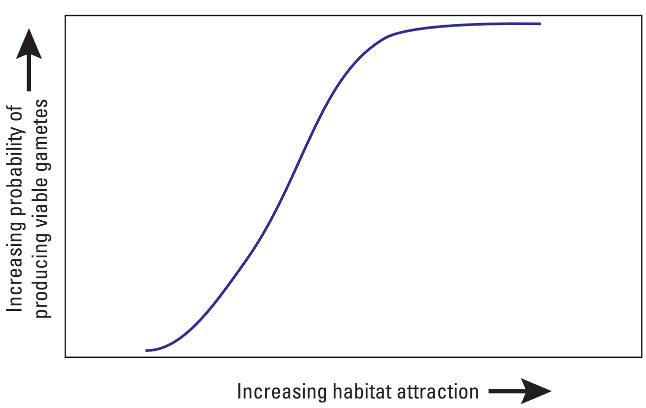


Figure 62. Hypothetical relation between attraction of spawning habitat and probability of producing viable gametes.

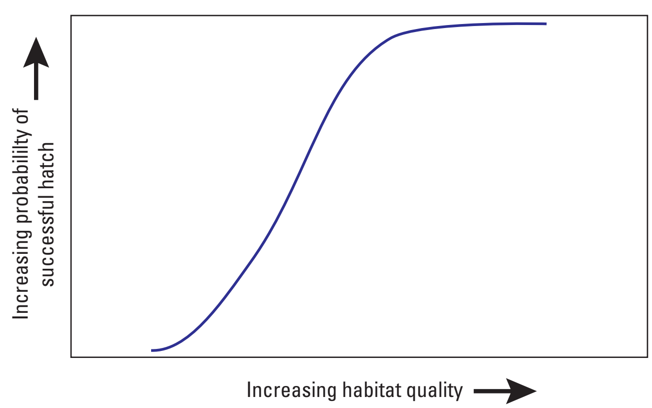


Figure 63. Hypothetical relation between quality of spawning habitat and probability of successful hatch.

for navigation, but construction and maintenance of features to provide more hydraulically suitable habitat could interact with sediment transport in complex ways. Changes in channel configuration, in turn, could possibly require higher flow releases to maintain navigation depths and, thereby, affect system regulation.

Working Management Hypothesis in Adaptive Management Context

The substantial uncertainty associated with this management action indicates that implementation would involve risk of failure as well as risk of negative interactions with authorized purposes. The fundamental uncertainties about what defines functional spawning habitat are being addressed in current research and field studies. It is possible that an additional 2–3 years of research progress will allow for implementation of well-designed field experiments.

Working Management Hypothesis 17—Channel Reconfiguration to Increase Food-Producing Habitats

Hypothesis 17 asserts that reconfiguration of the channel to create more food-producing habitats will allow for greater growth and survival of pallid sturgeon exogenously feeding larvae to age-1. The hypothesis is based on the assumptions that food is a limiting resource and that food-producing habitats can be adequately modeled with existing data and understanding.

Spatial Context and Interactions

The geographic context for this hypothesis is the Lower Missouri River downstream from Gavins Point Dam (fig. 2*B*). Because free embryos drift and disperse for considerable distance, it is logical that food-producing habitat would be more important downstream from spawning locations.

When free embryos exhaust the food resources in their yolk sac, they must immediately find food or they will starve. This event has been called the “critical period” (Gisbert and Doroshov, 2003) or the point of no return. The food must be of sufficient size (small enough to ingest) and nutritional content to allow the first-feeding larvae to grow and develop so they can survive through the first winter and recruit to the population. The locations of food-producing habitats are critical—at the end of the drifting period, wherever the free embryo is located, food must be available to it. One possibility is that the thalweg and microenvironments (areas in the boundary layer, on the lee side of sand dunes) may provide food and suitable energetic conditions. Another possibility is that the thalweg lacks food, is energetically unsuitable for growth (or both), in which case hydraulic conditions must be amenable to transporting or allowing the free embryo to exit the thalweg (interception habitats, hypothesis 19) and move into channel-marginal habitats with the combination of food-producing habitats and hydraulic conditions conducive to effective foraging (foraging habitats, hypotheses 18). Spawning habitat location, drift distance, interception habitat, food-producing habitat, and foraging habitat are all interrelated, and any could be limiting to recruitment. For convenience, interception, food-producing, and foraging habitat may be thought of as a complex of habitats for rearing of age-0 pallid sturgeon. All hydraulically defined functional processes are also related to flow regime, as the combination of flow and channel form determines hydraulic conditions.

Lines of Evidence to Support Working Management Hypothesis

Evidence from other sturgeon species and developmental theory supports the idea that food availability can be critical and may be limiting at the transition from free embryo to exogenously feeding larvae (Doroshov, 1985; Gisbert and Doroshov, 2003). Diet studies on pallid sturgeon document that first foods are generally Chironomidae or Ephemeroptera (Chipps and others, 2008; Andvik and others, 2010; Spindler and others, 2012; French, Graeb, Bertrand, and others, 2013; Harrison and others, 2014). These food items are abundant in depositional habitats of the Missouri River (fig. 2) (Poulton and others, 2003; Poulton, 2010; Poulton and Allert, 2012; Harrison and others, 2014), but they are probably not abundant in the thalweg where the sand substrate is mobile or coarser substrate is not amenable to burrowing (Modde and Schmulbach, 1977).

Gape or mouth size, among other factors, influence the type of prey on which a fish can forage (Bremigan and Stein, 1994). To determine if the prey indicated for older juvenile pallid sturgeon may be also used by the youngest larval fish, gape size of laboratory reared exogenously feeding larvae were measured in conjunction with ongoing USGS developmental research (Aaron DeLonay, U.S. Geological Survey, written commun.). Previous laboratory feeding studies suggest most pallid sturgeon reared at 18 °C begin feeding at around 14 dph and may exhibit symptoms of starvation beginning at 23 dph (James Candrl, U.S. Geological Survey, unpub. data). Mean measurements of the mouths of 14 and 23 dph larva were 1.73 and 1.93 mm, respectfully, with gape ranges from 1.58 to 2.04 mm. Definitive sizes for Chironomidae, Trichoptera, and Ephemeroptera species within the Missouri River are not available; however, the size of mesh in sampling gear was used to estimate the size of these potential prey species based on the premise that the mesh size indicates the desire to capture the smallest individuals present. Sample collection for a Chironomidae study used mesh of between 0.2 and 0.4 mm (Ferrington, 1984), and sample collection for a Trichoptera and Ephemeroptera study required meshes of 0.1–1.0 mm (MacFarlane and Waters, 1982), both of which are substantially smaller than the measured gape size of first-feeding pallid sturgeon larvae. It is notable that larvae of this age have also been observed cannibalizing each other, indicating that gape can be enlarged under some circumstances. These data and observations strongly suggest that gape size is not limited, and even the smallest pallid sturgeon larva could feed upon these prey species if the habitat is suitable to produce the insects and for larval foraging. Additional detailed studies are needed to verify these findings.

It is not clear, however, that lack of food or nutritional value of food is limiting to growth and survival of age-0 pallid sturgeon. Research is currently underway under the auspices of the USACE Habitat Assessment and Monitoring Program (HAMP) on stomach and lipid contents of age-0 *Scaphirhynchus* spp. caught in channel-marginal habitats in the Lower Missouri River (Todd Gemeinhardt, U.S. Army Corps of Engineers, written commun.). The results of this study may not be available for several years but should provide essential context for this hypothesis. In addition, the continued growth, recruitment, and survival of shovelnose sturgeon, which are thought to share dietary requirements with pallid sturgeon at this life stage, argue against food as a limiting factor.

Applicable Models

The CEMs indicate a hypothetical pathway from flow regime and channel configuration to hydraulics and substrate, to habitat suitability and food availability (Jacobson, Parsley, and others, 2015). Food availability in the CEMs is linked with moderate importance to survival for free embryos and exogenously feeding larvae, but this hypothesis was raised in importance in later hypothesis filtering process (Jacobson and others, 2016).

Existing hydrodynamic models were modified for the EA to assess availability of food-producing habitats in the Lower Missouri River (fig. 2*B*). The models use the criteria discussed earlier of velocities <0.08 m/s as being indicative of stable, depositional substrate amenable to burrowing Chironomidae. For the purposes of assessing effectiveness of channel reconfigurations, we compare food-producing habitats by flow scenarios at the channelized Miami, Mo., and Little Sioux, Iowa, hydrodynamic reaches and the best-available habitat at Lisbon-Jameson, Mo., and Hamburg Bends reaches, Iowa, reaches (fig. 37). Food-producing habitat is sparse in the upstream channelized site (Little Sioux, Iowa, reach) but increases substantially from 1.8 times median discharge to about 2.5 times median discharge when flow overtops the banks. At the Miami, Mo., reach, food-producing area is initially small when flows are less than about 0.7 times median discharge. As discharge increases above 0.7 times median discharge, water accesses complex areas downstream and bankward of wing dikes where slow velocities are dominant. The Miami, Mo., reach continues to provide about 30 acres/mi of food-producing habitat to about 2.5 times median discharge and then increases substantially as flows overtop the banks. Food-producing habitats at the Lisbon-Jameson, Mo., reach are substantially higher at low relative discharge because of large areas in backwater in overflow channels in the flood plain. The Lisbon-Jameson, Mo., reach produces about 40 acres/mi of food-producing habitat to about 3 times median discharge, at which point habitat increases rapidly with widespread overbank flooding (not shown in fig. 37). Food producing habitat at the Hamburg, Iowa, best-available reach has a notable increase in availability at about 1.7 times median discharge, peaks at about 225 acres/mi at 2.3 times median discharge, and decreases to about 90 acres/mi at 2.8 times median discharge. The rapid increase and peak in food-producing habitat availability is due to flood plain connectivity at relatively frequent flows. The discharge functions serve to illustrate that reconfigured channels with low impediments to flood plain connection have substantial potential to increase food production for components of the Lower Missouri River ecosystem and perhaps to contribute to age-0 pallid sturgeon growth.

We calculated temporal distributions of food-producing habitat by driving the discharge-food habitat relation with flow-regime time series. The comparison between Miami and Lisbon-Jameson, Mo., reaches (fig. 64*A*) shows that during May–August, food-producing habitats are substantially more available at the Lisbon-Jameson, Mo., reach compared to the Miami, Mo., reach. Differences between channelized to best-available sites are all statistically significant (Wilcox sign sum, $p<0.001$). Differences among flow scenarios for given channel reconfigurations are substantially smaller, although only five pairwise comparisons are not significantly different from one another (Wilcoxon rank sum, $p<.001$). Comparisons for the upper section at Little Sioux and Hamburg, Iowa, reaches show that the best-available channel configuration has substantially greater variability for all flow scenarios. The medians of CWCP and M540F0 scenarios for the Hamburg, Iowa, reach are actually lower than the corresponding medians for the Little Sioux, Iowa reach, but the more naturalized flow regimes all have substantially higher medians (fig. 64*B*).

Linking physical indicators of food-producing habitat availability to growth and survival will require resolution of the general question of whether or not food is limiting to growth. If food is limiting, then we would expect that increased food production would increase growth and, therefore, survival to age-1, with the rate of survival approaching an asymptote as food becomes more available (fig. 65).

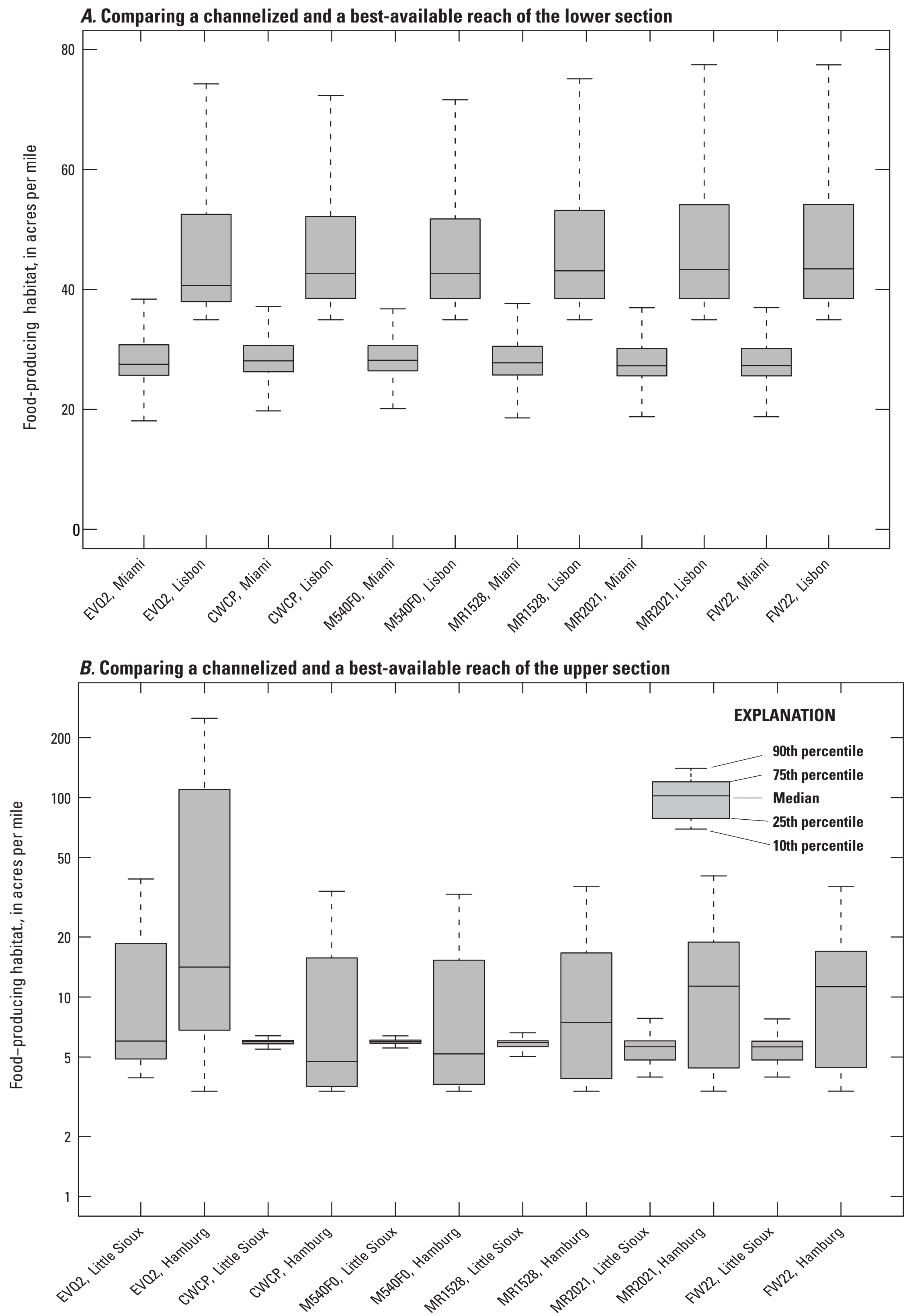


Figure 64. Boxplots of distributions of food-producing habitat area for *A*, the Miami channelized and Lisbon-Jameson best-available hydrodynamic model reaches and *B*, the Little Sioux channelized and Hamburg best-available hydrodynamic model reaches.

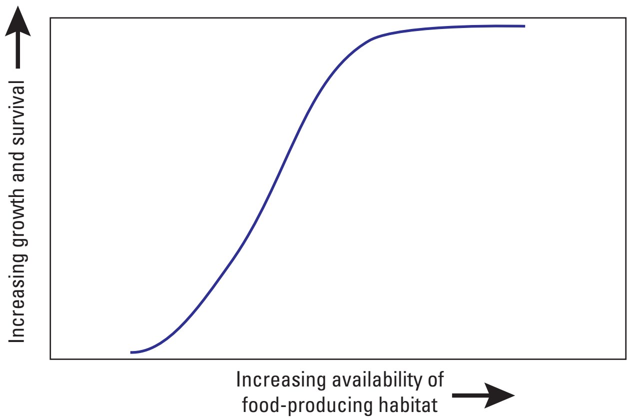


Figure 65. Hypothetical relation between availability of food-producing habitat and growth and survival of age-0 pallid sturgeon.

Uncertainty Assessment

The greatest uncertainty in this hypothesis is the question of whether or not age-0 pallid sturgeon are actually food limited. If it is determined that they are food limited, the next question is what sort of food is required and can its availability be modeled by habitat indicators? It is also possible that a habitat that is not limiting at one point in time could become limiting as other limitations are removed. The uncertainties associated with flow scenario models and hydraulic models are substantially less than these fundamental biological uncertainties. Both sources of uncertainty can be addressed through focused laboratory and field research, including continuation of the existing studies on age-0 diet and nutrition. If these studies confirm food limitation, field studies on habitat controls on food items would be warranted.

Potential Interactions with Authorized Purposes

Channel reconfigurations to increase food-producing habitats require creating channel-marginal habitats that can be inundated frequently during the growing season and with low velocities. Channel reconfigurations have the potential to alter velocity distributions and sediment transport, which could affect bank erosion, flooding, and navigation depths. In general, these channel reconfigurations would be expected to increase flow conveyance and decrease flood risk. Changes in channel configuration could possibly require changes in flow releases to maintain navigation depths and thereby affect system regulation.

Areas of slow current velocity already exist in many areas in the Lower Missouri River (fig. 2*B*) associated with river-training structures, so increased food-producing habitats and the navigation channel may be compatible. Channel reconfigurations also have the potential to trigger changes in flow releases if necessary to support navigation or mitigate flooding.

Working Management Hypothesis in Adaptive Management Context

To a large extent, expansion of food-producing habitat has already been implemented on the Lower Missouri River (fig. 2*B*) because some part of the channel reconfigurations associated with SWH construction undoubtedly fits the interim definition being used here. A more refined inventory process for SWH could be used to evaluate how much would qualify as potential food-producing habitat and where it is located. Existing SWH construction has been within acceptable risk tolerance, although criticism has noted that the biological relevance to pallid sturgeon populations has not been demonstrated (National Research Council, 2011). Continued implementation of SWH is, therefore, likely also to entail acceptable risk and may be justified if research, monitoring, and assessment are coordinated to test specific hypotheses based on improved and biologically defensible definitions of types of SWH. The present research on diets and nutritional value would be critical to this effort; and if studies support the hypothesis that food availability is indeed limiting, specific field experiments could be designed to accompany channel reconfigurations designed to increase food-producing habitats. Such experiments could also be designed to address interception and foraging habitat designs within IRCs and optimal locations along the river.

Working Management Hypothesis 18—Channel Reconfiguration to Increase Availability and Quality of Foraging Habitat

Hypothesis 18 asserts that foraging habitat—habitat needed by age-0 pallid sturgeon to forage for drifting food items—is limiting, and removing that limitation would increase growth and survival. The hypothesis hinges on a defensible definition of foraging habitat and the strength of information indicating it is limiting to growth and survival.

Spatial Context and Interactions

The geographic context for this hypothesis is the Lower Missouri River downstream from Gavins Point Dam (fig. 2*B*). Because free embryos drift and disperse for considerable distance, it is logical that foraging habitat would grow in importance downstream from spawning locations. For successful transition to exogenously feeding larvae, free embryos must have access to food and have bioenergetically favorable conditions for foraging for that food. The hypothetical function of foraging habitats is, therefore, closely linked to quality and location of interception (hypothesis 19) and food-producing (hypothesis 17) habitats, as well as to flow regimes that may alter hydraulics and energetic requirements (hypothesis 13). Spawning habitat location, drift distance, interception habitat, food-producing habitat, and foraging habitat are all interrelated and any could be limiting to recruitment. All hydraulically defined functional processes are also related to flow regime, as the combination of flow and channel form determines hydraulic conditions.

Lines of Evidence to Support Working Management Hypothesis

If they are to grow, first-feeding larvae need to find sufficient food in sufficient amounts that the caloric value of the food outpaces energy expenditures associated with acquiring the food. Conceptually, food items usually found in age-0 pallid sturgeon are produced in stable, depositional environments that support burrowing invertebrates but which are unsuitable for a rheophilic benthic fish. A logical foraging strategy would be for age-0 pallid sturgeon to position themselves on the slope of depositional bars, between the bank and the thalweg, where the current brings drifting food items to them but velocities are not so great that they require undue energy to hold position. Such a strategy could also make use of boundary-layer hydraulics associated with sand dunes or ripples that create local energy refugia.

This conceptual idea of foraging has not been verified with field observations or data at the fine scale that would be needed to infer hydraulic controls on foraging. Sample collections of age-0 *Scaphirhynchus* spp., however, provide some support as they indicate selection of (0.5–0.7 m/s) velocity and depth of about 1–3 m (Ridenour and others, 2011). Similar to food-producing habitat, however, there is no compelling evidence to support the hypothesis that foraging habitat is limiting, beyond lack of age-0 CPUE in the narrow Big Sioux and Platte River (fig. 2*A*) segments (appendix 2). Ongoing field studies under the auspices of the HAMP are targeting specific areas where age-0 *Scaphirhynchus* spp. seem to be most abundant (Todd Gemeinhardt, U.S. Army Corps of Engineers, written commun.), and these studies may prove to refine understanding of age-0 habitat associations.

Applicable Models

The CEMs indicate a pathway with high importance and moderate uncertainty from physical habitat, and associated water quality conditions, to habitat suitability for exogenously feeding larvae; growth and condition then link to survival to age-1 (Jacobson, Parsley, and others, 2015). Physical habitats are linked back to channel reconfiguration and flow regime.

Accepting the interim definition of foraging habitat as 0.5–0.7 m/s and 1–3 m depth, comparisons of foraging habitat availability among the Little Sioux, Iowa; Hamburg, Iowa; Miami, Mo.,; and Lisbon-Jameson, Mo., hydrodynamic modeling reaches provide some indication of the role of channel reconfiguration and flow regime in altering distributions of foraging habitat. The functional relation between foraging habitat availability and discharge is very similar for both channelized reaches, being maximum at the lowest discharges (20–30 acres/mi) and decreasing to near zero as flows overtop bars and wingdikes. Availability begins to increase modestly at the Little Sioux, Iowa, reach above about 2 times median discharge as some areas of low-lying lands adjacent to the flood plain are inundated. Availability in the Hamburg, Iowa, reach is similar to the channelized reaches as much as about 2.2 times median discharge and then increases rapidly with discharge as flows go overbank. Availability in the best-available Lisbon-Jameson, Mo., reach is substantially greater than the channelized reaches at discharges between the 75th and 25th percent flow exceedance because areas that fit the foraging definition exist in the Lisbon and Jameson chutes and along large sandbars. Availability continues to decrease in overbank flows at Lisbon-Jameson, Mo., reach (not shown, off chart, fig. 38) because low velocities in the extensive overbank area do not fit foraging velocity criteria.

We calculated temporal distributions of foraging habitat by driving the discharge-foraging habitat relation (fig. 38) with flow-regime time series. The comparison between Miami and Lisbon-Jameson, Mo., reaches (fig. 66*A*) shows that during May–August, foraging habitats are substantially more available at the Lisbon-Jameson, Mo., reach compared to the Miami, Mo., reach. Differences from channelized to best-available reaches are all statistically significant (Wilcox sign sum, p<0.001). Differences among flow scenarios for similar channel reconfigurations are smaller. At the Miami, Mo., reach, foraging habitat increases significantly from the EVQ2 natural flow regime to the managed flow regime, and the median is highest with the environmental MR2021 and USFW22 scenarios, which incorporate summer low flows. In contrast, the highest median values for foraging habitat at the Lisbon-Jameson, Mo., reach happened with the CWCP and M540F0, the flow regimes that are managed most for authorized purposes and which lack summer low flows, indicating the potential for beneficial interactions between channel reconfiguration and flow regimes that support Missouri River (fig. 2) authorized purposes. Six pairwise comparisons are not significantly different from one another (Wilcoxon rank sum, p<.001). Similarly, the upper section the Hamburg, Iowa, reach has about 4 times the foraging habitat as the Little Sioux, Iowa, reach and substantially more variability (fig. 66*B*). Among the flow scenarios EVQ2, MR1528, MR2021, and FW22 have significantly greater medians compared to CWCP and M540F0 (Wilcoxon rank sum, p<.001).

The predictive capability of these models is diminished to the extent that it is unknown if foraging habitat is actually limiting to growth and survival of age-0 pallid sturgeon. If it is a limiting factor, we would expect an increase in foraging habitat to be associated with higher survival rates because fish would be in more favorable conditions to forage and grow. The increase in survival would rise to an asymptote defined by conditions when foraging habitat is no longer limiting (fig. 67).

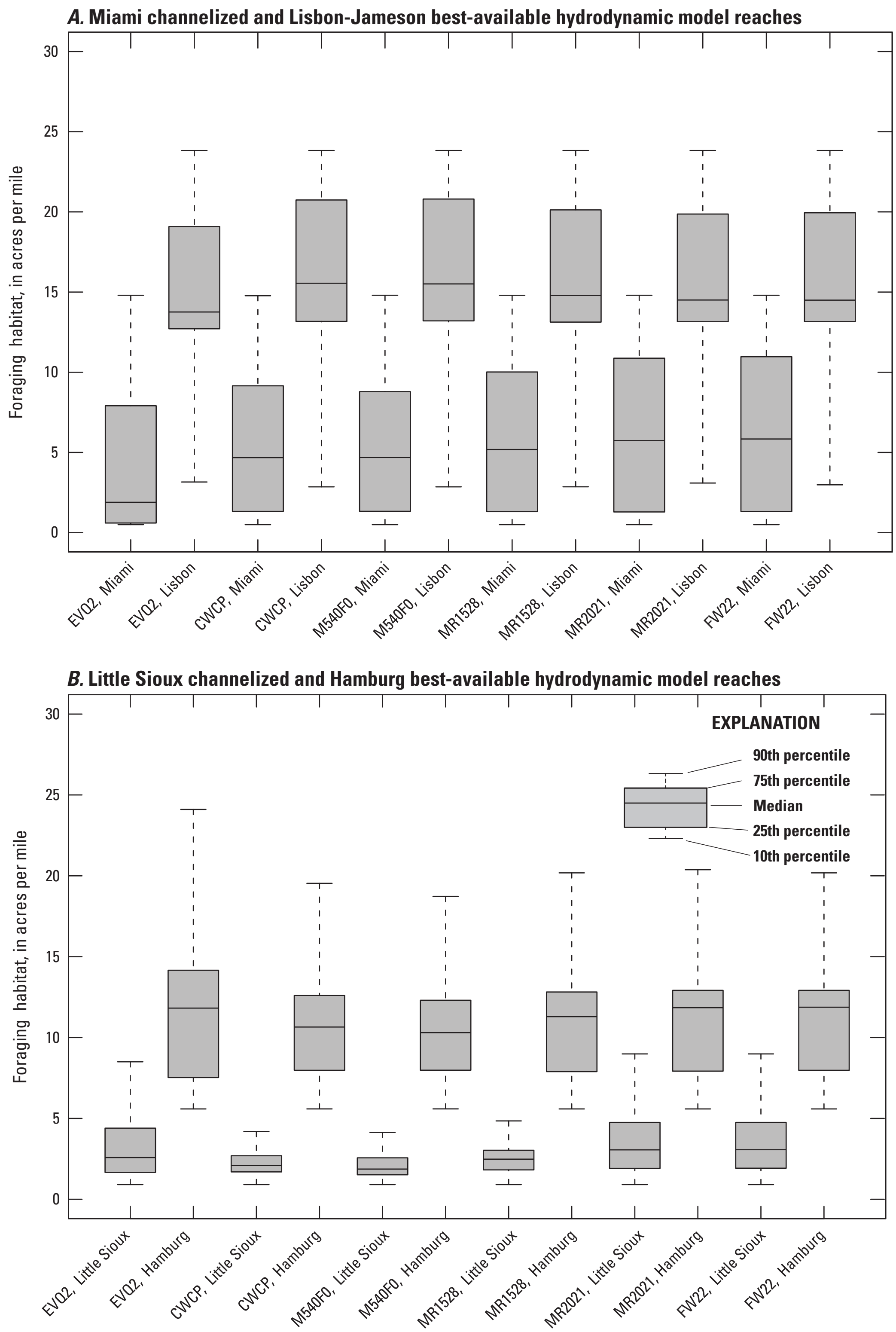


Figure 66. Boxplots of distributions of foraging habitat area by flow-regime scenarios for *A*, the Miami channelized and Lisbon-Jameson best-available hydrodynamic model reaches and *B*, the Little Sioux channelized and Hamburg best-available hydrodynamic model reaches.

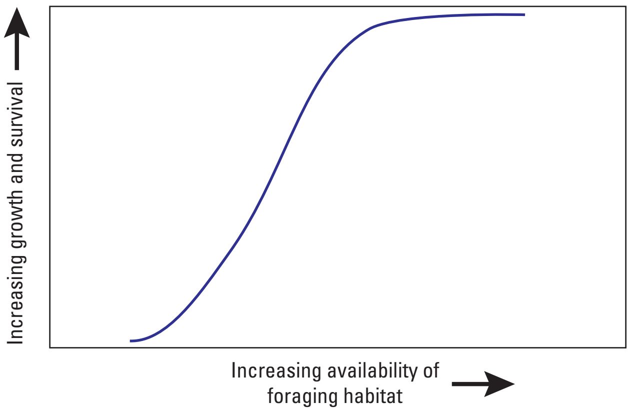


Figure 67. Hypothetical relation between availability of foraging habitat and growth and survival of age-0 pallid sturgeon.

Uncertainty Assessment

The greatest uncertainty in this hypothesis is the question of whether or not age-0 pallid sturgeon are actually limited by foraging habitat availability. If so, the next greatest uncertainty is if we have correctly defined and quantified habitats. The uncertainties associated with flow-scenario models and hydraulic models are substantially less than these fundamental biological uncertainties. These sources of uncertainty are extremely difficult to assess because of the difficulty in understanding foraging processes, growth, and survival under field conditions—and the need to disentangle possible limitations of foraging habitat from limitations related to food-producing and interception habitats. Associations between foraging habitat availability and CPUE may provide supporting evidence for the hypothesis but are unlikely to produce a causal understanding without detailed, laboratory-based studies to establish habitat preferences, bioenergetic optima, or both.

Potential Interactions with Authorized Purposes

If the interim definition of foraging habitat is correct, increases would entail channel reconfigurations that would increase top width and provide additional sloping area adjacent to the navigation channel, or other bathymetric complexity that would provide similar hydraulic conditions. These reconfigurations would affect velocity distributions and sediment transport in ways that might interact with the navigation channel or local flood stages; in general, however, these channel reconfigurations would be expected to increase flow conveyance and decrease flood risk. Changes in channel configuration could possibly require changes in flow releases to maintain navigation depths and thereby affect system regulation.

Working Management Hypothesis in Adaptive Management Context

To a large extent, expansion of foraging habitat has already been implemented on the Lower Missouri River (fig. 2*B*) because some part of the channel reconfigurations associated with SWH construction undoubtedly fits the interim definition being used here. A more refined inventory process for SWH could be used to evaluate how much would qualify as potential foraging habitat and where it exists along the river. Existing SWH construction has been within acceptable risk tolerance, with the previously noted caveat that the biological relevance to pallid sturgeon populations has not been demonstrated (National Research Council, 2011). Continued implementation of SWH is, therefore, likely also to entail acceptable risk and may be justified if research, monitoring, and assessment are coordinated to test specific hypotheses. Hypothesis-driven monitoring of CPUE of age-0 pallid sturgeon would improve associations between habitat conditions and occupancy and, if pursued in a randomized design, could be used to establish habitat selection. Imparting causality to selection, however, would require laboratory-based bioenergetic and habitat preference studies that might be challenging and expensive if designed to replicate field conditions. An alternative investment might be replicate field-based experiments. Such experiments could also be designed to address interception and foraging habitat designs and locations.

Working Management Hypothesis 19—Reconfiguration of the Navigation Channel for Interception of Free Embryos

Hypothesis 19 asserts that specific hydraulic conditions are needed to help pallid sturgeon free embryos exit the highly engineered, highly efficient navigation channel to find food and energetically supportive foraging habitats when they have used up their yolk sac and must transition to first feeding.

Spatial Context and Interactions

The geographic context for this hypothesis is the Lower Missouri River downstream from Gavins Point Dam (fig. 2*B*). Because free embryos drift and disperse for a considerable distance, it is logical that interception habitat would grow in importance downstream from spawning locations. The interception habitat hypothesis is inextricably linked to flow regime effects on drift dynamics (hypothesis 14), food-producing habitats (hypothesis 17), and foraging habitats (hypothesis 18). The validity of those three hypotheses is based on the assumption that free embryos cannot transition to exogenously feeding larvae and thrive while in the thalweg. If that assumption is valid, then interception habitats need to be at the proper distance downstream from hatch and adjacent to supportive food-producing and foraging habitats.

Lines of Evidence to Support Working Management Hypothesis

The hypothesis that interception habitats may be limiting to pallid sturgeon recruitment is based on the understanding that fish must successfully negotiate the critical transition to first feeding or they will starve, and the rationale that the hydraulic efficiency of the heavily altered navigation channel of the Lower Missouri River (fig. 2*B*) may be such that drifting free embryos have limited opportunity to exit the thalweg once entrained. Some empirical evidence exists to support the hypothesis. As presented in appendix 2, if persistent sandbars are used as an indicator of where hydraulic conditions support transport of material from the thalweg to channel-marginal positions, the strong statistical relation between channel morphology variables and sandbar occurrence presents a model for where free embryos should accumulate along the river. On the other hand, CPUE distribution data for age-0 (<109 mm) *Scaphirhynchus* spp. are poorly predicted by the same geomorphic variables and fail to correlate with persistent sandbars. The lack of correlation may be explained by a more complex model in which locations of age-0 pallid sturgeon are preconditioned by their upstream spawning location and characteristic drift distance, as determined by prevailing velocities, hydraulic interactions, and development rate. This model would explain age-0 interception and retention locations as the joint occurrence of drifting free embryos at the right stage of development plus physical hydraulic characteristics that serve to intercept them. Much of the river with interception-supporting hydraulic characteristics may not intercept and retain drifting sturgeon because they were already intercepted upstream or because free embryos had not yet developed to the stage where they can survive in retention habitats. It is also possible that CPUE of age-0 pallid sturgeon using conventional methods is not sufficiently precise to understand factors determining their distribution.

The lines of evidence to support this hypothesis and provide some insight into the nature of the interception process are relatively weak because the hypothesis has only recently emerged. The logic, based on the hydraulic efficiency of the channel, is compelling but there is no empirical information to indicate that interception habitat is limiting to pallid sturgeon populations. We cannot rule out the idea that hydraulic complexity in the channel is sufficient everywhere to promote some exchange of free embryos between the thalweg and channel-marginal habitats.

Applicable Models

The CEMs capture the concept of interception habitat on the Lower Missouri River (fig. 2*B*) as a combination of flow regime and channel morphology, that result in hydraulic habitat conditions that are not conducive to retention, resulting in starvation in the thalweg. The statistical models presented in appendix 2 attempt to provide a spatial prediction based on channel morphology variables, and relative success in explaining persistent sandbars as an indicator would suggest some value to this model. On the other hand, the model works poorly in explaining age-0 *Scaphirhynchus* spp. CPUE, which may be explained by the biological complexity of spawning location and drift distance, interacting with channel morphology, or by poor performance of the CPUE dataset in application to this question.

The advection/dispersion drift models being developed as part of the EA promise to serve as a framework for understanding the potential locations for interception for a given spawning location and development rate. The interaction of advection/dispersion results with the spatial data indicating potential for interception may eventually be a powerful tool for explaining the spatial distribution of age-0 pallid sturgeon and also for understanding the hydraulic conditions that lead to interception and retention. Assessments of age-0 pallid sturgeon distributions relative to hydraulic conditions may also provide design criteria for enhancing interception. The value of enhanced interception would depend on the existence of supporting food-producing and foraging habitat in complexes where food would be transported to foraging locations.

The lack of robust understanding of what defines interception habitat produces considerable uncertainty into any models forecasting effectiveness in pallid sturgeon population dynamics. If the concepts developed to date are valid, the relation between interception habitat and survival would be sigmoidal, but with a steep slope indicating that once a threshold of exchange was reached, survival would increase rapidly (fig. 68).

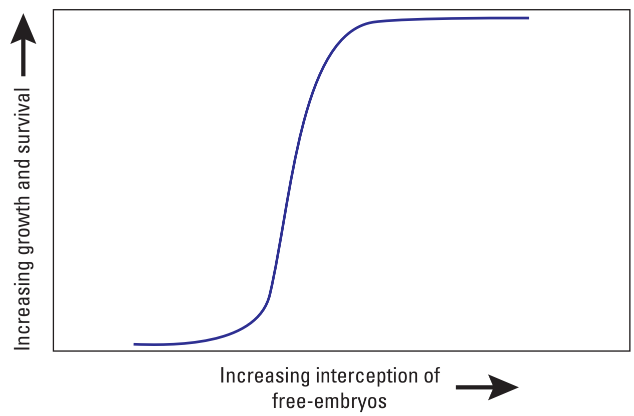


Figure 68. Hypothetical relation between degree of interception and growth and survival of age-0 pallid sturgeon.

Uncertainty Assessment

Uncertainties in the definition of interception habitat and whether or not it may be limiting to pallid sturgeon populations dominate the assessment. Although the logic for interception habitat limitation is compelling, uncertainty will remain high until field data support the concept. The uncertainties may be decreased through additional collection and analysis of CPUE data from the PSPAP, hypothesis-driven monitoring under HAMP, field-based tracer experiments, and (or) hydraulic particle-tracing model experiments.

Potential Interactions with Authorized Purposes

If interception habitat is validated as a significant limitation on pallid sturgeon recruitment, and if analysis provides design guidelines for channel reconfigurations that would enhance interception in locations that would support age-0 growth and survival, the associated management actions could interact with various authorized purposes. Because interception potential is likely related to channel width and width variability, channel reconfigurations would likely be similar to some ongoing SWH construction, involving increased channel top width and potentially varied dike lengths. These designs could affect local velocity fields and sediment transport, which could propagate to interactions with the navigation channel and flood stages; in general, however, these channel reconfigurations would be expected to increase flow conveyance and decrease flood risk. Changes in channel configuration, in turn, could possibly require changes in flow releases to maintain navigation depths and thereby affect system regulation.

Working Management Hypothesis in Adaptive Management Context

To some extent, changes in interception habitat may have been already implemented on the Lower Missouri River (fig. 2*B*) as a result of SWH construction. The degree to which this is true is unknown because definition of interception habitats have not been in place to guide inventory efforts. A more refined inventory process for SWH could be used to evaluate if SWH efforts have likely had an effect on interception and where. Existing SWH construction has been generally within acceptable risk tolerance, with the previously noted caveat that the biological relevance to pallid sturgeon populations has not been demonstrated (National Research Council, 2011); but because interception habitat is a relatively new concept and poorly defined, implementation would be considered risky at this point. Continued hypothesis-driven monitoring of CPUE of age-0 would be valuable in helping establish associations between interception potential and occupancy. Field-based experiments, including tracers and computational modeling, in existing channel configurations could provide substantial information about interception processes. Such experiments could also be designed to address interception and foraging habitat designs and locations.

Working Management Hypothesis 20—Improved Stocking Strategies by Optimizing Stocked Size Classes

Hypothesis 20 asserts that stocking hatchery-origin fish at an ideal size will increase survival during the critical first years of life (age-0 to age-1) and eventually result in a greater number of reproductive pallid sturgeon adults in the future. This will allow the stocked pallid sturgeon to obtain an ideal condition factor and a more stable life stage in a controlled hatchery setting before experiencing the stresses of the Lower Missouri River (fig. 2*B*). The USFWS and states share authority and responsibility for stocking decisions through the pallid sturgeon recovery team and workgroups; therefore, the MRRP implementation of management actions to address this hypothesis would require coordination with those groups.

Spatial Context and Interactions

This hypothesis includes the Missouri River from Gavins Point Dam downstream to the confluence with the Mississippi River, accessible parts of major tributaries, and an unknown distance down the Mississippi River (fig. 2). This hypothesis interacts with all other hypotheses that relate to habitat suitability because habitats are necessary to support the stocked fish. Altered flows, water temperatures, and channel configurations may all contribute to growth and survival of stocked fish.

Lines of Evidence to Support Working Management Hypothesis

The lines of evidence to support the stocking size hypothesis in the Lower Missouri River are identical to those for the Upper Missouri River (fig. 2*B*). Absolute size distributions may vary between the upper river and the lower river, but the hypothesis similarly asserts that larger, older fish have higher survival than smaller, younger fish and that optimization of the tradeoffs with producing older fish may help increase survival and population growth.

Applicable Models

The applicable conceptual models for the Lower Missouri River are identical to the Upper Missouri and Yellowstone Rivers (fig. 2*B*), although the data behind the models would be different. Similar to the upper river, quantitative models do not exist to forecast survival of different size classes or optimize risks and benefits of alternative rearing investments. Notwithstanding these uncertainties, the assumed functional relation between size and survival is asymptotic but with a fairly gentle rate of increase (fig. 69).

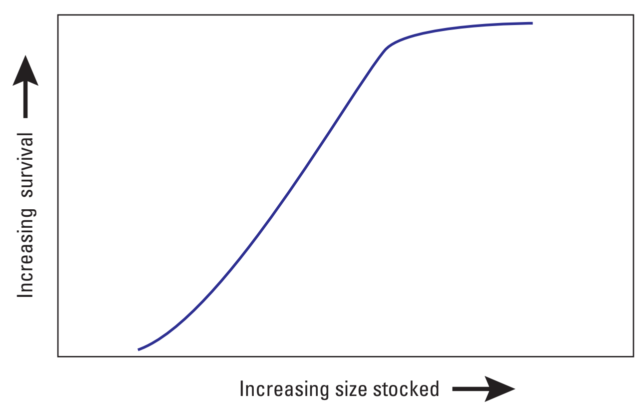


Figure 69. Hypothetical relation between size at stocking and survival.

Uncertainty Assessment

Uncertainties for this hypothesis are thought to be relatively low when considering size and survival. Extending models to the optimization of rearing techniques to achieve desired size classes includes substantially more uncertainty. Uncertainties are identical to those of the upper river with perhaps some variation related to present hatchery capacities.

Potential Interactions with Authorized Purposes

This hypothesis does not presumably interact with authorized purposes. Because augmentation stocking is currently ongoing, it is unlikely that current river-generated activities and authorized purposes will not be affected by the proposed hypothesis.

Working Management Hypothesis in Adaptive Management Context

Because supplemental stocking is already being implemented, changes in current hatchery protocols that increase stocking size and limit hatchery stressors would allow implementation of this hypothesis with minimal risk. Empirical data from records of pallid sturgeon stocking could provide an initial strategy to optimize stocking size. Additional factors that may contribute to overall pallid sturgeon fitness and survival including broodstock contaminant levels and genetics could also be investigated (Buckler, 2011; Saltzgiver and others, 2012; Jacobson, Parsley, and others, 2015). Continued monitoring of stocking survival through field sampling and hatchery evaluation will be needed to ensure adequate assessment of this hypothesis.

Working Management Hypothesis 21—Improved Stocking Strategies by Optimizing Genetic Diversity

Hypothesis 21 asserts that selection of genetically diverse broodstock in population augmentation can increase population viability of pallid sturgeon (that is, the ability of the population to sustain itself demographically) (Hallerman, 2003). Managing for genetic variation that approximates that of the natural population will result in greater fitness of the lower river population as a whole. The USFWS and states share authority and responsibility for stocking decisions through the pallid sturgeon recovery team and workgroups; therefore, the MRRP implementation of management actions to address this hypothesis would require coordination with those groups.

Spatial Context and Interactions

This hypothesis includes the Missouri River from Gavins Point Dam downstream to the confluence with the Mississippi River, accessible parts of major tributaries, and an unknown distance down the Mississippi River (fig. 2). This hypothesis interacts with all other hypotheses that relate to habitat suitability because habitats are necessary to support the stocked fish. Altered flows, water temperatures, and channel configurations may all contribute to growth and survival of stocked fish; moreover, optimal management of genetic parentage interacts with optimal size distributions for stocking (hypothesis 20).

Lines of Evidence to Support Working Management Hypothesis

The lines of evidence to support optimization of genetic parentage are very similar to those of the upper river (hypothesis 9), but the genetics issues are blurred somewhat by the incomplete understanding of the natural, underlying genetic structure of the pallid sturgeon population and if the structure coincides with the MUs as drawn (U.S. Fish and Wildlife Service, 2014). Heist and others (2013) suggest a loss of offspring fitness if stocking does not happen in the location the broodstock originated. This would suggest that only progeny from broodstock collected in the Central Lowlands and Interior Highlands MUs, which includes the scope of this hypothesis, should be stocked in the Lower Missouri River (fig. 2*B*). Unfortunately, low numbers of broodstock exist in the Lower Missouri River, historically (U.S. Fish and Wildlife Service, 2008).

In conservation stocking when populations are small, strategies to limit inbreeding and domestication are also a concern. Inbreeding not only limits fitness of offspring (reproductive impairments, reduced survival and growth, and physical abnormalities) but limits genetic diversity (Heist and others, 2013). Optimization of genetic selection for families to avoid inbreeding, outbreeding, and domestication may benefit genetic variation and stocking survival.

Applicable Models

The CEMs for the Lower Missouri River (fig. 2) are identical to the upper river. More quantitative models to explore results of parentage strategies have not been developed for pallid sturgeon in the Missouri River like they have for white sturgeon (Jager and others, 2001). Such models might provide insights into risks and benefits associated with alternative genetics management strategies.

Uncertainty Assessment

Uncertainties for this hypothesis are thought to be relatively low because present population augmentation plans follow best-management practices and limit stocking to local fish (by MU) that are presumably adapted to local river conditions; presently available genetic tools identify parentage sufficiently to support the family crossing decisions. Continued optimization of current hatchery protocols regarding genetic sampling and genetic information used to select for families that will enhance population viability may be achieved with limited perceived risk. If, however, proposals were made to stock large numbers of fish among MUs, there would be considerable uncertainty about the long-term effect.

Potential Interactions with Authorized Purposes

This hypothesis does not presumably interacted with authorized purposes. As augmentation stocking is currently ongoing, it is thought that current river-generated activities and authorized purposes will not be affected by the proposed hypothesis.

Working Management Hypothesis in Adaptive Management Context

Population modeling results indicate that stocking will be needed to contribute to recovery of the pallid sturgeon population in the Missouri River (figs. 17–22), and ongoing assessment of survival of stocked fish will increase knowledge of the role of genetic parentage in fitness. The advancement of genetic techniques and their use in stocking optimization may act to limit problems associated with conservation breeding programs (inbreeding, outbreeding and domestication). Practices such as the cryopreservation of milt and increased family crosses would help to ensure increased genetic diversity and limit the effects of inbreeding (Heist and others, 2013; U.S. Fish and Wildlife Service, 2014).

Discussion

This EA report is intended to integrate the development of CEMs, information status, and working management hypotheses generated in the previous EA reports and apply that understanding to assessment of efficacy of management actions in achieving fundamental species objectives for the pallid sturgeon in the Missouri River (fig. 2). The report addresses 21 working management hypotheses that emerged from the conceptual models and expert-driven hypothesis filtering (Jacobson, Parsley, and others, 2015; Jacobson and others, 2016). A final step used by the USACE and USFWS filtered out management actions that were not within agency authorities to arrive at a set of initially modeled hypotheses.

The concept of modeling is used very broadly here because it includes conceptual, statistical, simulation/forecasting, and expert-opinion models. This is necessitated by the heterogeneous set of emergent hypotheses—which cover a broad range of actions, abiotic processes, and biotic processes—and potential population responses. The quality and quantity of scientific information available to address these hypotheses is highly varied, so different levels of analysis and uncertainty have been applied to the lines of evidence for each hypothesis. The objective of this section is to discuss and emphasize some important aspects of the Missouri River related to pallid sturgeon population dynamics.

Pallid Sturgeon in the Geographic Context of the Missouri River

The pallid sturgeon life cycle is based on long upstream reproductive migrations and long downstream dispersal, a reproductive strategy that results in different life-stage transitions taking place in different locations in the river. The evolutionary strategy for long migrations is unclear and subject to some debate in the literature, but it is believed that reproductive migrations were often tied to distinct landscape characteristics that provided essential habitats, such as specific upstream spawning location with substrate and hydraulic characteristics, and specific downstream habitats that produced food and provide for successful foraging (Kynard and others, 2002, 2007). Emerging information on genetic structuring in the pallid sturgeon population (Schrey and others, 2006, 2011; Elchelberger and others, 2014) suggests that subpopulations may have existed with their life cycles tied to different locations on the landscape, although we lack the historical information that would validate this idea.

Whether one or multiple subpopulations existed, fragmentation of the Mississippi-Missouri River system has certainly affected how pallid sturgeon use the river. It is possible that fragmentation by dams is the major factor affecting populations, and management actions in nondammed segments will always be inadequate to recover the species. The critical information to evaluate this is documentation of how the existing pallid sturgeon population uses the river provided to them, and whether or not successful completion of their life cycles can be documented on the existing landscape.

Fragmentation is also an important concept for understanding and modeling present-day population processes, in particular, what group of fish or part of the river can be considered a breeding subpopulation (or members of a genetic neighborhood). In the upper river, the fish in the Upper Missouri and Yellowstone Rivers (fig. 2) (bounded by Fort Peck Dam, Lake Sakakawea, and an undetermined length of the lower Yellowstone River), can probably be considered an isolated, breeding subpopulation for population-modeling purposes, as we have treated them in this report. We also treated the lower river, bounded by Gavins Point Dam and undetermined lengths of some tributaries and the Mississippi River, as one subpopulation; however, this assumption is at odds with the official definition of MUs, which divides the lower river between the Central Lowlands and Interior Highlands MUs (fig. 2). Although ecoregional units (U.S. Fish and Wildlife Service, 2014) or distinct landscape characteristics like the Late Pleistocene glacial boundary and bedrock influences of the Ozarks Plateaus (Laustrup and others, 2007) may have influenced geographic distributions of pallid sturgeon subpopulations in the historical river, it is not clear how fragmentation and channelization of the present day river have altered interactions, immigrations, and emigrations. Improving this geographic understanding will be critical to improving statistical models of survival and abundance, population targets, and population dynamics models.

Upper Missouri and Yellowstone River Interactions

The effects of fragmentation are clearest in the Upper Missouri-Yellowstone River sections, where Fort Peck Dam (fig. 2) presents a distinct barrier to upstream migration, other dams provide barriers or impediments (Intake Diversion Dam, Cartersville Dam, and Vandalia Dam), and the headwaters of Lake Sakakawea presents an inhospitable environment for larval and adult pallid sturgeon. Available drift/dispersal distance emerges as a fundamental limitation on recruitment in the upper river. Under the immediate drift hypothesis and assuming mostly passive transport, calculated drift times indicate that management actions on the Upper Missouri River are generally ineffective at increasing drift distance sufficiently for free embryos to settle before reaching presumably lethal headwaters of Lake Sakakawea. Under a delayed drift hypothesis (interstitial residency), and if spawning happens close to Fort Peck Dam, combinations of low discharges and high temperatures from Fort Peck Dam, and drawdown of Lake Sakakawea, can possibly result in sufficient drift distance.

Retarded drift—hypothesized interactions between biologic and hydraulic processes that would work to slow drift substantially below passive drift rates—could also contribute to management flexibility in the Upper Missouri River.

In contrast, if reproductive pallid sturgeon are attracted to migrate up the Yellowstone River, able to bypass Intake Diversion Dam in sufficient numbers, and attracted to migrate far enough upstream to spawn (and perhaps up tributaries like the Powder River), management actions on the Upper Missouri may not be necessary. The success of each of these steps is certainly not ensured; and depending on how far upstream the fish migrate, interstitial residency, retarded drift, and drawdown of Lake Sakakawea might still be required for sufficient drift distance.

Key scientific uncertainties and the potential tradeoff between management actions on the Yellowstone and Upper Missouri Rivers suggest a decision-tree approach to decision making. The decision tree presented here (fig. 70) focuses on information needs for making decisions. The key uncertainties determining decisions are verification that Lake Sakakawea is anoxic or otherwise lethal, followed by validation that fish migrate successfully up the Yellowstone River. If reproductive adults do not migrate up the Yellowstone River, and interstitial residency or other sources of retarded drift happen to delay drift by as much as 5 days, management options are available on the Upper Missouri River. On the Missouri River side, reproductive fish need to be attracted sufficiently upstream, find supporting habitats, find mates, and spawn successfully. If spawn, fertilization, incubation, and hatch are successful, then minimizing velocities, maximizing temperature, and drawdown of Lake Sakakawea may be viable options. If fish do migrate up the Yellowstone River, the next question is whether or not they spawn sufficiently far upstream at locations that would provide adequate distance for immediate drifters. If true, then recruitment potential exists. If not, the questions of interstitial residency and retarded drift again become important to resolve to determine if drawdown of Lake Sakakawea is a useful action.

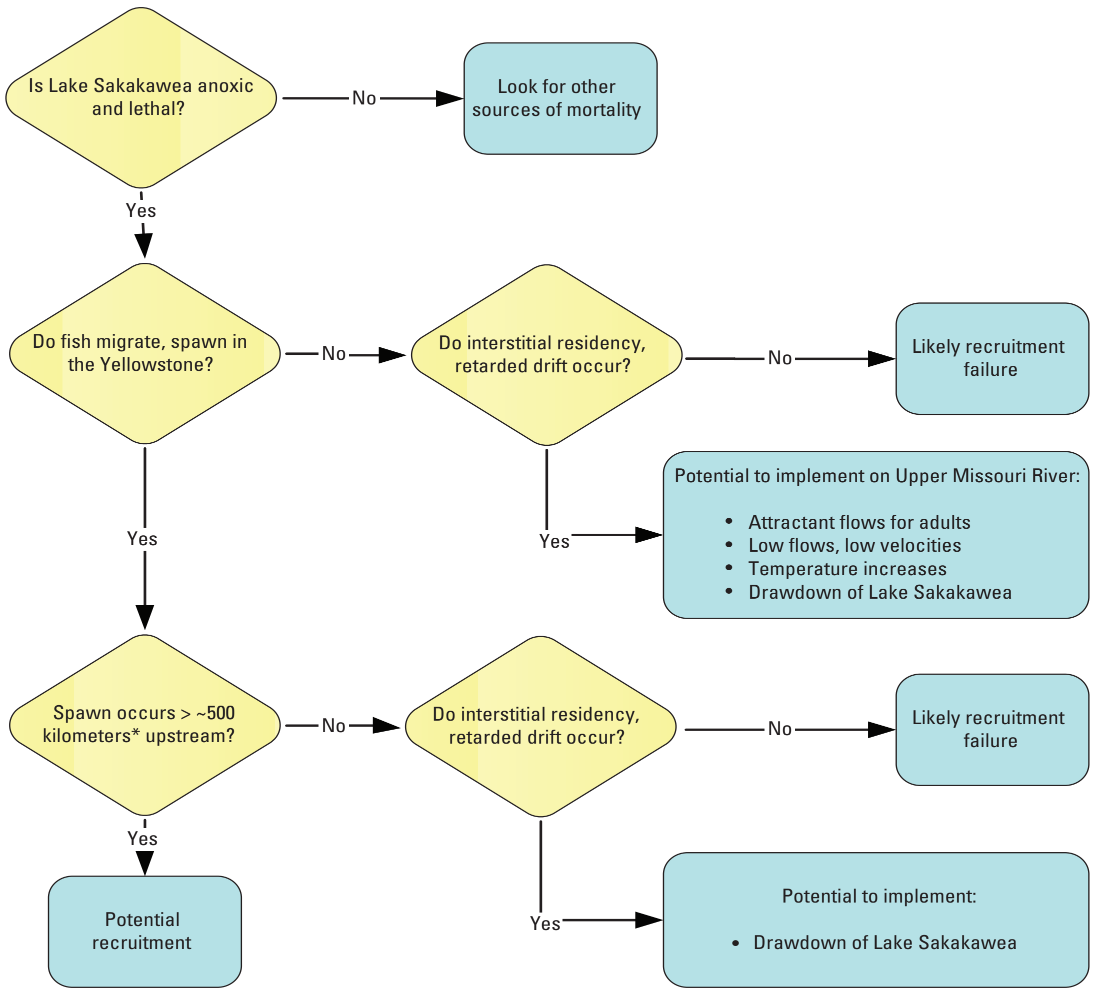
Lower Missouri River

Uncertainties also exist on the Lower Missouri River in regard to how pallid sturgeon use the 811 mi of the river, tributaries, and Mississippi River (fig. 2). These uncertainties have a bearing on decisions about flow releases and locations of channel reconfiguration projects. For flow releases, the uncertainties involve whether or not change of a given magnitude propagates to a specific location where it is hypothesized to have a specific biological response (for example, a flow pulse intended to evoke an aggregation response). For channel reconfigurations, the uncertainties involve the need to configure specific functional habitats to match the spatial pattern of upstream migration and downstream dispersal (for example, construction of food-producing habitats where free embryos are likely to settle from the drift).

The key uncertainties on the Lower Missouri River also suggest a decision-tree approach, with decisions being contingent on developing information (fig. 71). Decisions to pursue flow manipulations or channel reconfigurations to support survival of free embryos and exogenously feeding larvae would logically follow after demonstration of successful fertilization, incubation, and hatch. If not demonstrated, then flow manipulations, stocking densities, and channel reconfigurations for spawning habitat would be implementation options. The next question is if there is information on whether or not velocities and turbulence are lethal to drifting free embryos. The question of whether or not free embryos can survive turbulence is also related to the interstitial residency hypothesis because delayed drift may result in greater fitness. If hydraulic conditions are lethal, implementation options include decreasing discharges to decrease velocities and turbulence, or perhaps manipulating spawning substrates to allow greater access of free embryos to interstitial spaces. If survival of turbulence is not a limiting factor, the next logical question is if free embryos being transported in the navigation channel will starve unless they can settle into supportive, channel-margin habitats—or if instead they can transition to first feeding, find food, and grow to the point where they are mobile enough to seek habitats on their own. If persistence in the thalweg results in starvation, then actions to implement more interception habitats, in correct locations, would be indicated. For either case that free embryos can thrive in the thalweg or that they require specific interception habitats to move out of the thalweg, the exogenously feeding larvae will eventually need food; hence, the next logical question is whether food or foraging habitats are limiting in the channel-margin habitats. If so, there would be potential to increase food-producing and (or) foraging habitat quantity and quality. If not, the decision tree would indicate that another hypothesis would have to be generated to explain recruitment failure.

The directionality of the decision tree follows life stages, and addressing each life stage in sequence would be the most systematic approach to understanding recruitment failure. Useful information can be generated outside of the sequence as well; for example, using age-0 shovelnose sturgeon as a surrogate species may allow for cautious inference about food limitations of pallid sturgeon and allow for emphasis on other hypotheses.

Effectiveness of management actions on the Missouri River may also depend on exchange of fish with the Mississippi River. If early life stages disperse into the Mississippi River, management actions on the Missouri River to increase growth and survival of those life stages would be ineffective. If adult fish migrate back into the Missouri River, however, actions to improve spawning habitats may be effective in increasing reproduction rates. Understanding how much of the river the fish use during their lifetimes—the reproductive range—is, therefore, critical to many management decisions. If subpopulations exist within the Lower Missouri River, then multiple reproductive ranges may need to be defined, each with a characteristic set of spawning locations, drift distance, and rearing



* 500 kilometers distance upstream is a coarse guideline because it would provide about 9 days for drift and development under purely passive drift assumptions.

Figure 70. Decision tree for addressing contingent information in the Upper Missouri and Yellowstone Rivers.

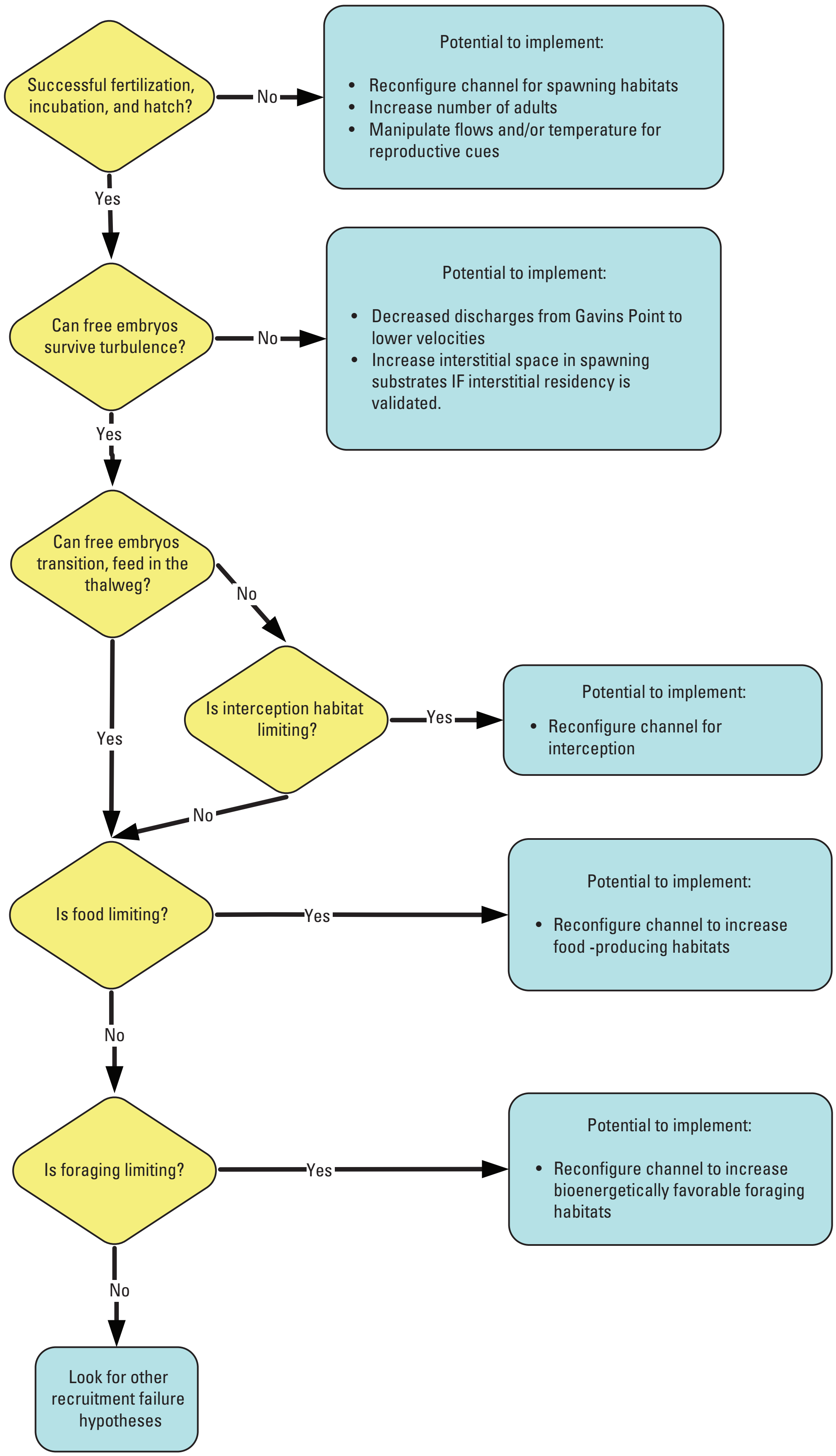


Figure 71. Decision tree for addressing contingent information in the Lower Missouri River.

locations. Continued application of telemetry tracking of adults (DeLonay, Chojnacki, Jacobson, Albers, and others, 2016) and genetic and microchemistry tracers (Todd Gemeinhardt, written commun.) have promise in helping define the reproductive ranges, and particularly the amount of exchange with the Mississippi River.

Use of Functional Habitats in Decision Making

A substantial proportion of the quantitative modeling in this report is based on functional habitat definitions. It should be emphasized that we consider the definitions to be hypothetical statements about how potentially limiting habitats can be measured. As interim definitions, they are open to revision as ecological understanding improves. It is useful to think of hypotheses as being arranged in a set such that hypotheses relating to definitions or design are nested within the working management hypothesis; for example, the interception habitat working management hypothesis asserts that channel reconfiguration can improve interception and survival of free embryos. Nested within that hypothesis are hypotheses that interception habitat can be modeled under some quantitative definition and that, knowing the definition, interception habitat can be designed and constructed on the Missouri River (fig 2). We anticipate that the AM structure for the MRRP will support continued refinement of functional habitat definitions.

Assessments of functional habitat dynamics in this report focused on the variation of habitat availability with changes to flow regime and channel reconfigurations (morphology). Results from the Hamburg Bends, Iowa, hydrodynamic modeling reach provided the additional insight that dynamics vary with geomorphic adjustments of the channel. Food-producing habitat at the Hamburg Bends, Iowa, hydrodynamic modeling reach shows a rapid increase in area at discharges equivalent to about 1.8 times the median discharge compared to a similar increase at the Lisbon-Jameson, Mo., reach at about 2.5–2.8 times the median discharge (fig. 37). The difference is attributable to location of the Hamburg Bends, Iowa, model reach in an aggrading section of the Missouri River downstream from the Platte River confluence (fig. 72). The other three modeling reaches are in areas of modest degradation or channel stability; as a result, connection of flow with low-lying lands and overbank areas happens at higher relative discharge. There are several implications of this finding. The first is the clear need to establish how representative modeled reaches are within the spatial variation of the Lower Missouri River. The four current habitat models are based on those that were available to be synthesized in the EA, and the extent to which they deviate from average conditions needs to be acknowledged in interpolation and extrapolation of results from these models. For future modeling needs, selection of representative reaches might consider the status of geomorphic adjustment as a stratifying variable.

The second implication stems from the evident sensitivity of connectivity metrics to the state of geomorphic adjustment, which is known to be an ongoing process (Fischenich and others, 2014). As channel adjustments continue and locations of degradation and aggradation continue to shift, habitat availability will shift as well, and models to project future habitat availability will need to take this into account.

Improvement of functional habitat models to forge the linkages from habitats to growth and survival will continue to be a challenge. Some additional insight will be provided by increasing accuracy and understanding of habitats occupied by age-0 and juvenile pallid sturgeon, but present understanding indicates that occupancy alone does not explain growth and survival. Rather, growth and survival likely depend on habitats occupied within the context of many other factors that may include properties of adjacent habitats, food production, energetic expenditure, water quality, and predator populations. Bioenergetics research and modeling are promising approaches to understanding these complex interactions. Useful bioenergetics models will need to address water temperature (a dominant potential management variable in the Upper Missouri River) and current velocity (a dominant potential management variable in the Lower Missouri River).

Population Augmentation Strategies

Population augmentation, or stocking, is addressed in this report in two hypotheses that have been applied to the upper and lower rivers. The first hypothesis asserts that there may be a size for stocking hatchery-origin fish that would optimize growth and survival. By extension, this hypothesis includes concerns about hatchery-related diseases because there is a tradeoff between time that fish are kept in the hatchery (to achieve greater size) and the probability that they will be exposed to disease. The second hypothesis asserts that there are approaches to selecting parentage that would optimize genetic diversity and viability of the population. These actions contribute to building the population of pallid sturgeon to achieve a sufficient number of adults with suitable genetic diversity to stave off extinction, whereas the effects of other management actions contribute to survival and recruitment. The most recent recovery criteria include genetically diverse self-sustaining populations of at least 5,000 adult pallid sturgeon per MU (U.S. Fish and Wildlife Service, 2014).

Population augmentation is recognized as necessary and beneficial for the short term (U.S. Fish and Wildlife Service, 2008). At the same time, risks have been identified with augmentation, including potential inbreeding depression, outbreeding depression, competition with congenerics or other native fishes for scarce resources, and propagation of hatchery-related diseases (U.S. Fish and Wildlife Service, 2008). These risks indicate that augmentation strategies should be pursued cautiously and should be based on robust information on the fate of stocked fish and the health of the population. Although other working management hypotheses explored in this report are amenable to focused research and experimentation, the stocking-related hypotheses will require an extensive and ongoing monitoring program to track survival, condition, and reproductive status of stocked fish.

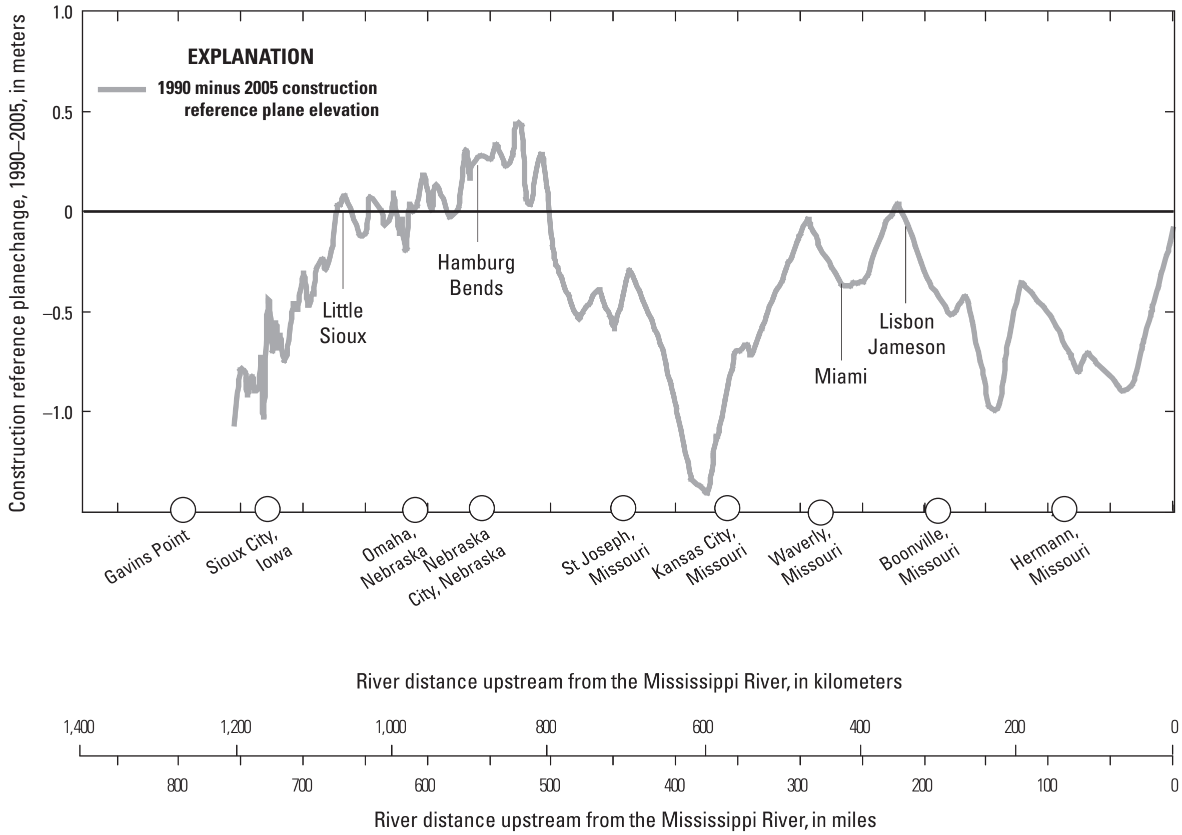


Figure 72. Longitudinal graph of channel degradation and aggradation of the Missouri River indicated by recent changes in the construction reference plane elevation (modified from Jacobson and others, 2009).

Effects Analysis and Adaptive Management

The substantial uncertainty surrounding factors that affect pallid sturgeon population dynamics does not support definitive statements about efficacy of specific management actions. Instead, this EA process has focused on documenting what is known and what is not known, and on framing how AM of the pallid sturgeon in the Missouri River (fig. 2) can be used to increase learning and reduce uncertainties about management actions.

The ideal goal of an EA modeling process is to provide a comprehensive population model similar to a population viability assessment (Murphy and Weiland, 2011). The comprehensive model would include linkages from management actions through abiotic and biotic responses, to survival probabilities for each critical life-stage transition, and it would use the resulting probabilities to forecast population responses. Fundamental gaps in understanding of pallid sturgeon biology and large uncertainties concerning demographic rates preclude development of a comprehensive population response model at this time (2016). The modeling framework presented in this report, however, consisting of the population-level model, the life-stage component models, and the supporting hydrologic, hydraulic, and habitat models, provides a foundation for future data assimilation, hypothesis generation, and model improvements.

Hypothesis Routing

Our assessments of the 21 working management hypotheses acknowledge varying levels of uncertainties, risks, and benefits by discussing “routing” of the hypotheses to several types of implementation (table 12). The sections entitled “Working Management Hypothesis in Adaptive Management Context” discuss the weight of evidence that a management action would have a beneficial effect on pallid sturgeon populations, relative to the uncertainties and attendant risk of failure. We defined three general groups of implementation options. If the benefit is clearly and quantitatively supported by data and models with low uncertainty, an action might be considered for implementation as a management action, coupled with the requisite level of monitoring and assessment to verify performance. If the benefit is supported by one or more lines of evidence, but has considerable uncertainty, an action might be considered for implementation as a field-scale, manipulative experiment in limited areas. Well-designed field experiments have potential to provide systematic, hypothesis-driven information to reduce critical uncertainties. For actions that have the highest levels of uncertainty and attendant risks, the hypothesis might be routed to directed research or field-based studies that take advantage of present-day variations in conditions on the landscape. We envision that the AM program for pallid sturgeon in the Missouri River (fig. 2) would have a mix of these three types of implementations, with an attempt to prioritize learning implementations where information is most influential to pending management actions.

Table 12. Summary table of working management hypotheses, findings, and routings

Action	Number	Working management hypothesis	Findings	Potential routing
Upper Missouri River				
Alter flow regime at Fort Peck Dam	1	Naturalized flows, food, and energetic demands	Theoretical support but inadequate data to model and forecast.	Research on bioenergetics, hydrodynamic models, comparative field experiment.
	2	Attractant flows, aggregation, and spawning cues	Theoretical support, inference from other sturgeon species, but inadequate data to model and forecast.	Research, monitor responses to events, possible pulsed flow experiment.
	3	Decreased spring flows and velocities, reduced drift	Potential effective action, subject to contingent information.	Research to resolve anoxia, use of Yellowstone, interstitial hiding, retarded drift.
Temperature control, Fort Peck Dam	4	Increased temperature, increased productivity	Theoretical support but inadequate data to model and forecast.	Research on bioenergetics, hydrodynamic models, comparative field experiment.
	5	Increased temperature, increased growth, decreased drift	Potential effective action, subject to contingent information.	Research to resolve anoxia, use of Yellowstone, interstitial hiding, retarded drfit.
Sediment augmentation, Fort Peck Dam	6	Increased turbidity, decreased predation	Theoretical support, but laboratory data equivocal; no specific models.	Research on predation egg, embryos, free embyros.
Yellowstone River				
Passage at Intake Diversion Dam	7	Increased potential drift distance	Potential effective action, subject to contingent information.	Implementation under way. Complement with robust monitoring and evaluation.
Upper Missouri and Yellowstone Rivers				
Upper basin propagation	8	Improved stocking strategy, size classes	Potential effective action, subject to hatchery capacities.	Implemented, validate with monitoring, assessment. Research on optimization.
	9	Improved stocking strategy, parentage, and fitness	Theoretical support, no specific data, models to forecast for pallids	Research on linking parentage and population viability.
Lake Sakakawea				
Drawdown, Lake Sakakawea	10	Increased potential drift distance	Potential effective action, subject to contingent information.	Research to resolve anoxia, use of Yellowstone, interstitial hiding, retarded drift.

Table 12. Summary table of working management hypotheses, findings, and routings.—Continued

Action	Number	Working management hypothesis	Findings	Potential routing
Lower Missouri River				
Alter flow regime at Gavins Point Dam	11	Naturalized flows, aggregation, and spawning cues	Theoretical support, inference from other sturgeon species, but inadequate data to model and forecast.	Research, monitor responses to events, possible pulsed flow experiment.
	12	Naturalized flows, increased productivity	Theoretical support, inference from hydrodynamic models, but data inadequate to model, forecast.	Research on bioenergetics, comparative field experiments, possible pulse flow experiment.
	13	Naturalized flows, decreased energetic demands	Theoretical support, inference from hydrodynamic models, but data inadequate to model, forecast.	Research on bioenergetics, comparative field experiments, possible pulse flow experiment.
	14	Decreased spring flows and velocities, reduced drift	Theoretical support, inference from hydrodynamic models, but data are equivocal as limiting factor	Research into drift dynamics.
Temperature management, Gavins Point Dam	15	Naturalized temperatures, increased aggregation and spawning cues	Theoretical support, inference from other sturgeon species, data equivocal about magnitude of change.	Research, monitor responses to events.
Channel reconfiguration	16	Reconfigure channel for spawning habitats	Theoretical support, supporrt from sturgeon species, hydrodynamic models, but data are equivocal as limiting factor	Research in spawning dynamics, comparative field experiment.
	17	Reconfigure channel for food production habitats	Theoretical support, inference from hydrodynamic models, but data are equivocal as limiting factor.	Implemented, comparative field experiment, validate with monitoring, assessment.
	18	Reconfigure channel for foraging habitats	Theoretical support, inference from hydrodynamic models, but data are equivocal as limiting factor.	Implemented, comparative field experiment, validate with monitoring, assessment.
	19	Reconfigure channel for interception habitats	Theoretical support, inference from hydrodynamic models, but data are equivocal as limiting factor.	Implemented (?), validate with monitoring, assessment, comparative field experiment.
Propagation lower basin	20	Improved stocking strategy, size classes	Potential effective action, subject to hatchery capacities.	Implemented, validate with monitoring, assessment. Research on optimization.
	21	Improved stocking strategy, parentage, and fitness	Theoretical support, no specific data, models to forecast for pallids	Research on linking parentage and population viability.

Effects Analysis Phases 2 and 3

Within the context of AM, this EA report can be seen as a punctuation mark in the ongoing AM narrative. The need for EA functions of data assimilation, analysis, model updates, and hypothesis generation will be enduring. We envision that the EA process will continue in some form to support the learning function of AM and serve as the conduit of new information into the decision making process.

In the next phase of the EA, team members will work with the USACE, USFWS, scientists, and stakeholders to design research, monitoring, and evaluation processes and provide continued analysis of new data to inform alternatives for the MRRMP (phase 2; fig. 73). The product envisioned for phase 2 is a robust AM plan that will provide a roadmap for addressing scientific uncertainties and learning as alternatives are implemented. As part of phase 2, the EA team will continue to refine the collaborative population model, and we anticipate a role in helping model and evaluate alternatives. This process will set the stage for implementation of whatever alternatives come out of the MRRMP (phase 3) and ongoing AM.

As documented in this report, the considerable uncertainties about how many management actions may be linked to population responses support a need for substantive science efforts directed at key information gaps. Reducing uncertainties may be achieved through directed science components during the AM process, including foundational research, field experimentation, and robust monitoring and assessment of implemented alternatives.

Summary and Conclusions

The Missouri River Pallid Sturgeon Effects Analysis was designed in collaboration with the Missouri River Recovery Management Plan to address three components of an assessment of how management may affect pallid sturgeon population dynamics: collection of reliable scientific information, critical assessment and synthesis of available data and analyses, and analysis of the effects of management actions on listed species and their habitats. This report is built on and synthesizes three precursor reports that document development of conceptual ecological models, assessment of the status of information relevant to the *Scaphirhynchus albus* (pallid sturgeon) EA, and development of a filtered set of working management hypotheses. All three components have presented challenges because of the varying quality and rapidly evolving nature of pallid sturgeon science, the wide range of expert opinion on the causes for recruitment failure, and the inherent high uncertainties in fundamental pallid sturgeon biology and demographic rates.

The hypothesis filtering process produced 21 working management hypotheses almost evenly divided between the Upper Missouri/Yellowstone Rivers and Lower Missouri River. The objective of this report has been to document lines of evidence for the 21 working management hypotheses and develop quantitative models of effects of management actions where possible. Quantitative models are the desired outcome for the Effects Analysis because of the need for quantitative forecasts in decision making. The ability to

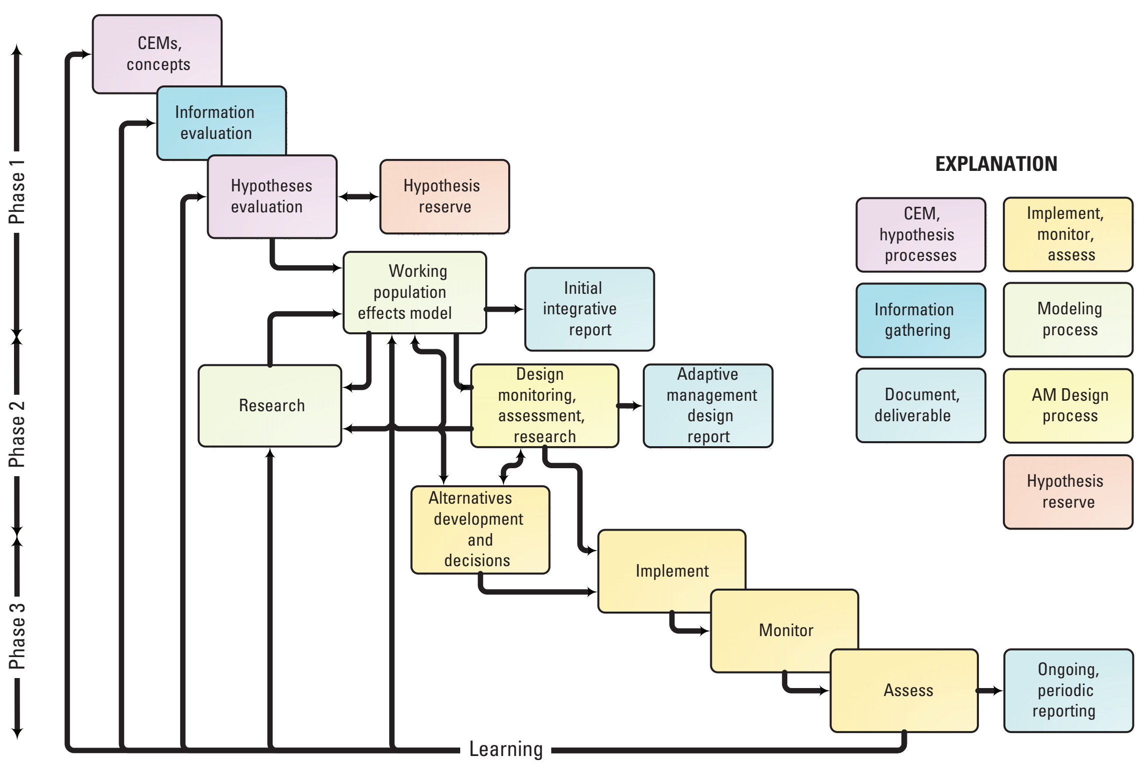


Figure 73. Phases 1, 2, and 3 sequence of tasks and timeline for the Missouri River Pallid Sturgeon Effects Analysis.

quantify the stressor-response relations in pallid sturgeon population dynamics, however, is substantially compromised by fundamental information gaps. For some of the 21 hypotheses, information is so sparse that lines of evidence are limited to theoretical deduction, inference from sparse empirical datasets, or expert opinion; nevertheless, useful models have been developed of the effects of management actions on survival of drifting free embryos in the upper river, and for assessing effects of flow and channel-reconfigurations on habitat availability in the lower river. We have also developed a population model that can be used to assess sensitivity of life stages, assess some hypotheses related to stocking decisions, and explore a limited number of management actions. The model is intended to provide a framework to guide future science priorities. Although we have been able to develop models that link management actions to abiotic changes and interim definitions of functional habitat units, available information is not sufficient to link habitat characteristics through to survival rates or other demographic variables. This report documents those challenges to guide development of future science priorities.

Sensitivity analyses completed with the population model confirmed that early life-stage survival values were the most uncertain and have the most leverage on population dynamics. Comparisons of the population model results with current average stocking rates and zero stocking confirmed the present-day dependence of population persistence on stocking; the zero-stocking model runs typically predicted negative growth rates and quasi extinction. Model runs were also used to estimate early life-stage survival rates needed to sustain a population under current average stocking rates. These numbers provide benchmarks against which to evaluate stocking and to guide refinement of survival rates.

One-dimensional advection/dispersion models have been developed through the EA process to assess drift dynamics of free embryos. The results of the models are instrumental in documenting the conditions under which flow management, temperature management, and drawdowns of Lake Sakakawea have the potential to affect survival of drifting free embryos and the distances upstream on the Yellowstone River that adults would need to migrate to have their drifting free-embryo progeny survive. Drift models on the Lower Missouri River are important for documenting the length of river traversed by drifting free embryos and indicating locations along the river where foraging and food-producing habitats for free embryos might be constructed.

Functional habitat assessments using two-dimensional hydrodynamic models provide an understanding of how availability of functional habitats varies jointly with flow regime and channel reconfigurations. Comparison of channelized and best-available channel configurations by six flow-regime scenarios demonstrate that the influence of flow regime on functional habitat availability diminishes substantially downstream from Kansas City, Missouri, where unregulated flows contribute variability to discharges, although statistical comparisons among flow regimes documented that almost all pairwise comparisons were significantly different. Among the functional habitats modeled, food-producing and foraging habitats were substantially greater in the best-available habitat model reaches (Hamburg, Iowa, and Lisbon-Jameson, Mo.). Water residence time did not vary much between upstream/downstream or channelized/best-available reaches, indicative of the overwhelming transport efficiency of the engineered river.

These analyses indicate that flow regime is effective in altering distributions of habitats in upstream reaches, channel reconfigurations are effective in altering distributions of habitats in all reaches, and the combination of the two can be especially effective in altering distributions of some habitats. The continuing challenge with functional habitat analyses is to increase the biological realism of habitat definitions so that they have demonstrable relevance to pallid sturgeon growth and survival.

Each of the 21 working management hypotheses includes a discussion of hypothesis "routing;" that is, how the degree of uncertainty and risk associated with each hypothesis may guide implementation toward full field implementation of an action, limited implementations as field-scale experiments, or (in the case of greatest uncertainty and risk) emphasis on research and opportunistic experiments or gradient studies. Analysis of relations among different management actions indicates some strong contingencies in which decisions are highly dependent on precursor information. These contingencies have been presented in the format of decision trees.

Finally, recognizing the substantial uncertainties associated with pallid sturgeon population dynamics and the need to continually assimilate and assess new information, we have proposed that the Effects Analysis process should be considered an integral part of ongoing Missouri River adaptive management. The Effects Analysis process will allow for the most effective use of the foundation of information and modeling tools that have been developed by the Effects Analysis.

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Appendix 1. Pallid Sturgeon Spawning Habitat on the Lower Missouri and Yellowstone Rivers

Spawning Habitat

Gravid female *Scaphirhynchus albus* (pallid sturgeon) have been tracked each spring during 2008–13 through migrations to probable spawning patches on the Lower Missouri River in Missouri, Kansas, Iowa, and Nebraska; and during 2012–14 on the Lower Yellowstone River on the Montana and North Dakota border (DeLonay and others, 2009, 2014; DeLonay, Chojnacki, and others, 2016). Habitats of 10 spawning patches for 10 individual female pallid sturgeon were mapped on the Lower Missouri River during 2008–13, and 3 spawning patches used by 4 females were mapped on the Yellowstone River for spawning events during 2012–14 (table 1–1). Habitat assessments used previously documented methods to map depth, velocity, and substrate (Elliott and others, 2004; Reuter and others, 2008; DeLonay and others, 2009). A multibeam echosounder was used to map depths and visualize substrates at all sites on the Lower Missouri River. Depths were mapped on the Lower Yellowstone River using an acoustic Doppler current profiler. Velocity flow fields at all sites were mapped using an acoustic Doppler current profiler. Substrate assessments on both rivers used side-scan sound and navigation ranging (sonar), and additional substrate sampling was completed on the Yellowstone River in 2014 using a bed-material sampler and an underwater microscope. Repeat longitudinal profiles (parallel to flow) were measured on the Yellowstone River in 2014 to assess the stability of the substrate and bedforms within the spawning patch and reach.

Lower Missouri River

Documentation of spawning downstream from Gavins Point Dam has not been sufficient to determine whether the distribution is patchy or continuous. Spawning has been documented as far upstream as reaches near Gavins Point Dam in 2008 (DeLonay and others, 2009, 2014; DeLonay, Chojnacki, and others, 2016). The downstream extent of documented spawning events on the Lower Missouri River is near river mile (RM) 200 (DeLonay, Chojnacki, and others, 2016). Evidence of spawning has also been documented on the Platte River, but discrete locations are not known and spawning habitat has not been mapped on the Platte River (DeLonay, Jacobson, and others, 2016).

Reaches (several kilometers in length centered on the spawning patch) mapped include a wide range of habitats within a channel bend. All 10 of the spawning patches (100s of meters in length) mapped on the Lower Missouri River are in or adjacent to the thalweg on outside bends, armored with coarse bank revetment rock. Patches were determined based on 8–50 acoustic telemetry re-locations of tagged, reproductive female pallid sturgeon. Although individual depths recorded at spawning patches have a fairly wide range (2.18–10.59 meters [m]), mean depth at spawning locations is 6.58 m (table 1–1; fig. 1–1). The mean depth-averaged velocity for Lower Missouri River spawning telemetry locations is 1.40 meters per second (m/s) (range 0.46–2.36 m/s), which is considerably faster than many adjacent environments within the spawning reaches in the Lower Missouri River (table 1–1; fig. 1–1). On the Lower Missouri River, pallid sturgeon are spawning generally in deep high-velocity patches.

The locations of egg release and deposition are known with an accuracy of no more than meters to tens of meters, yet all locations on the Lower Missouri River are adjacent to coarse substrate and moving sand dunes. Multibeam bathymetry and side-scan sonar mapping document that several of the Lower Missouri River spawning patches (near RM 202 and 216; table 1–1) contain large limestone bedrock outcrops and topographic evidence for patches of gravel deposits. Two additional sites (near RM 399 and 423) contain small bedrock exposures and gravel deposits. All Lower Missouri River sites have coarse bank revetment adjacent to them and the potential for gravel deposits to exist at the base of the revetment and margin of sand dunes in the channel. Repeat single-beam echosounder bedform measurements (Elliott and others, 2009) and multibeam dune mapping indicate that large sand dunes are moving in the channel thalweg at most discharges and would not remain static during the several days required from egg deposition to embryo hatch. Bank revetments and bedrock substrates at Missouri River spawning patches seem to be stable during periods of days to years.

Yellowstone River

On the Lower Yellowstone River, four female pallid sturgeon have been tracked using radio telemetry to probable spawning patches within one large reach between RM 7 and 5 in June of 2012, 2013, and 2014 (table 1–1; fig. 1–2). These spawning patches are associated with aggregations of 3–12 males, which typically have been present in the reach for several days to weeks before spawning. Two females spawned in the channel thalweg near RM 6.8 over a gravel patch in 2012 and 2013 (table 1–1; fig. 1–2). One female spawned in a shallower location near RM 5.9 in 2013. In 2014, a female was tracked to a confirmed spawning patch near RM 5.5.

Table 1–1. Spawning habitat summary, Missouri and Yellowstone Rivers, 2008–14.

[NTU, nephelometric turbidity unit; –, not applicable]

Pallid sturgeon	Spawning dates	River mile (reach center)	Mean water temperature, in degrees Celcius	Discharge range, in cubic feet per second	Substrate		Depth, in meters	Depth-averaged velocity, in meters per second	Turbidity range in NTUs
Missouri River									
PLS08-004	5/4/2008–5/5/2008	230	15.9	[1]84,400–98,600	Sand, dunes, revetment	Mean	6.65	1.31	
						Range	2.18–10.59	0.57–1.62	[3]210–390
PLS08-008	5/8/2008–5/9/2008	366	17.8	[2]56,900–61,800	Sand, dunes, revetment	Mean	8.09	1.49	–
						Range	2.20–9.53	0.58–1.77	–
PLS08-009	5/7/2008–5/8/2008	369	17.0	[2]54,800–56,900	Sand, dunes, revetment	Mean	6.42	1.39	–
						Range	5.00–8.11	0.97–1.88	–
PLS09-007	4/25/2009–4/26/2009	206	17.4	[3]59,400	Sand, dunes, revetment	Mean	7.66	1.33	
						Range	5.21–8.94	0.49–1.58	50–683
PLS10-006	4/31/2010–5/1/2010	202	16.6	[3]135,000	Sand, revetment, bedrock, potential gravel	Mean	8.55	1.58	–
						Range	3.65–10.27	1.25–1.80	–
PLS11-008	5/16/2011–5/19/2011	216	17.1	[1]120,000–123,000	Sand, revetment, bedrock, potential gravel	Mean	7.21	1.59	–
						Range	2.45–10.01	0.46–2.36	–
PLS11-007	3/31/2012	322	19.4	[4]62,500	Sand, revetment	Mean	6.50	1.33	–
						Range	6.17–6.93	1.27–1.38	–
PLS09-011	4/26/2012	580	16.8	[5]38,000	Sand, revetment	Mean	4.55	1.4	–
						Range	3.53–5.32	0.52–1.72	–
PLS08-035	5/10/2013–5/11/2013	423	16.1	[6]38,800	Sand, revetment, bedrock, potential gravel	Mean	5.12	1.24	–
						Range	2.21–7.95	0.69–1.39	[6]51–130
PLS13-035	5/10/2013–5/11/2013	399	16.1	[6]38,800	Sand, revetment, bedrock, potential gravel	Mean	5.07	1.32	–
						Range	2.85–6.97	0.72–1.55	[6]51–130
Mean			**17.0**				**6.58**	**1.40**	

Table 1–1. Spawning habitat summary, Missouri and Yellowstone Rivers, 2008–14.—Continued

[NTU, nephelometric turbidity unit; –, not applicable]

Pallid sturgeon	Spawning dates	River mile (reach center)	Mean water temperature, in degrees Celcius	Discharge range, in cubic feet per second	Substrate		Depth, in meters	Depth-averaged velocity, in meters per second	Turbidity range in NTUs
				Yellowstone River[7]					
Radio code 30	6/19/2012–6/20/2012	6.8	20.3	21,000–21,500	Sand, gravel	Mean	3.54	1.18	–
						Range	2.09–4.49	0.74–1.43	–
Radio code 41	6/20/2013	6.8	22.1	24,500	Sand, gravel	Mean	3.54	1.18	–
						Range	2.09–4.49	0.74–1.43	–
Radio code 40	6/25/2013–6/26/2013	5.9	22.2	18,500–23,000	Sand, gravel	Mean	2.20	0.8	–
						Range	1.75–2.81	0.70–0.89	–
Radio code 39	6/26/2014–6/27/2014	5.4	20.5	32,200–33,600	Sand, gravel, dunes	Mean	3.96	1.27	110–280[7]
						Range	1.47–5.61	1.04–1.36	–
Mean			**21.3**				**3.31**	**1.11**	

[1]Discharge measurements are from the U.S. Geological Survey streamgage 06906500 Missouri River at Glasgow, Missouri.

[2]Discharge measurements are from the U.S. Geological Survey streamgage 06893000 Missouri River at Kansas City, Missouri.

[3]Discharge and turbidity measurements are from the U.S. Geological Survey streamgage 06909000 Missouri River at Boonville, Missouri.

[4]Discharge measurements are from the U.S. Geological Survey streamgage 06895500 Missouri River at Waverly, Missouri.

[5]Discharge measurements are from the U.S. Geological Survey streamgage 06807000 Missouri River at Nebraska City, Nebraska.

[6]Discharge and turbidity measurements are from the U.S. Geological Survey streamgage 06818000 Missouri River at St. Joseph, Missouri.

[7]Discharge and turbidity measurements are from the U.S. Geological Survey streamgage 06329500 Yellowstone River at Sidney, Montana.

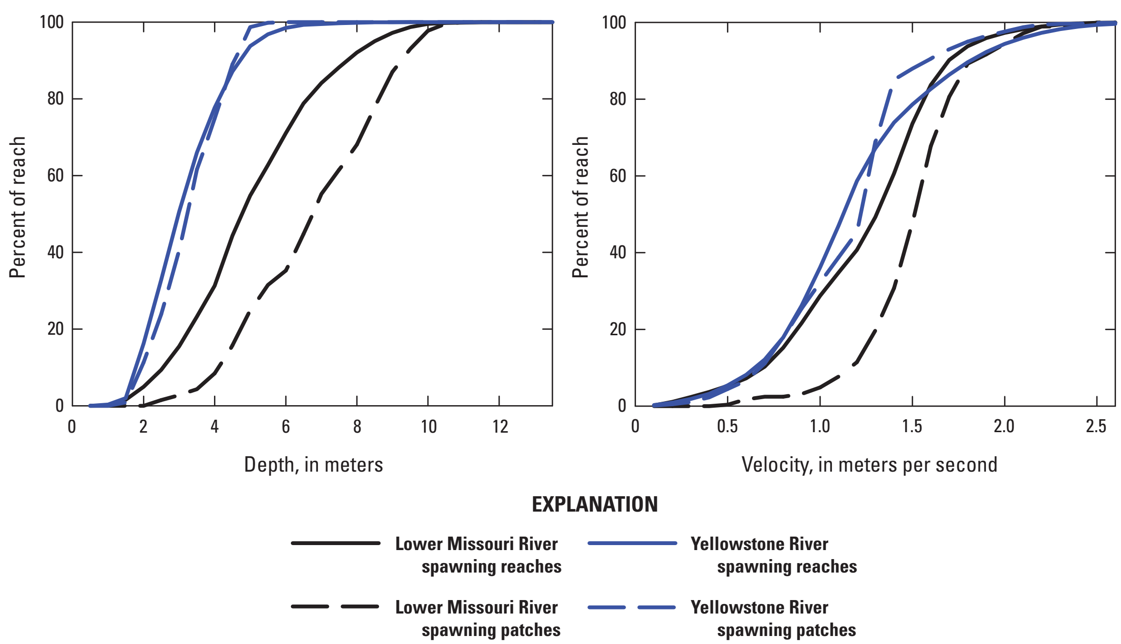
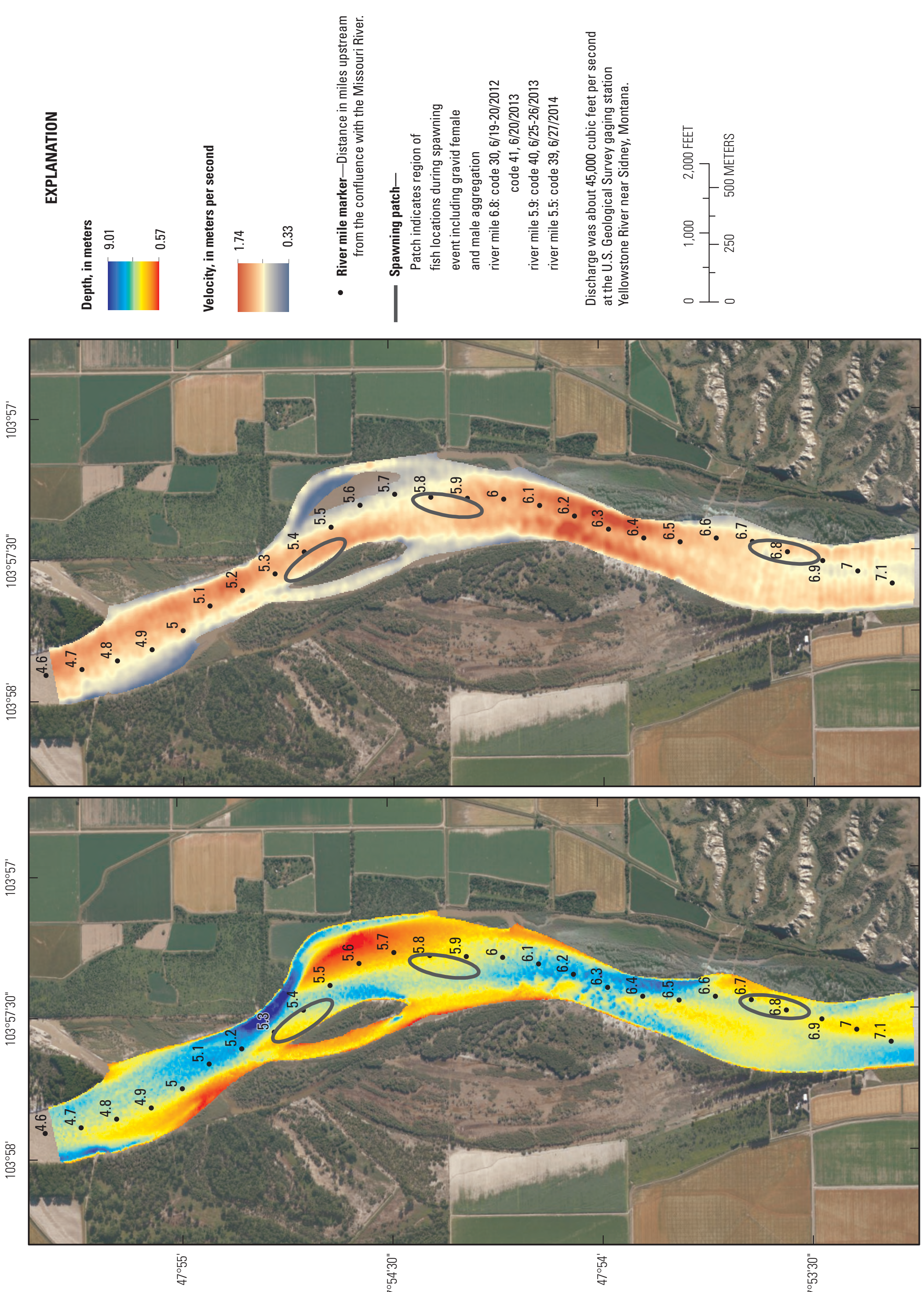


Figure 1–1. Cumulative distributions of depths and depth-averaged velocities at spawning patches within spawning reaches on the Lower Missouri and Yellowstone Rivers.



Base data from U.S. Geological Survey digital data, 1999

Figure 1–2. Yellowstone River spawning reaches and patches, river miles 4.6–7.1.

Depths at Yellowstone River spawning patches are similar to those in the adjacent reach (figs. 1–1 and 1–2). Depths are considerably lower than Missouri River spawning patches, with mean Yellowstone River patch range of 1.45–5.61 m and a mean depth of 3.31 m (table 1–1; fig. 1–1). Yellowstone River spawning patches are characterized by fairly high velocity, with a mean velocity of 1.11 m/s and range from 0.74 to 1.43 m/s (table 1–1). Repeat mapping in 2013 and 2014 indicates that these patches are not static; the depths, velocities, and substrates at specific patches in the Lower Yellowstone River are highly dynamic; and changes in the arrangement of the bed happen from year to year and within a year with changes in discharge. Substrate within the spawning reach is dominantly sand with patches of gravel. Side-scan sonar, bed-material sampling, and photographs of the bed taken with an underwater microscope show that deposits exist as irregular gravel patches (actually pebble- to cobble-sized sediments) within a field of sand dunes. The size and extent of the gravel patches are highly variable: some gravel patches within the spawning reach are tens of meters in size and others exist in very small, discrete polygons (less than 5 m in size). Repeat bed profiling in 2013 through part of an occupied spawning patch near RM 5.3 to 5.5 documented the presence and migration of about 1-m high dunes during the course of as little as 1.5 hours (fig. 1–3). Changes in dune form were characterized during a 6-day period close to the spawning date, and these data demonstrated the dynamic moving habitat present in some parts of the spawning reach (fig. 1–3).

Summary

Probable *Scaphirhynchus albus* (pallid sturgeon) spawning habitat on the channelized Lower Missouri River exists on outside revetted bends in relatively deep and high-velocity conditions in an extended area (600 miles of river). Substrate does vary somewhat by site, with some sites containing varying degrees of bedrock and gravel deposits; however, sand dunes and revetment are present at all Missouri River spawning patches. The Lower Yellowstone River has a braided channel with active channel migration regions. Spawning has been documented to happen in a range of depths and velocities generally less than those of the Lower Missouri River but higher than adjacent nonselected habitats. Gravel substrate has been documented in small patches surrounded by sand dunes. On the Yellowstone River, documented spawning is restricted to a 3-mile reach although locations of spawning patches vary from year to year within the reach. Sand bedforms are dynamic and migrate through the reach, changing velocity fields and patch structure on hourly to daily periods. This contrasts with Lower Missouri River spawning patches where repeat mapping documents that depths and velocities in spawning reaches and patches are likely to be similar from year to year. Many Lower Missouri River spawning patches have a spatial arrangement of stable revetment or bedrock in close proximity to rapidly migrating sand dunes.

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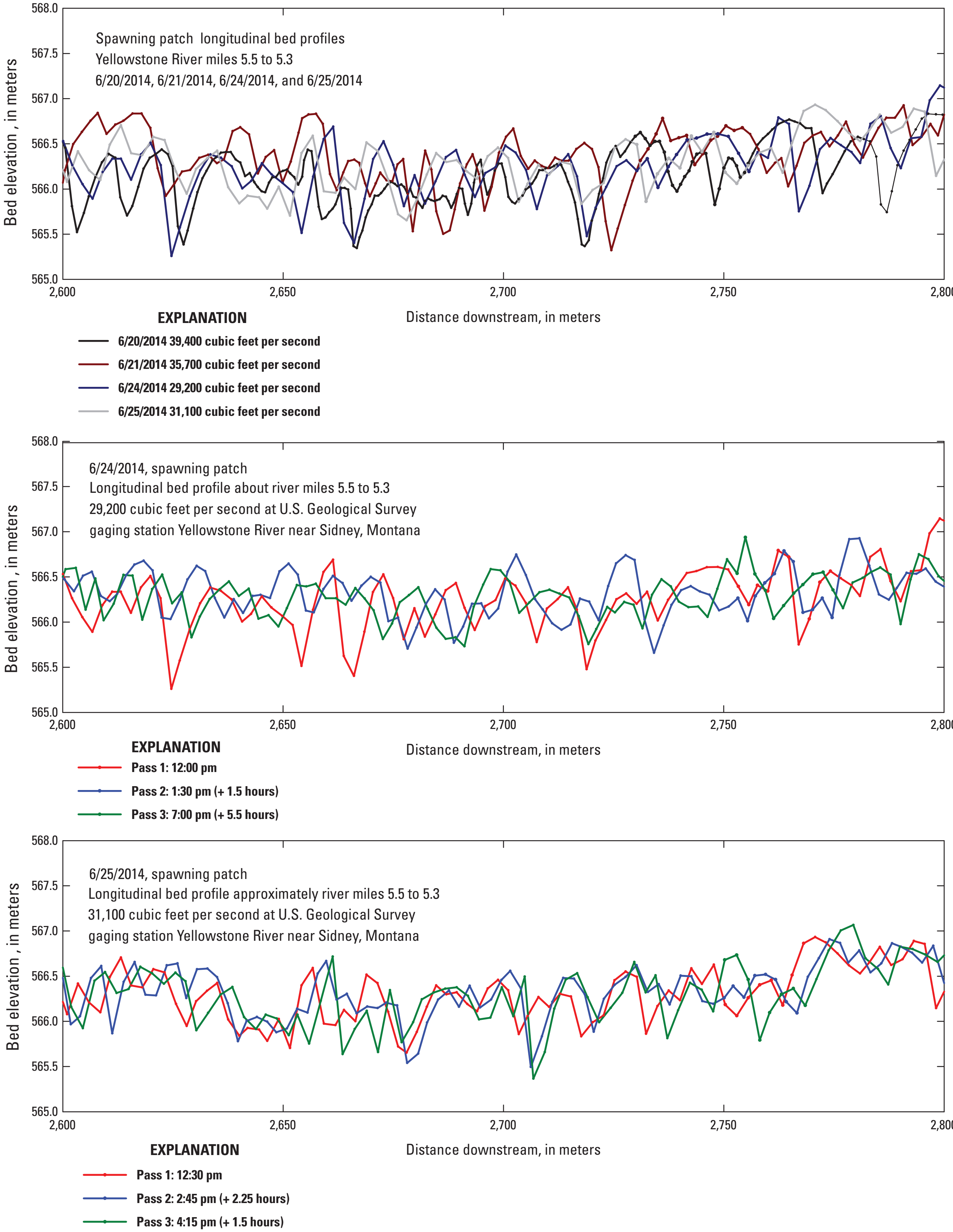


Figure 1–3. Longitudinal profile data showing dune movement at 2013 Yellowstone River spawning patches.

Appendix 2. Spatial Distributions of Interception Habitat Potential, Lower Missouri River

Interception Habitat

The hypothesis that interception habitat might be limiting for survival of age-0 *Scaphirhynchus albus* (pallid sturgeon) has prompted analysis to refine the concept of interception processes and evaluate if existing data support the hypothesis. The interception habitat hypothesis asserts that newly hatched free embryos are not able to exit the thalweg (navigation channel) and transition to first feeding; they, therefore, starve because the Lower Missouri River lacks hydraulic conditions that would transport them into supportive channel-margin habitats with food and protection.

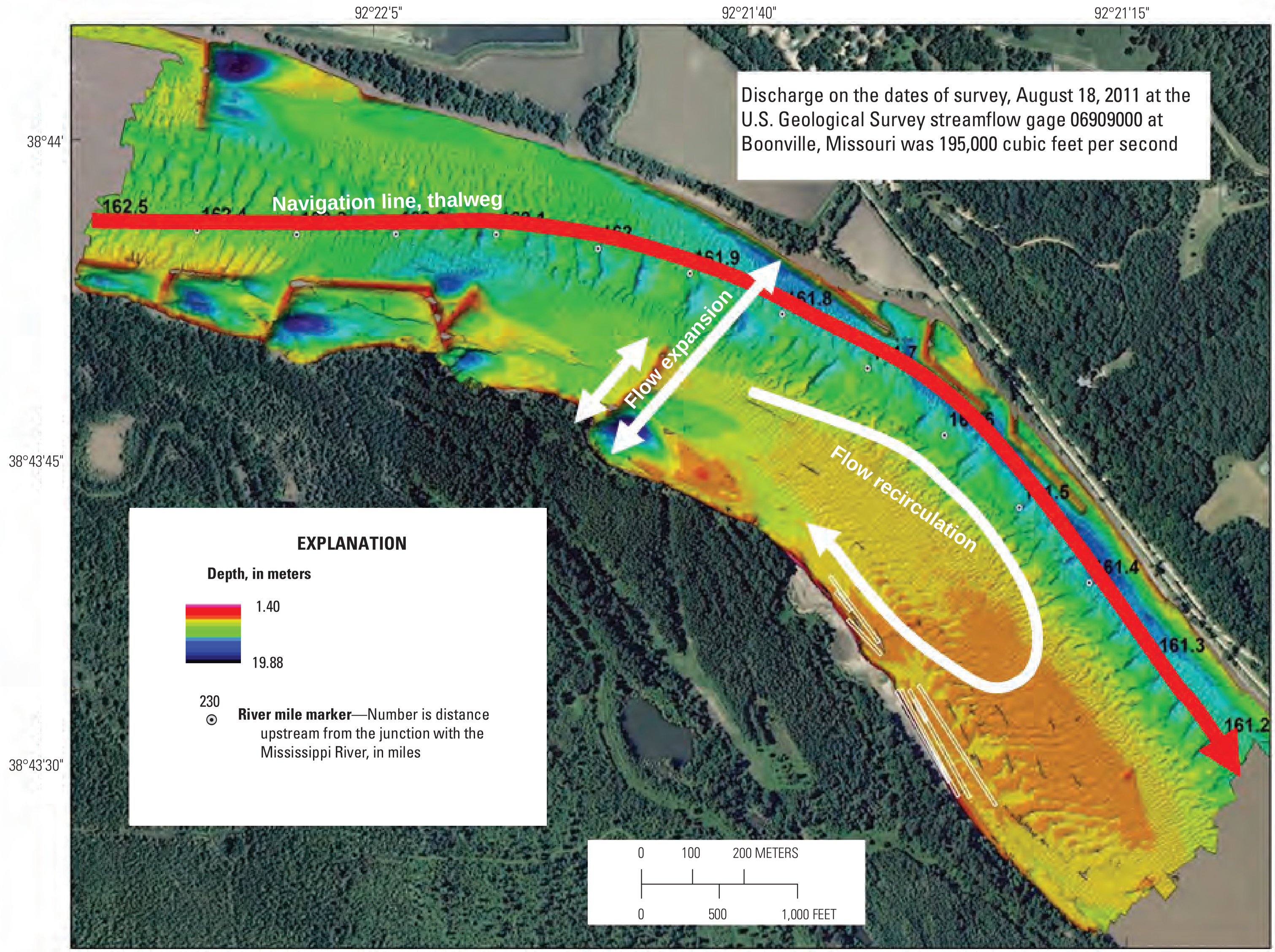
Approach

This analysis attempts to use readily available geographic information system (GIS) and remote sensing data at a regional scale to infer processes taking place at the millimeter scale. The GIS data are accurate to 0.1 meter (m), but because these data are geomorphic features—channel geometry, river-training structures, tributary positions—they can only be considered indicators of dynamic processes of transport at scale of free embryos (less than [<] 25 millimeters [mm]). The analysis requires candidate independent variables that are thought to have an influence on transport, interception, or retention, and one or more dependent variables. For independent variables, we developed GIS data of channel widths, wing dike characteristics, channel sinuosity (degree of curvature) at various scales, and locations of tributary junctions. These datasets were thought to provide some insights into channel complexity that were hypothesized to be related to interception and retention of free embryos. Specifically, we hypothesized that a combination of flow expansion downstream of wing dikes, dike spacing, and (or) channel curvature would be related to interception because these geometric features control formation and intensity of secondary currents. This hypothesis is illustrated in figure 2–1, a multibeam bathymetric image from near Hartsburg, Missouri, showing the conceptual effect of flow expansion and channel curvature on secondary currents. The orientations of sand dunes on the sand bar on the right descending bank indicate vectors of sand transport from the main channel, obliquely up the sand bar and toward the right bank. Detailed information like this was only available in a few reaches along the river so could not be used to evaluate the hypothesis over the entire Lower Missouri River.

We evaluated three candidate dependent variables. The variable of most interest is catch per unit effort (CPUE) of age-0 sturgeon (all shovelnose sturgeon [*Scaphirhynchus platorynchus*], <109 mm) captured during randomized sampling of the Pallid Sturgeon Population Assessment Project; this dataset is similar to that examined by Gemeinhardt and other (2015) but extends through the entire 811 miles of the Lower Missouri River, whereas the Gemeinhardt and others (2015) analysis was confined to the downstream 500 miles. These fish were captured in 16-foot otter trawls deployed in 0.7 to 3.4 m depth. Effort was randomized and fairly well balanced except for a noticeable increase above average near the mouth of the Platte River, which may have elevated CPUE at miles 590–620. Because CPUE was likely to be affected by biotic processes—in particular spatial biases related to origin of drifting free embryos—we also wanted to look at independent surrogates that might have less of that bias. A second dependent variable was based on a human-origin trash survey that was completed by the group Missouri River Relief in 2009. Volunteers obtained Global Positioning System coordinates of trash accumulations and assigned attributes about the nature of the trash and relative size of the trash accumulation on a scale from 1 to 4. For our dependent variable, we used the floating trash category and preferentially filtered out small accumulations by considering only categories 2, 3, and 4. This dependent variable is an indicator of where floating particles may tend to accumulate but is also subject to potential spatial bias because of nonuniform distributions of sources along the river.

The least spatially biased dependent variable we developed is persistent sandbar area. Although sand is substantially denser than a free embryo, both are transported at or near the bottom (Braaten and others, 2010). Sand is ubiquitously present along the river, with the possible exception of just downstream from Gavins Point Dam where channel incision and armoring have occurred (Jacobson and others, 2009), so presence should not be biased by distance to source. We developed the persistent sandbar layer by adding sand-classified pixels from 30 years of Landsat Thematic Mapper surface reflectance data between Julian dates 116 and 296 (average of 95 scenes per location; 1,918 scenes total) and filtering for sandbars that existed at least 20 percent of the time. The inventory of persistent sand averages out fluctuations in sandbar identification that would happen with variation in stage and erosional/depositional processes, and reduces noise from classification errors resulting from clouds and atmospheric effects. The value of the persistent sand dependent variable is that it is expected to respond purely physically, with no interacting biological effects because of spawn location or ontogenetic development.

Independent and dependent variables were summarized by 256 bends and associated with a mean river mile (upstream from the Mississippi River). The summary bends were defined from crossover to crossover, as expressed in the navigation channel.



Base from U.S. Department of Agriculture National Agriculture Imagery Program, digital data, 2011
Universal Transverse Mercator projection
Zone 15

River miles from U.S. Army Corps of Engineers, 1960.

Figure 2–1. Multibeam bathymetric image from the Missouri River near Hartsburg, Missouri, showing concepts of free-embryo transport and factors related to interception habitats.

Results

Longitudinal profiles of selected variables were plotted to evaluate general spatial associations (fig. 2–2); plots are by river mile with river mile (RM) 800 (just downstream from Gavins Point Dam) on the left and RM 0 at the Mississippi River confluence on the right. Persistent sandbar area as a percent of bend area is notable for the relative lack of sandbar area upstream of the Kansas River. Downstream from the Kansas River, persistent sandbar area increases dramatically and is punctuated with large and small values. Most of the large accumulations are point bars on the inside of bends. Small accumulations associated with individual wing dikes are aggregated at this scale. Trash hot spots pick up downstream from the Platte River (the trash reconnaissance extended all the way to Gavins Point Dam); and the distribution is suggestive of clumped accumulations, but associations are difficult to discern. The CPUE of age-0 pallid sturgeon is very low downstream from the Big Sioux River and is interrupted by a concentration upstream from the Platte River; as indicated earlier, this is one spot with especially high effort, so this clump may be an artifact. The CPUE starts to pick up around RM 640, and the distribution is characterized by a great deal of spatial variability between peaks and troughs downstream to the Osage River. From the Osage River to the Mississippi River, CPUE peaks tend to diminish. The overall distribution suggests a punctuated, bell-shaped curve with a broad peak between the Kansas and Grand Rivers.

The lower two graphs are candidate independent variables. The suite of candidate variables was filtered based on examination of regressions and ordination plots to determine which variables had redundant information. The shapes of the channel width and standard deviation of constricted channel width correspond to the persistent sandbar distribution, suggesting an association. Channel width is a measure of overall accommodation space for sandbars (or other habitat complexity features). Channel widths were measured every 0.1 mile and averaged by bend. Constricted width is channel width minus wing dike projected length perpendicular to the thalweg. The standard deviation of constricted width is a measure of variability of channel width as the channel is alternately constricted and allowed to expand downstream of wing dikes. The bottom panel of figure 2–2 shows average dike spacing in red and channel sinuosity measured over 24 kilometers (km) in blue. Dike spacing increases substantially at RM 500, which is the boundary between the Omaha and Kansas City U.S. Army Corps of Engineers District offices. Some prominent peaks in sinuosity seem like they may be associated with CPUE and sandbar peaks (for example, the peak at about RM 280), but many sinuosity peaks show no corresponding CPUE peaks.

Associations between CPUE and sand, and candidate independent variables were explored with general linear models. The best model identified for persistent sandbar percent area had an adjusted multiple coefficient of determination (R^2) value of 0.54, and significant p values for mean width and standard deviation. Models that included sinuosity and dike spacing had equivalent multiple R^2 values; p values for sinuosity and dike spacing were not significant.

The same model for predicting CPUE had an adjusted multiple R^2 of 0.04 and neither mean width nor standard deviation of constricted width had a p value less than 0.2.

Discussion

The graphical and statistical associations between two channel geometry variables and persistent sandbar area confirm that a measurable, physical basis exists for predicting where particles in passive transport are intercepted and retained on the Lower Missouri River. The bend-average scale of the analysis undoubtedly does not capture the details of river mechanics responsible for the sandbar persistence, but the association between sand and channel geometry variables is physically reasonable. Sinuosity did not contribute significantly to the distribution of sand, which indicates that constriction and expansion of flow associated with wingdikes probably has a greater effect than the secondary currents associated with channel curvature. Average spur-dike spacing per bend did not contribute significantly either, and it may be that averaging over a bend does not capture the specific role of dike spacing at the downstream end of bends where a short spacing can interrupt eddy formation.

The graphical depiction of CPUE is notable for the lack of catch upstream from about RM 540, but otherwise visible associations with independent variables (and with sandbars) are elusive. Lack of CPUE upstream from RM 540 may be related to the narrow channel and short wingdike spacing in this part of the Missouri River navigation channel. Short spacing of wing dikes may not allow for lateral eddies to form completely; therefore, the spacing does not promote interception retention of free embryos or sand. It is also likely that transporting free embryos have not developed to the point where they are ready to transition to settle out and begin feeding in channel-margin habitats. This explanation implies that transport is not entirely passive; and some active movement on the part of a free embryo may be necessary, with or without supporting hydraulics, for it to move to lateral habitats. The diminished CPUE downstream from RM 200 could be the result of fewer available free embryos because most had already been retained upstream. Interpretations of the CPUE distribution are complicated by the fact that the age-0 sturgeon are shovelnose sturgeon, which are thought to be more likely to spawn in tributaries than pallid sturgeon, and may therefore have originated in tributaries to the main stem Missouri River; moreover, CPUE may also vary considerably with fishing conditions and skill. The linear model using parameters that were influential in predicting sand distribution worked poorly in predicting CPUE.

Results of this analysis were similar to those of Gemeinhardt and others (2015), which confirmed that no significant spatial relation exists between CPUE and availability of shallow water habitat, simply defined as depths <1.5 m. Several factors may be responsible for this lack of relation including: (a) processes in areas identified as shallow-water habitat are not limiting to sturgeon populations, (b) relevant physical and

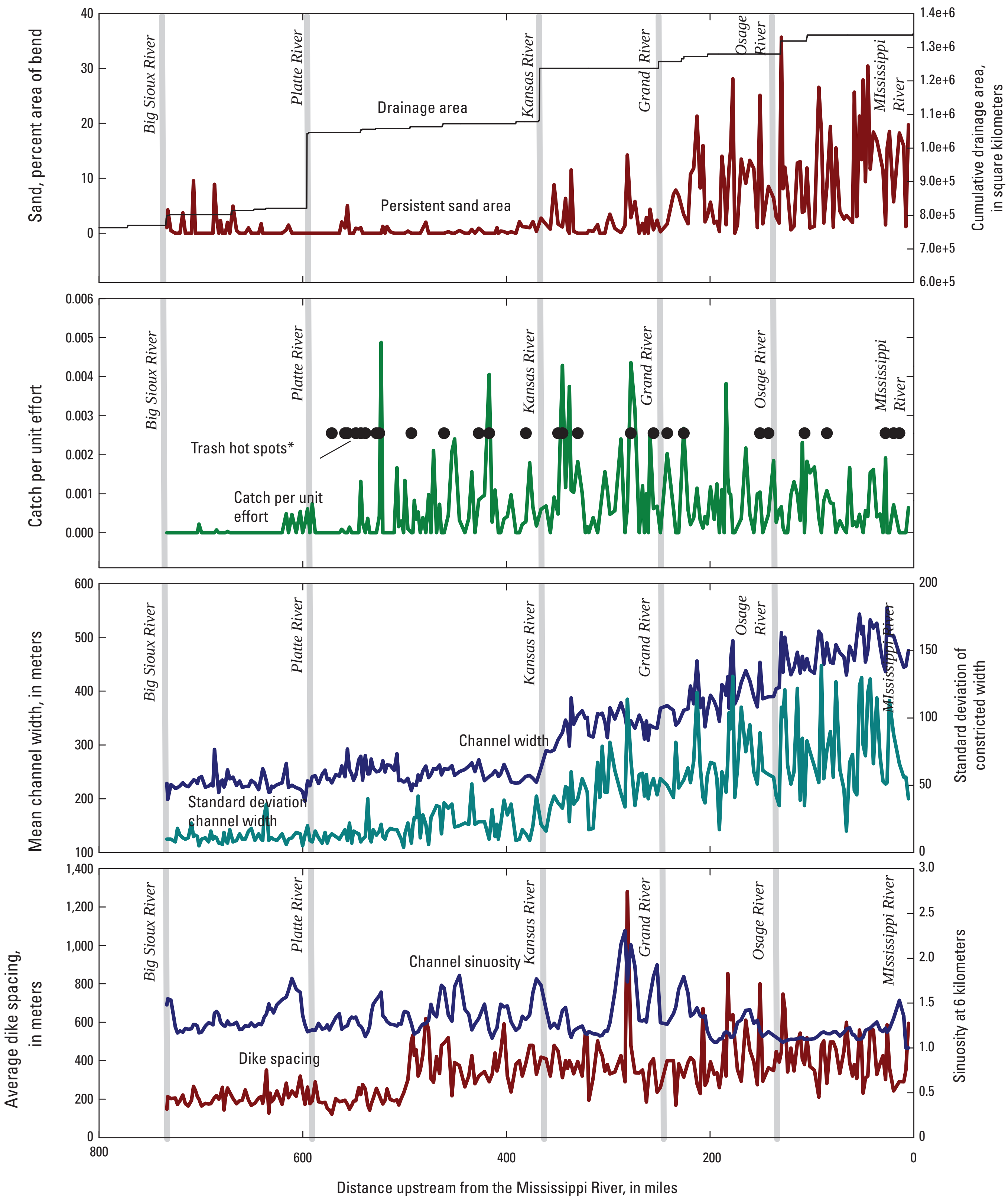


Figure 2–2. Longitudinal plots of dependent variables (persistent sand area, catch per unit effort, floating trash hot spots) compared to candidate independent variables, 0–800 river miles from the Mississippi River confluence.

biological habitat conditions are not captured in the conventional definition or if the velocity component of the definition is ignored, or (c) CPUE using conventional sampling techniques is not sufficiently selective to document occupancy of shallow-water habitat by age-0 sturgeon. If depths <1.5 m are an important measure of larval rearing habitat, those shallow depths probably need to co-occur with hydraulics that contribute to interception and retention of free embryos.

Summary

This investigation supports in part the hypothesis that physical variables can define interception habitat and their effects can be discerned. Poor associations between physical variables and age-0 sturgeon catch per unit effort (relative to sand) indicate that the physical realism and resolution of the geographic information system model are not sufficient to resolve actual factors affecting interception and retention or, more likely, that the biologic effects of spawning location, development rate, and nonpassive transport obscure physical effects. This does not mean that channel reconfigurations would not be effective in increasing interception and retention of *Scaphirhynchus albus* (pallid sturgeon) free embryos. It likely means that physical controls are secondary after the need to have drifting free embryos present at the correct stage of development at the right location. If validated, this interpretation could be used to optimize locations of interception, food-producing, and foraging habitats, given understanding of spawning locations and free-embryo dispersal rates.

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