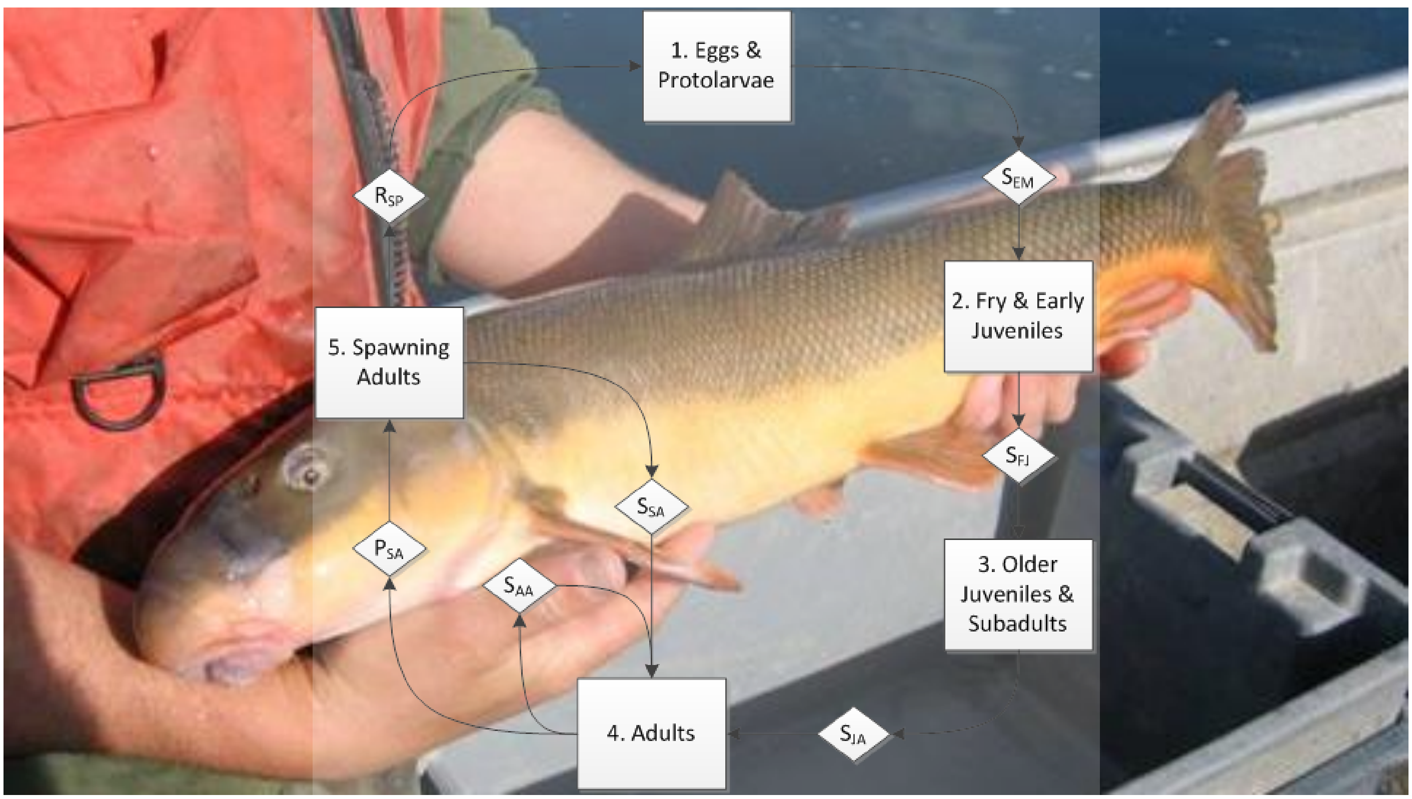
Lower Colorado River Multi-Species Conservation Program

Balancing Resource Use and Conservation

Flannelmouth Sucker (*Catostomus latipinnis*) (FLSU) Basic Conceptual Ecological Model for the Lower Colorado River



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U.S. DEPARTMENT OF THE INTERIOR
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June 2015

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Lower Colorado River
Multi-Species Conservation Program

Flannelmouth Sucker
(*Catostomus latipinnis*) (FLSU)
Basic Conceptual Ecological Model for the Lower Colorado River

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ACRONYMS AND ABBREVIATIONS

AGFD	Arizona Game and Fish Department
BONY	bonytail (*Gila elegans*)
BP	Before Present
CEM	conceptual ecological model
cfs	cubic feet per second
CI	confidence interval
cm	centimeter(s)
DO	dissolved oxygen
FLSU	flannelmouth sucker (*Catostomus latipinnis*)
km	kilometer(s)
LCR	lower Colorado River
LCR MSCP	Lower Colorado River Multi-Species Conservation Program
LCRB	Lower Colorado River Basin
m	meter(s)
m/s	meters per second
m^3/s	cubic meters per second
mm	millimeter(s)
NISIC	National Invasive Species Information Center
NRC	National Research Council
POM	particulate organic matter
RASU	razorback sucker (*Xyrauchen texanus*)
Reclamation	Bureau of Reclamation
TL	total length
UCRB	Upper Colorado River Basin
UDWR	Utah Department of Natural Resources – Division of Wildlife Resources
USFWS	U.S. Fish and Wildlife Service
USGS	U.S. Geological Survey
YOY	young-of-year

Symbols

≈	approximately
°C	degrees Celsius (*aka* Centigrade)
>	greater than
≥	greater than or equal to
≤	less than or equal to
%	percent
±	plus or minus

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Foreword

The Lower Colorado River Multi-Species Conservation Program (LCR MSCP) Habitat Conservation Plan requires the creation, and long-term stewardship, of habitat for 20 covered species. This is both an exciting and daunting challenge – exciting, in that success would mean a major conservation achievement in the lower Colorado River landscape, and daunting, in that we need to simultaneously manage our lands for the benefit of 20 species in a mosaic of land cover types. To do so, we need to develop a common understanding of the habitat requirements of each species and the stewardship required to meet those needs.

To provide a framework to capture and share the information that forms the foundation of this understanding, conceptual ecological models (CEMs) for each covered species have been created under the LCR MSCP's Adaptive Management Program. The LCR MSCP's conceptual ecological models are descriptions of the functional relationships among essential components of a species' life history, including its habitat, threats, and drivers. They tell the story of "what's important to the animal" and how our stewardship and restoration actions can change those processes or attributes for the betterment of their habitat. As such, CEMs can provide:

- A synthesis of the current understanding of how a species' habitat works. This synthesis can be based on the published literature, technical reports, or professional experience.
- Help in understanding and diagnosing underlying issues and identifying land management opportunities.
- A basis for isolating cause and effect and simplifying complex systems. These models also document the interaction among system drivers.
- A common (shared) framework or "mental picture" from which to develop management alternatives.
- A tool for making qualitative predictions of ecosystem responses to stewardship actions.
- A way to flag potential thresholds from which system responses may accelerate or follow potentially unexpected or divergent paths.
- A means by which to outline further restoration, research, and development and to assess different restoration scenarios.

- A means of identifying appropriate monitoring indicators and metrics.
- A basis for implementing adaptive management strategies.

Most natural resource managers rely heavily upon CEMs to guide their work, but few explicitly formulate and express the models so they can be shared, assessed, and improved. When this is done, these models provide broad utility for ecosystem restoration and adaptive management.

Model building consists of determining system parts, identifying the relationships that link these parts, specifying the mechanisms by which the parts interact, identifying missing information, and exploring the model's behavior (Heemskerk et al. 2003[1]). The model building process can be as informative as the model itself, as it reveals what is known and what is unknown about the connections and causalities in the systems under management.

It is important to note that CEMs are not meant to be used as prescriptive management tools but rather to give managers the information needed to help inform decisions. These models are conceptual and qualitative. They are not intended to provide precise, quantitative predictions. Rather, they allow us to virtually "tweak the system" free of the constraints of time and cost to develop a prediction of how a system might respond over time to a variety of management options; for a single species, a documented model is a valuable tool, but for 20 species, they are imperative. The successful management of multiple species in a world of competing interests (species versus species), potentially conflicting needs, goals, and objectives, long response times, and limited resources, these models can help land managers experiment from the safety of the desktop. Because quantitative data can be informative, habitat parameters that have been quantified in the literature are presented (in attachment 2) in this document for reference purposes.

These models are intended to be "living" documents that should be updated and improved over time. The model presented here should not be viewed as a definitive monograph of a species' life history but rather as a framework for capturing the knowledge and experience of the LCR MSCP's scientists and land stewards. While ideally the most helpful land management tool would be a definitive list of do's and don'ts, with exact specifications regarding habitat requirements that would allow us to engineer exactly what the species we care about need to survive and thrive, this is clearly not possible. The fact is, that despite years of active management, observation, and academic research on many of the LCR MSCP species of concern, there may not be enough data to support developing such detailed, prescriptive land management.

[1] Heemskerk, M., K. Wilson, and M. Pavao-Zuckerman. 2003. Conceptual models as tools for communication across disciplines. Conservation Ecology 7(3):8: http://www.consecol.org/vol7/iss3/art8/

The CEMs for species covered under the LCR MSCP are based on, and expand upon, methods developed by the Sacramento-San Joaquin Delta Ecosystem Restoration Program (ERP): https://www.dfg.ca.gov/ERP/conceptual_models.asp. The ERP is jointly implemented by the California Department of Fish and Wildlife, U.S. Fish and Wildlife Service, and National Marine Fisheries Service. The Bureau of Reclamation (Reclamation) participates in this program. (See attachment 1 for an introduction to the CEM process.)

Many of the LCR MSCP covered species are migratory. These models only address the species' life history as it relates to the lower Colorado River and specifically those areas that are potentially influenced by LCR MSCP land management. The models DO NOT take into account ecological factors that influence the species at their other migratory locations.

Finally, in determining the spatial extent of the literature used in these models, the goals and objectives of the LCR MSCP were taken into consideration. For species whose range is limited to the Southwest, the models are based on literature from throughout the species' range. In contrast, for those species whose breeding range is continental (e.g., yellow-billed cuckoo) or west-wide, the models primarily utilize studies from the Southwest.

How to Use the Models

There are three important elements to each CEM:

(1) The narrative description of the species' various life stages, critical biological activities and processes, and associated habitat elements.

(2) The figures that provide a visual snapshot of all the critical factors and causal links for a given life stage.

(3) The associated workbooks. Each CEM has a workbook that includes a worksheet for each life stage.

This narrative document is a basic guide, meant to summarize information on the species' most basic habitat needs, the figures are a graphic representation of how these things are connected, and the accompanying workbook is a tool for land managers to see how on-the-ground changes might potentially change outcomes for the species in question. Reading, evaluating, and using these CEMs requires that the reader understand all three components; no single component provides all the pertinent information in the model. While it seems convenient to simply read the narrative, we strongly recommend the reader have the figures and workbook open and refer to them while reviewing this document.

It is also tempting to see these products, once delivered, as "final." However, it is more accurate to view them as "living" documents, serving as the foundation for future work. Reclamation will update these products as new information is available, helping to inform land managers as they address the on-the-ground challenges inherent in natural resource management.

The knowledge gaps identified by these models are meant to serve only as an example of the work that could be done to further complete our understanding of the life history of the LCR MSCP covered species. However, this list can in no way be considered an exhaustive list of research needs. Additionally, while identifying knowledge gaps was an objective of this effort, evaluating the feasibility of addressing those gaps was not. Finally, while these models were developed for the LCR MSCP, the identified research needs and knowledge gaps reflect a current lack of understanding within the wider scientific community. As such, they may not reflect the current or future goals of the LCR MSCP. They are for the purpose of informing LCR MSCP decisionmaking but are in no way meant as a call for Reclamation to undertake research to fill the identified knowledge gaps.

John Swett, Program Manager, LCR MSCP
Bureau of Reclamation
September 2015

Executive Summary

This document presents a conceptual ecological model (CEM) for the flannelmouth sucker (*Catostomus latipinni*) (FLSU). The purpose of this model is to help the Bureau of Reclamation (Reclamation), Lower Colorado River Multi-Species Conservation Program (LCR MSCP), identify areas of scientific uncertainty concerning FLSU ecology, the effects of specific stressors, the effects of specific management actions aimed at species habitat restoration, and the methods used to measure FLSU habitat and population conditions. (Note: Attachment 1 provides an introduction to the CEM process. We recommend that those unfamiliar with this process read attachment 1 before continuing with this document.)

The identified research questions and gaps in scientific knowledge that are the result of this modeling effort serve as examples of topics the larger scientific community could explore to improve the overall understanding of the ecology of this species. These questions may or may not be relevant to the goals of the LCR MSCP. As such, they are not to be considered guidance for Reclamation or the LCR MSCP, nor are these knowledge gaps expected to be addressed under the program.

CONCEPTUAL ECOLOGICAL MODELS

CEMs integrate and organize existing knowledge concerning: (1) what is known about an ecological resource, with what certainty, and the sources of this information; (2) critical areas of uncertain or conflicting science that demand resolution to better guide management planning and action; (3) crucial attributes to use while monitoring system conditions and predicting the effects of experiments, management actions, and other potential agents of change; and (4) how we expect the characteristics of the resource to change as a result of altering its shaping/controlling factors, including those resulting from management actions.

The CEM applied to FLSU expands on the methodology developed for the Sacramento-San Joaquin River Delta Regional Ecosystem Restoration Implementation Plan (DiGennaro et al. 2012). The model distinguishes the major life stages or events through which the individuals of a species must pass to complete a full life cycle. It then identifies the factors that shape the likelihood that individuals in each life stage will survive to the next stage in the study area and thereby shapes the abundance, distribution, and persistence of the species in that area.

Specifically, the FLSU conceptual ecological model has five core components:

- **Life stages** – These consist of the major growth stages and critical events through which an individual FLSU must pass in order to complete a full reproductive cycle.
- **Life-stage outcomes** – These consist of the biologically crucial outcomes of each life stage, including the number of individuals recruited to the next life stage or age class within a single life stage (recruitment rate), or the number of offspring produced (fertility rate).
- **Critical biological activities and processes** – These consist of activities in which the species engages and the biological processes that take place during each life stage that significantly beneficially or detrimentally shape the life-stage outcome rates for that life stage.
- **Habitat elements** – These consist of the specific habitat conditions, the abundance, spatial and temporal distributions, and other qualities that significantly beneficially or detrimentally affect the rates of the critical biological activities and processes for each life stage.
- **Controlling factors** – These consist of environmental conditions and dynamics – including human actions – that determine the abundance, spatial and temporal distributions, and other qualities of the habitat elements for each life stage. Controlling factors are also called "drivers."

The CEM identifies the causal relationships among these components for each life stage. A causal relationship exists when a change in one condition or property of a system results in a change in some other condition or property. A change in the first condition is said to cause a change in the second condition. The CEM method applied here assesses four variables for each causal relationship: (1) the character and direction of the effect, (2) the magnitude of the effect, (3) the predictability (consistency) of the effect, and (4) the certainty of a present scientific understanding of the effect. CEM diagrams and a linked spreadsheet tool document all information on the model components and their causal relationships.

CONCEPTUAL ECOLOGICAL MODEL STRUCTURE

The FLSU conceptual ecological model addresses the FLSU population along the river and the lakes of the lower Colorado River (LCR). The basic sources of information for the FLSU conceptual ecological model include Bezzerides and

Bestgen (2002), Mueller and Marsh (2002), Snyder and Muth (2004), Reclamation (2005, 2008), Rees et al. (2005), Utah Department of Natural Resources – Utah Division of Wildlife Resources (2006), Carman (2007), and Minckley and Marsh (2009). These studies summarize and cite large bodies of earlier studies across the entire Colorado River basin, predominantly across the Upper Colorado River Basin, reflecting the historic distribution of the species. The model also integrates information from more recent publications, information on current research projects, and the expert knowledge of LCR MSCP fish biologists. Our purpose is not to provide an updated literature review but to integrate the available information and knowledge into a CEM so it can be used for adaptive management.

The FLSU conceptual ecological model distinguishes and assesses five life stages and their seven associated outcomes as follows:

1. Eggs and protolarvae
    - Egg and protolarval survival rate
2. Fry and early juveniles
    - Fry and early juvenile survival rate
3. Older juveniles and subadults
    - Older juvenile and subadult survival rate
4. Adults
    - Adult survival rate
    - Adult reproductive participation rate
5. Spawning adults
    - Spawning adult survival rate
    - Spawning adult fertility rate

The model distinguishes 12 critical biological activities or processes relevant to 1 or more of these life stages, 16 habitat elements relevant to 1 or more of these critical biological activities or processes for 1 or more life stages, and 7 controlling factors that affect 1 or more of these habitat elements. Because the LCR comprises a highly regulated system, the controlling factors almost exclusively concern human activities.

The 12 critical biological activities and processes identified across all life stages are: chemical stress, competition, disease, drifting, foraging, hybridization, long-distance movement, mechanical stress, predation, resting, swimming, and thermal stress. The 16 habitat elements identified across all life stages are: aquatic macrophytes, aquatic vertebrates, birds and mammals, fishing encounters, flow network fragmentation, infectious agents, invertebrates and particulate organic matter (POM), macrohabitat geometry, mesohabitat geometry/cover, scientific study, substrate texture/dynamics, turbidity, water chemistry, water depth, water flow/turbulence, and water temperature. The seven controlling factors identified across all habitat elements are: channel and off-channel engineering, fishing activity and fisheries management, motorboat activity, nuisance species introduction and management, tributary inflows, wastewater and other contaminant inflows, and water storage-delivery system design and operation.

KEY RESULTS

The assessment of the causal relationships among controlling factors, habitat elements, critical biological activities and processes, and life-stage outcomes indicates the following strong (high-magnitude) causal relationships. These results specifically refer to LCR Reach 3:

- Two controlling factors consistently have high-magnitude direct effects on multiple habitat elements across all FLSU life stages, listed here in order of impact: water storage-delivery system design and operation and channel and off-channel engineering.

- Five habitat elements consistently have high-magnitude direct effects on multiple critical biological activities and processes across all FLSU life stages, listed here in order of impact: mesohabitat geometry/cover, aquatic vertebrates, aquatic macrophytes, invertebrates and POM, and substrate texture/dynamics.

- Six habitat elements consistently have high-magnitude direct effects on other habitat elements and thereby have strong *indirect* effects on one or more critical biological activities or processes across all FLSU life stages. These six elements are listed here in order of impact: aquatic vertebrates, macrohabitat geometry, mesohabitat geometry/cover, water depth, water flow/turbulence, and water temperature. Two habitat elements, aquatic vertebrates and mesohabitat geometry/cover, thus have high-magnitude direct *and indirect* effects on one or more critical biological activities or processes across all FLSU life stages.

- Two critical biological activities or processes consistently have high-magnitude direct effects on multiple life-stage outcomes across all FLSU life stages, listed here in order of impact: foraging and predation. Four critical biological activities or processes consistently have high-magnitude direct effects on other critical biological activities or processes and thereby have strong *indirect* effects on one or more life-stage outcomes across all FLSU life stages. These four activities or processes are listed here in order of impact: resting, competition, swimming, and foraging. One critical biological activity or process, foraging, thus has high-magnitude direct *and indirect* effects on one or more life-stage outcomes across all FLSU life stages.

The assessment of causal relationships also identified those with high magnitude but low understanding. Seven habitat elements have high-magnitude but poorly understood direct effects either on one or more other habitat elements or on one or more critical biological activities or processes. Five of these seven habitat elements with poorly understood impacts affect more than one other habitat element or more than one critical biological activity or process: aquatic macrophytes, aquatic vertebrates, mesohabitat geometry/cover, substrate texture/dynamics, and water flow/turbulence.

Seven critical biological activities or processes also have high-magnitude but poorly understood direct effects either on one or more other critical biological activities or processes or one or more life-stage outcomes. Four of these seven critical biological activities or processes with poorly understood impacts affect more than one other critical biological activity or process or more than one life-stage outcome: competition, foraging, predation, and swimming. Additionally, drifting, another of these seven critical biological activities or processes with poorly understood impacts, strongly indirectly affects survivorship of FLSU fry. Drifting affects only a single life stage, but it has a strong—even though indirect—effect on that life stage. The low level of understanding of this relationship therefore warrants special recognition along with the habitat elements proposed to affect drifting itself.

FLSU differ from other native fishes of the LCR in their apparent ability to persist along the river and even re-establish themselves in reaches from which they had disappeared. Reviews of the status of the species across the Colorado River basin in general consistently propose that, as with the other native species of the basin, it has suffered from the combined impacts of habitat loss and fragmentation, predation by non-native species, water pollution, altered turbidity, and altered hydrology and water temperatures. However, development of the CEM did not turn up clear evidence that water pollution currently affects the overall distribution or health of the species. Similarly, FLSU appear to be able to spawn in river sections with highly altered temperature and flow regimes, although the present assessment did not evaluate the possible limits of this range of tolerance. Further, development of the CEM did not turn up clear evidence that predation by non-native species threatens the persistence of FLSU in the basin or in any individual river reach. A broad spectrum of non-native vertebrates and possibly also invertebrates (e.g., crayfish) undoubtedly do prey on FLSU. However, the CEM suggests that FLSU numbers and distribution may be more sensitive to other constraints, specifically the abundance and quality of food materials; the availability of hydrologically and geomorphically suitable spawning, drifting, and nursery and other resting habitat, including habitat with aquatic macrophyte cover; and the presence of barriers to long-distance movement.

The research questions and gaps in scientific knowledge identified in this modeling effort serve as examples of topics the larger scientific community could explore to improve the overall understanding of the ecology of FLSU. These questions may or may not be relevant to the goals of the LCR MSCP. As such, they are not to be considered guidance for Reclamation or the LCR MSCP, nor are these knowledge gaps expected to be addressed under the program.

Chapter 1 – Introduction

This document presents a conceptual ecological model (CEM) for the flannelmouth sucker (*Catostomus latipinnis*) (FLSU). The purpose of this model is to help the Bureau of Reclamation (Reclamation), Lower Colorado River Multi-Species Conservation Program (LCR MSCP), identify areas of scientific uncertainty concerning FLSU ecology, the effects of specific stressors, the effects of specific management actions aimed at species habitat restoration, and the indicators used to measure FLSU habitat and population conditions. The CEM methodology follows that developed for the Sacramento-San Joaquin River Delta Regional Ecosystem Restoration Implementation Plan (DiGennaro et al. 2012), with modifications. (Note: Attachment 1 provides an introduction to the CEM process. We recommend that those unfamiliar with this process read attachment 1 before continuing with this document.)

The model addresses the FLSU population along the river and the lakes of the lower Colorado River (LCR). However, FLSU currently consistently occupy only a single section of the river, specifically the section of Reach 3 between Davis Dam and Lake Havasu. The assessment of causal relationships in the CEM consequently focuses on this section of the river wherever possible.

FLSU historically occurred in the Colorado River basin from the present-day U.S.-Mexico border upstream to elevations of approximately 1880 meters (m) (approximately 6170 feet) (Bezzerides and Bestgen 2002). This distribution included the entire Gila River basin, within which the original and several subsequent other early-type specimens were collected (Gilbert and Scofield 1898). The species is now considered extirpated throughout the Gila River basin (Bezzerides and Bestgen 2002; NatureServe 2014). FLSU in the LCR today occupy only a single river reach, between Davis Dam and Lake Havasu, isolated from the remainder of the FLSU distribution across the Upper Colorado River Basin (UCRB) (Bezzerides and Bestgen 2002; Mueller and Wydoski 2004; Best and Lantow 2012).

The basic sources of the information for the FLSU conceptual ecological model include studies by Bezzerides and Bestgen (2002), Mueller and Marsh (2002), Snyder and Muth (2004), Reclamation (2005, 2008), Rees et al. (2005), Utah Department of Natural Resources – Division of Wildlife Resources (UDWR) (2006), Carman (2007), and Minckley and Marsh (2009). These studies summarize and cite large bodies of earlier studies across both the upper and lower Colorado River basins. Most of these studies concern the upper basin, reflecting the historic distribution of the species (Bezzerides and Bestgen 2002). The model also integrates information from more recent publications, information on current research projects, and the expert knowledge of LCR MSCP fish biologists. The purpose of this effort is not to provide an updated literature review but to integrate the available information and knowledge into a CEM so it can be used for adaptive management.

This document is organized as follows: The remainder of chapter 1 provides an overview of the reproductive ecology of FLSU as currently understood, specifically its adaptation to the pre-regulation LCR hydrogeomorphic environment, and introduces the underlying concepts and structure of the CEM. Chapter 2 presents a life-stage model for FLSU with which to build a CEM. Succeeding chapters present and explain the CEM for FLSU in the LCR and identify potentially important causal relationships for management, monitoring, and research consideration.

FLANNELMOUTH SUCKER REPRODUCTIVE ECOLOGY

FLSU have at least 5 million years of evolutionary history in the LCRB, following earlier evolution in the UCRB during the Miocene Epoch and the subsequent merging of the upper and lower basins (Minckley 1991; Douglas and Douglas 2007; Spencer et al. 2008). Consequently, as with the other native fishes of the Colorado River, FLSU have a long evolutionary history of interaction with, and adaptation to, the natural environmental conditions and other endemic species of the Colorado River.

Similar to many fish species adapted to large flood plain rivers in desert basins, FLSU have a reproductive strategy characterized by high fecundity and the release of numerous eggs during each spawning season, participation of only a portion of the adult population in spawning in any single year, a complete lack of parental investment in offspring, low larval survivorship, large adult body size, and a long adult lifespan (Minckley et al. 2003; Zeug and Winemiller 2007). Although perhaps less strongly than is the case with other large fishes of the Colorado River (e.g., bonytail [*Gila elegans*] [BONY]) (Mueller 2006), FLSU reproduction matches the criteria for a "skip spawner" (Johnston 1999) or "periodic" reproductive strategist (Winemiller and Rose 1992), an adaptation associated with strongly seasonal riverflow regimes (Mims et al. 2010; Mims and Olden 2012).

FLSU female fecundity ranges from 4,000 to 40,000 ova per individual and varies approximately with body length (McAda and Wydoski 1985), with females in their first year of maturity (approximately age-4) being both smaller and less fecund than females age-8 and older. Mueller and Wydoski (2004) estimated that an average female FLSU in the LCR can spawn for 15 years or more; however, only a fraction of the mature females spawn in a given year. The estimated male:female ratios at spawning sites range from 1:1 up to 3:1 (Weiss 1993; McKinney et al. 1999). Mueller and Wydoski (2004) found an average annual recruitment rate of 15 percent (%) over 4 years along LCR Reach 3 between Davis Dam and Lake Havasu. They noted that this recruitment rate was sufficient to maintain the population in that reach, assuming an average male:female spawning ratio of 2:1 and an average fecundity per female of 15,000 ova during fertile years. Assuming a lifetime fecundity of 120,000 ova (8 fertile years x 15,000 ova per fertile year), individual FLSU in Reach 3 thus have a very low average lifetime reproductive success rate of approximately 0.00166% (2 individuals surviving to reproduce out of every 120,000 ova).

The timing of FLSU spawning in the LCR correlates seasonally with the rise in water temperature following the winter low but prior to the Colorado River spring flood pulse following snowmelt in the Rocky Mountains (Bezzerides and Bestgen 2002; Rees et al. 2005; Reclamation 2008; Minckley and Marsh 2009; Zelasko et al. 2011) (see chapters 2, 4, and 6). FLSU deposit their eggs into the substrate, where they must remain to develop and hatch. Spawning sites therefore must provide substrates that remain stable over the course of embryo development, hatching, and larval development prior to swim-up. Otherwise, eggs and newly hatched larvae in/on these substrates potentially could be churned up, buried, or exposed during the rise and fall of the spring flood pulse following spawning. The timespan in the wild during which FLSU embryos and early larvae (prior to swim-up) are vulnerable to such disruption of their natal site ranges from 10 days at 20 degrees Celsius (°C) to more than 30 days at 12 °C (see chapter 2).

Further, FLSU spawn in locations at some distance from locations suitable for nursery habitat. FLSU larvae must find their way to suitable nursery habitat following swim-up (see chapters 3, 4, and 6). However, FLSU, immediately following swim-up (approximately 13–14 millimeters [mm] total length [TL]), lack the strength or environmental familiarity to navigate in the river exclusively under their own power and depend on currents (drifting) to help transport them into nursery habitat. Excessively weak or strong currents from a drought or flood pulse during this period of drift could transport the small larvae too little or too far, preventing their settling into suitable nursery habitat. Flood pulse variability therefore would have posed significant risks for FLSU larval survival.

Once they reach suitable nursery habitat, young FLSU remain there for approximately 3–5 months before dispersing back into the river (see chapter 2) (Snyder and Muth 2004; Reclamation 2008). Suitable natural nursery environments consist of low-velocity (< 0.2 meter per second [m/s]) environments along shorelines and in embayments, shallow near-shore pools, and backwater areas wetted and/or connected to the main channel during the spring flood pulse (see chapters 2, 3, 4, and 6). These environments must remain connected to the river, or become reconnected before drying out following spring flooding, to allow the maturing FLSU juveniles (see chapter 2) to move back into the river. Off-channel nursery habitat that becomes disconnected from the river following the spring flood pulse would become inhospitable to young FLSU due to rising water temperatures and salinity as the habitat dried out. FLSU fry and juveniles in wild nursery habitats therefore faced yet additional environmental risks to survival.

Historically, the timing and magnitude of the Colorado River spring flood pulse in fact varied greatly from year to year and over longer timespans (Ely et al. 1993; O'Connor et al. 1994; Woodhouse et al. 2010; Reclamation 2011a). In turn, Piechota et al. (2004) identified approximately 11 droughts lasting 5 years or more affecting the discharge of the Colorado River between 1923 and 2004. In turn, Woodhouse et al. (2010) identified numerous short- and long-term droughts over the preceding 1,200 years, providing a larger context for understanding the historic record. A severe drought in 2000–2004, for example, produced the lowest 5-year period of flow on the Colorado River in the historic gauge record up to that time (1906–2005) but ranked as only the seventh worst drought in the last 500 years (Piechota et al. 2004; Woodhouse et al. 2010). The timing of the annual flood pulse along the LCR varies with the timing of onset of snowmelt in different parts of the Rocky Mountains and the timing of spring rain storms, including rain-on-snow events. Prolonged droughts can put aquatic species under severe selective pressure, force them into refugia, and create genetic bottlenecks. Douglas et al. (2003) in fact found strong evidence for such a bottleneck for FLSU, apparently a consequence of an extreme drought across intermountain western North America circa 7,500 years BP. Over the centuries, therefore, the spring period of FLSU spawning, larval dispersal, and maturation in nursery habitat has always been a period of wide hydrologic variability.

Air temperature also affects FLSU embryo-larval and fry-juvenile development by affecting water temperatures and evaporation rates. For example, the speed and success rate for FLSU embryo maturation falls off at water temperatures above and below the optimal range of 18–20 °C (see chapters 2–4). Periods of spring high air temperatures do not necessarily correspond with periods of drought: historic and prehistoric droughts in the Colorado River basin result from lower winter precipitation in the Rocky Mountains but not necessarily higher temperatures along the LCR (Cayan et al. 2010; Woodhouse et al. 2010). Over the centuries, therefore, the spring period of FLSU spawning, larval dispersal, and maturation in nursery habitat was always a period of wide temperature variability along the LCR, independent of the variability in riverflows.

FLSU thus evolved in an ecosystem prone to wide variation in air temperatures and the availability of water. Prior to river regulation, this variation affected the spatial pattern, extent, timing, and duration of flooding; the timing and duration of flood recession; water temperatures; and the rate of drying of disconnected waters across the flood plain following flood recession. The rate of drying also depended on the intensity and timing of the onset of the naturally hot, dry spring and summer weather—another set of variables affected by long-term variation in weather—in this case, specific to the LCR valley itself.

The evidence therefore suggests that environmental variability naturally would have subjected FLSU to significant mortality during the first few weeks and months following spawning. Some predatory fishes may also consume freshly broadcast FLSU eggs (Weiss et al. 1998). The concentration of eggs at spawning sites makes them particularly vulnerable to consumption, and their availability during the late winter or early spring would provide a food resource during a season of otherwise low productivity (Mueller 2006).

Additionally, numerous native species also likely prey on FLSU larvae, fry, and juveniles, including the carnivorous larvae of several native insects (see chapters 3, 4, and 6). However, the FLSU life history strategy may include adaptations to predation. FLSU produce eggs 3.8–3.9 mm in diameter, roughly a third larger than those of any other catostomid in the Colorado River basin (Snyder and Muth 2004) (see chapter 2). Conceivably, the larger egg size may reduce the potential pool of smaller species that will try to consume FLSU eggs. Further, FLSU grow to a greater size faster than any other large fish in the Colorado River (McAda and Wydoski 1985; Robinson and Childs 2001; Walters et al. 2006, 2012; Sweet et al. 2009). Conceivably, this may reduce the time during which FLSU are vulnerable to attack by the majority of both native and non-native predators in the system.

The FLSU reproductive strategy therefore may be adapted to the extremely low probabilities of survival faced by individual embryos (Minckley 1991; Minckley et al. 2003). The vast majority of eggs, early larvae, and fry would die in most years, but enough would survive in enough years to perpetuate the species. Juvenile and adult survival may not have been easy either, but it would have been less tenuous; and, FLSU become sexually mature after 4–8 years of life (see chapter 2), ready to start trying to produce offspring of their own.

CONCEPTUAL ECOLOGICAL MODEL PURPOSES

Adaptive management of natural resources requires a framework to help managers understand the state of knowledge about how a resource “works,” what elements of the resource they can affect through management, and how the resource will likely respond to management actions. The “resource” may be a population, species, habitat, or ecological complex. The best such frameworks incorporate the combined knowledge of many professionals accumulated over years of investigations and management actions. CEMs capture and synthesize this knowledge (Fischenich 2008; DiGennaro et al. 2012).

CEMs explicitly identify: (1) the variables or attributes that best characterize resource conditions, (2) the factors that most strongly shape or control these variables under both natural and altered (including managed) conditions, (3) the character, strength, and predictability of the ways in which these factors do this shaping/controlling, and (4) how the characteristics of the resource vary as a result of the interplay of its shaping/controlling factors.

By integrating and explicitly organizing existing knowledge in this way, a CEM summarizes and documents: (1) what is known, with what certainty, and the sources of this information, (2) critical areas of uncertain or conflicting science that demand resolution to better guide management planning and action, (3) crucial attributes to use while monitoring system conditions and predicting the effects of experiments, management actions, and other potential agents of change, and (4) how the characteristics of the resource would likely change as a result of altering its shaping/controlling factors, including those resulting from management actions.

A CEM thus translates existing knowledge into a set of explicit hypotheses. The scientific community may consider some of these hypotheses well tested, but others, less so. Through the model, scientists and managers can identify which hypotheses, and the assumptions they express, most strongly influence management actions. The CEM thus helps guide management actions based on the results of monitoring and experimentation. These results indicate whether expectations about the results of management actions—as clearly stated in the CEM—have been met or not. Both expected and unexpected results allow managers to update the model, improving certainty about some aspects of the model while requiring changes to other aspects, to guide the next cycle of management actions and research. The CEM, through its successive iterations, becomes the record of improving knowledge and the ability to manage the system.

CONCEPTUAL ECOLOGICAL MODEL STRUCTURE

The CEM methodology used here expands on that developed for the Sacramento-San Joaquin River Delta Regional Ecosystem Restoration Implementation Plan (DiGennaro et al. 2012). The expansion incorporates recommendations of Wildhaber et al. (2007, 2011), Kondolf et al. (2008), and Burke et al. (2009) to provide greater detail on causal linkages and outcomes and explicit demographic notation in the characterization of life-stage outcomes (McDonald and Caswell 1993). Attachment 1 provides a detailed description of the methodology.

The CEM methodology applied here produces a “life history” model, as is common for CEMs focused on individual species (Wildhaber et al. 2007, 2011). That is, the methodology distinguishes the major life stages or events through which the individuals of a species must pass to complete a full life cycle, including reproducing, and the biologically crucial outcomes of each life stage. These biologically crucial outcomes typically include the number of individuals recruited to the next life stage (e.g., juvenile to adult) or next age class within a single life stage (recruitment rate), or the number of viable offspring produced (fertility rate). It then identifies the factors that shape the rates of these outcomes in the study area and thereby shapes the abundance, distribution, and persistence of the species in that area.

The FLSU conceptual ecological model has five core components as explained further in attachment 1:

- **Life stages** – These consist of the major growth stages and critical events through which the individuals of a species must pass in order to complete a full life cycle.

- **Life-stage outcomes** – These consist of the biologically crucial outcomes of each life stage, including the number of individuals that survive to enter or "transition to" the next life stage (e.g., transition from juvenile to adult) or the next age class within a single life stage (recruitment rate), or the number of viable eggs produced (fertility rate). The rates of the outcomes for an individual life stage depend on the rates of the critical biological activities and processes for that life stage.

- **Critical biological activities and processes** – These consist of the activities in which the species engages and the biological processes that take place during each life stage that significantly affect its life-stage outcomes rates. Examples of activities and processes for a fish species may include spawning, foraging, avoiding predators, and avoiding other specific hazards. Critical biological activities and processes typically are "rate" variables.

- **Habitat elements** – These consist of the specific habitat conditions, the quality, abundance, and spatial and temporal distributions of which significantly affect the rates of the critical biological activities and processes for each life stage. Taken together, the suite of natural habitat elements for a life stage is called the "habitat template" for that life stage. Defining the natural habitat template may involve estimating specific thresholds or ranges of suitable values for particular habitat elements outside of which one or more critical life activities or processes no longer fully support desired life-stage outcome rates—if the state of the science supports such estimates.

- **Controlling factors** – These consist of environmental conditions and dynamics—including human actions—that determine the quality, abundance, and spatial and temporal distributions of important habitat elements. Controlling factors are also called "drivers." A hierarchy of such factors may affect the system at different scales of time and space (Burke et al. 2009). For example, the availability of spawning sites may depend on factors such as riverflow rates, sediment transport rates, and flow-path morphology, which in turn may depend on factors such as dam design, reservoir morphology, and dam operations, which in turn are shaped by watershed geology, vegetation, climate, land use, and water demand.

The CEM identifies these five types of core components and the causal relationships among them that affect life-stage outcome rates. Further, the CEM assesses each causal linkage based on four properties to the extent possible with the available information: (1) the character and direction of the effect, (2) the magnitude of the effect, (3) the predictability (consistency) of the effect, and (4) the status (certainty) of a present scientific understanding of the effect.

The CEM for each life stage thus identifies the causal relationships that most strongly support or limit the rates of its life-stage outcomes, support or limit the rate of each critical biological activity or process, and support or limit the quality, abundance, and distribution of each habitat element (as these affect other habitat elements or affect critical biological activities or processes). In addition, the CEM for each life stage highlights areas of scientific uncertainty concerning these causal relationships, the effects of specific management actions aimed at these relationships, and the suitability of the methods used to measure habitat and population conditions. Attachment 1 provides further details on the assessment of causal relationships, including the use of diagrams and a spreadsheet tool to record the details of the CEM and summarize the findings.

Chapter 2 – FLSU Life Stage Model

A life stage consists of a biologically distinct portion of the life cycle of a species during which individuals undergo distinct developments in body form and function, engage in distinct behaviors, use distinct sets of habitats, and/or interact with their larger ecosystems in ways that differ from those associated with other life stages. This chapter proposes a life stage model for FLSU in the LCR on which to build the CEM.

No single, formal classification of life stages exists for FLSU in either the upper or lower Colorado River basins. However, the species is relatively well studied, particularly in the UCRB, and the broad outline of its life history is relatively well understood. Bezzerides and Bestgen (2002), Mueller and Marsh (2002), Snyder and Muth (2004), Reclamation (2005, 2008), Rees et al. (2005), UDWR (2006), Carman (2007), and Minckley and Marsh (2009) summarize critical information on FLSU life history stages. Snyder and Muth (2004) formally distinguish larval developmental stages.

EVIDENCE FOR FLANNELMOUTH SUCKER LIFE STAGES

As summarized by Bezzerides and Bestgen (2002), Snyder and Muth (2004), Reclamation (2005, 2008), Rees et al. (2005), and Minckley and Marsh (2009), spawning FLSU deposit and fertilize their eggs directly on or immediately above shallow (depth 1–2 m) beds of sand, gravel, and cobbles with flow velocities of 0.5–1.0 m/s (McAda and Wydoski 1985; Mueller and Wydoski 2004). FLSU produce eggs 3.8–3.9 mm in diameter, roughly a third larger than those of any other catostomid fish (*aka* suckers) (Cooke et al. 2005) in the Colorado River basin (Snyder and Muth 2004). The eggs adhere to the substrate after settling to the bottom, with some settling into interstices among gravel and cobble. Eggs that do not adhere to or settle into interstitial spaces in the substrate may be swept up by currents, exposing them to predation or redepositing them in settings unsuitable for their further development (Robinson et al. 1996, 1998). Bestgen et al. (2011a) also noted that water flowing through interstitial spaces likely keeps developing eggs and newly hatched larvae well supplied with oxygen. Egg incubation time varies with temperature: McAda (1977) reported incubation times of 6–7 days at 15.6–17.8 °C; Haines (1995) reported incubation times of 6 days at 20 °C up to 16 days at 12 °C; and Ward (2001) reported that FLSU eggs at 20 °C began hatching 5 days following fertilization. Hatched larvae are 11–12 mm TL.

Thieme (1997) states that swim-up occurs 20–28 days following hatching along the Paria River in water averaging 12 °C, while Ward (2001) observed swim-up as early as 5 days following hatching at 20 °C in a laboratory setting. Snyder and Muth (2004) noted that swim-up coincides approximately with the transition from protolarval to flexion mesolarval morphology, when the larvae are 13–14 mm TL. Yolk assimilation is complete shortly following swim-up (Snyder and Muth 2004).

Following swim-up, FLSU larvae (fry) drift but control their movements into and out of currents. Robinson et al. (1996, 1998) observed that FLSU fry captured while drifting along the lower Little Colorado River on average consisted of approximately 25% protolarvae, 67% mesolarvae, and 8% metalarvae. The investigators also reported capturing drifting protolarvae and mesolarvae overwhelmingly in near-shore settings and drifting metalarvae mostly mid-channel. The initiation of drifting thus did not coincide exactly with the transition from proto- to mesolarval morphology, while the transition from meso- to metalarval morphology was associated with a relative shift in drifting behavior.

The investigations along the Little Colorado River by Robinson et al. (1996, 1998) also found that the timing of FLSU larval drift did not correlate strongly with the timing of higher or lower rates of river discharge. This finding indicates that the larvae controlled the timing of their drifting rather than drifting solely under the control of river currents. However, their study did not span any large runoff events, and both they and others (e.g., Thieme 1997; Zelasko et al. 2011) cited evidence that large runoff events can sweep drifting FLSU larvae far downstream. The literature is divided on whether FLSU larvae show any diel pattern in their drift (Robinson et al. 1996, 1998; Bezzerides and Bestgen 2002; Reclamation 2008; Rees et al. 2005). For example, Bezzerides and Bestgen (2002) cited one study that found more FLSU larval drifting at night than in the daytime along the main stem Colorado River, while Robinson et al. (1996, 1998) found the opposite along the lower Little Colorado River.

FLSU fry typically drift a moderate distance before moving into rearing (*aka* "nursery") habitat. Robinson et al. (1998) reported an average drift distance of 8.6 kilometers (km) along the lower Little Colorado River. Investigations conducted by Reclamation below Davis Dam have showed FLSU in rearing habitat up to 45 km downstream from the downstream-most spawning site below the dam (Best and Lantow 2012; E. Best 2015, personal communication).

FLSU fry drift and navigate to rearing habitats consisting of low-velocity (< 0.2 m/s) environments along shorelines and in embayments, shallow near-shore pools, and backwater areas. Mueller and Marsh (2002) noted a possible preferential use of submergent vegetation as cover. As discussed by Bezzerides and Bestgen (2002), Mueller and Marsh (2002), Rees et al. (2005), Reclamation (2008), and Minckley and Marsh (2009), the larvae feed primarily on aquatic invertebrates, including insect larvae, zooplankton, and phytoplankton, as well as particulate organic matter (POM) (Joseph et al. 1977; Maddux et al. 1987 cited in Bezzerides and Bestgen 2002; Childs et al. 1998).

FLSU larvae complete their transition to juvenile morphology over a timespan of 2–3 months, during which time they grow to approximately 30 mm TL (Snyder and Muth 2004; Reclamation 2008). They then mostly remain in these nursery environments for another 1–2 months before dispersing (see below). Valdez et al. (2000) classify FLSU larvae and juveniles within nursery habitats together as "Juvenile I," with a size range of approximately 15–50 mm TL. Investigations of FLSU along LCR Reach 3 between Davis Dam and Lake Havasu (Best and Lantow 2012; E. Best 2015, personal communication) occasionally find juveniles up to 62 mm TL in nursery habitats but none larger.

FLSU juveniles disperse from their nursery areas into habitats with a wider range of depths and flow velocities, including runs and edges of riffles (Holden 1999). Habitat use following dispersal from nursery sites along the LCR is not well understood. During investigations of FLSU along LCR Reach 3 between Davis Dam and Lake Havasu, it was found that once juveniles disperse from nursery sites, they become undetectable by existing monitoring methods until they reach age 2 or 3 (see below) (Best and Lantow 2012; E. Best 2015, personal communication). Investigations elsewhere indicate that FLSU continue to feed in benthic habitat following their dispersal from their nursery sites, focusing on aquatic and submerged terrestrial plant litter, algae, and aquatic invertebrates, but including increasingly large-sized matter (see "Foraging," chapter 3) (Bezzerides and Bestgen 2002; Rees et al. 2005; Reclamation 2008). Rees et al. (2005) reported no evidence of variation in food preference related to "… season, hydrological cycles, or migration, or between juvenile and adult stages."

FLSU, following dispersal from their nursery sites, achieve lengths of 90–100 mm TL by the end of their first year and 140–150 mm TL by age 1.5; reach sexual maturity after 4–6 years, as they reach 400–600 mm TL; and may live until age 15–30 and reach > 600 mm TL (McAda and Wydoski 1985), with all individuals mature by age 8 (Bezzerides and Bestgen 2002; Mueller and Marsh 2002; Reclamation 2005, 2008; Rees et al. 2005; Walters et al. 2006; Minckley and Marsh 2009). During investigations of FLSU along LCR Reach 3 between Davis Dam and Lake Havasu, small, sexually ripe males, 350–400 mm TL, have been occasionally found, but FLSU smaller than 400–500 mm TL have not been seen attempting to spawn (Best and Lantow 2012; E. Best 2015, personal communication).

Valdez et al. (2000) proposed identifying an age class, "Juvenile II," 50–200 mm TL, as a separate life stage, distinct from subadults and adults. However, other authors (e.g., Gido and Propst 1999; Best and Lantow 2012) found no biological or ecological reason to distinguish separate life stages among FLSU following dispersal from their nursery sites until they became sexually active. This life interval covers individuals roughly from 50 to 350 mm TL and ages roughly from 0.5 to 4–6 years. Investigations of FLSU conducted along LCR Reach 3 between Davis Dam and Lake Havasu have rarely resulted in detections or captures of individuals in this age/size range (Best and Lantow 2012; E. Best 2015, personal communication). This gap in detection suggests that FLSU in this age/size range use a different range of habitat settings and/or experience higher rates of predation than do larger individuals/adults.

FLSU typically spawn in March–April below Glen Canyon Dam and along the LCR, including in tributaries to these reaches, and in April to June further upstream (Angradi et al. 1992; Valdez et al. 2000; Bezzerides and Bestgen 2002; Rees et al. 2005; Reclamation 2008; Budy et al. 2009; Minckley and Marsh 2009; Zelasko et al. 2011; Best and Lantow 2012; Farrington et al. 2013; E. Best 2015, personal communication). Spawning occasionally may occur later in the year, too: Douglas and Douglas (2000) presented evidence of FLSU spawning mid-fall 1998 in Havasu Creek, a Grand Canyon tributary. The Arizona Game and Fish Department [AGFD] (2001) also recorded FLSU larvae drifting along the Little Colorado River "in Grand Canyon" in February 1994, indicating a spawning event sometime in December 1993 or January 1994. Males may become fertile sooner in the year than females and remain fertile longer (e.g., as summarized in UDWR 2006). Spawning may take place over a period of 6 or more weeks along individual tributaries and river reaches (Farrington et al. 2013) as summarized by Bezzerides and Bestgen (2002).

The onset of spawning along a given river reach and its tributaries appears to be triggered by changes in water temperature rather than river discharge (Bezzerides and Bestgen 2002; Rees et al. 2005; Reclamation 2008; Minckley and Marsh 2009; Zelasko et al. 2011) (see chapters 4 and 6). FLSU spawn today along the LCR between Davis Dam and Lake Havasu, a section of the river subject to highly unnatural discharges governed by demand for municipal and irrigation water supply unrelated to the natural flow regime (see "Water Flow/Turbulence," chapter 4). This section of the river experiences a modified thermal regime as well, but air temperatures have a strong effect on water temperatures, resulting in relatively natural annual and diurnal patterns of temperature *variation* around the modified annual and daily average temperatures (see "Water Temperature," chapter 4). However, a change in photoperiod has also been proposed as a spawning cue (Robinson et al. 1998; Hoffnagle et al. 1999).

Ripe adults may aggregate at or near spawning locations for several weeks prior to spawning (Valdez et al. 2000). However, the literature does not consistently identify such staging as a distinct period within the spawning cycle.

Spawning occurs at locations other than normal feeding habitat, and FLSU may travel some distance to reach a spawning site (Budy et al. 2009; Best and Lantow 2012). As discussed by Bezzerides and Bestgen (2002), the extent of movement to spawning sites may vary with several factors (see also Snyder and Muth 1990; Weiss et al. 1998). For example, spawning may occur at only a limited number of locations in the Grand Canyon, including tributary mouths. However, spawning sites appear to be much more widely available in the UCRB, possibly simply as a consequences of differences in river morphology (Holden and Stalnaker 1975).

FLSU spawning occurs in aggregations. For example, Mueller and Wydoski (2004) observed an aggregation of > 200 FLSU spawning along the LCR main stem between Davis Dam and Lake Havasu. As summarized by Mueller and Marsh (2002), "… males position themselves over the spawning area where they wait for females. When a female is ready to spawn, she enters the area and is joined by one or more males who fertilize her eggs as they are deposited over the gravel. When finished, she leaves, and the males resume their wait for another ripe female." Investigators report male:female ratios at spawning sites ranging from 1:1 up to 3:1 (Weiss 1993). These ratios suggest the possibility that only a fraction of the female adult population may participate in spawning in some years (see summaries by Rees et al. 2005; Reclamation 2008).

PROPOSED FLANNELMOUTH SUCKER LIFE STAGES

The evidence summarized above suggests that the CEM for FLSU should recognize five life stages and seven life-stage outcomes as follows and as summarized in table 1 and figure 1. The life stages are numbered sequentially beginning with the eggs and protolarvae:

Table 1.—FLSU life stages in the LCR ecosystem

Life stage	Life-stage outcome(s)
1. Eggs and protolarvae	• Egg and protolarval survival rate
2. Fry and early juveniles	• Fry and early juvenile survival rate
3. Older juveniles and subadults	• Older juvenile and subadult survival rate
4. Adults	• Adult survival rate • Adult reproductive participation rate
5. Spawning adults	• Spawning adult survival rate • Spawning adult fertility rate

1. **Eggs and protolarvae:** This life stage begins when spawning adults release their gametes and depart the scene of individual spawning events, continues through egg incubation and hatching, and ends with larval morphological transition from protolarval to flexion mesolarval morphology and swim-up at approximately 13–14 mm TL. This life stage has a single life-stage outcome, designated S_{EM}, the rate of survival of (recruitment from) the life stage.

2. **Fry and early juveniles:** This life stage begins with larval swim-up and dispersal to nursery habitat, includes the transformation from metalarval to juvenile body morphology, and ends with dispersal of transformed juveniles beyond their nursery habitat. The life stage spans approximately the first 4–5 months of life following swim-up, with growth to approximately 50 mm TL. Some juveniles may remain in their nursery habitat longer than others. The life stage has a single life-stage outcome, designated S_{FJ}, the rate of survival of (recruitment from) the life stage. LCR MSCP staff also move FLSU fry from Lake Mead, from its Colorado River inflow, to a rearing facility for use in research (Reclamation 2014). Under the program, approximately 100 reared juveniles are repatriated annually to the river below Davis Dam, where they constitute an additional source of recruits to the next life stage. The present CEM does not address this rearing program.

3. **Older juveniles and subadults:** This life stage begins after FLSU juveniles disperse from their nursery habitat, roughly around the middle of their first year. They grow from roughly 50 to 350 mm TL. This life stage ends when they reach sexual maturity, usually during their fourth to sixth year of life. This life stage has a single life-stage outcome, designated S_{JA}, the rate of survival of (recruitment from) the life stage.

4. **Adults:** This life stage covers all age classes of sexually mature FLSU, which may achieve lifespans approaching 30 years (see above), and individuals from roughly 350 to more than 600 mm TL. The adult life stage has two life-stage outcomes: (1) S_{AA}, the rate of survival of adults from year to year so that they remain part of the adult population (Rees et al. 2005), and (2) P_{SA}, the percentage of adult females that participate in and contribute gametes to spawning per year.

5. **Spawning adults:** This life stage covers adult FLSU during the times in which they participate in spawning. This life stage begins when would-be spawners leave their home territories to move toward spawning sites and ends when these individuals return to their home territories. This life stage thus encompasses the time FLSU spend at spawning sites, and the time they spend traveling to and from these sites. The life stage has two life-stage outcomes: (1) S_{SA}, the rate of survival of spawning adults to return to the adult population following spawning, and (2) R_{SP}, the rate of production of fertilized eggs (fertility rate) at spawning sites.

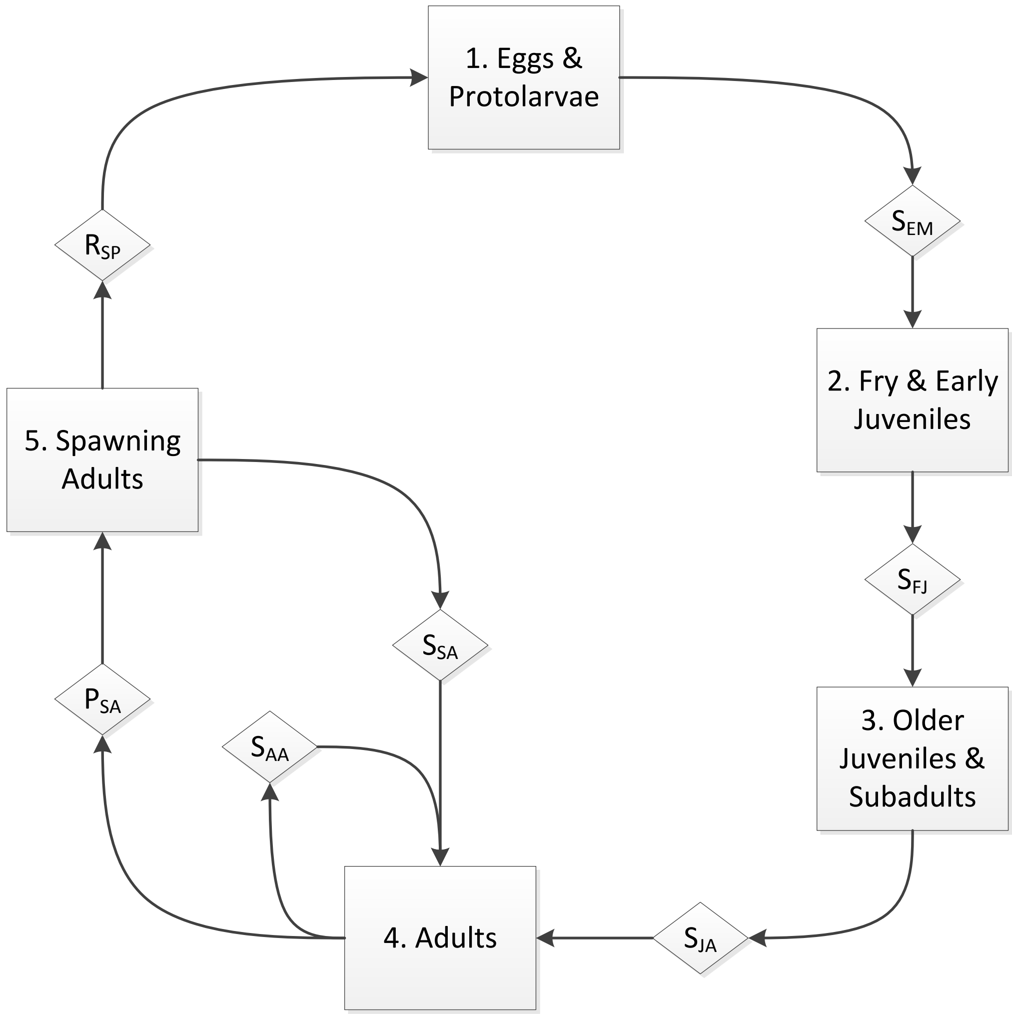

Figure 1.—Proposed FLSU life history model.
Squares indicate the life stage, and diamonds indicate life-stage outcomes.
S_{EM} = the rate of survival of (recruitment from) the eggs and protolarvae life stage,
S_{FJ} = the rate of survival of (recruitment from) the fry and early juveniles life stage,
S_{JA} = the rate of survival of (recruitment from) the older juveniles and subadults life stage,
S_{AA} = the rate of survival of adults from year to year so that they remain part of the adult population, P_{SA} = the percentage of adult females that participate in and contribute gametes to spawning per year, S_{SA} = the rate of survival of spawning adults to return to the adult population following spawning, and R_{SP} = the rate of production of fertilized eggs per spawning adult at spawning sites.

These life stages, illustrated on figure 1, provide the framework for a CEM addressing FLSU ecology, demography, and distribution in the LCR. The model does not address FLSU genetic dynamics. However, FLSU are known to hybridize occasionally with other native and non-native catostomids, including native razorback sucker (*Xyrauchen texanus*) (RASU) and bluehead sucker (*Catostomus discobolus*), and the non-native white sucker (*Catostomus commersonii*) (e.g., see discussions and citations of older literature in Bezzerides and Bestgen 2002; Mueller and Marsh 2002; Rees et al. 2005; Minckley and

Marsh 2009; Douglas and Douglas 2010). Hybrids may be fertile (Tyus and Karp 1990; Douglas and Marsh 1998; Bezzerides and Bestgen 2002; Bestgen et al. 2006; Douglas and Douglas 2010). Hybridization diminishes the effective fertility of non-hybrid FLSU spawning adults, and crosses may compete with non-hybrid FLSU for food or physical habitat (see "Hybridization," chapter 3).

Chapter 3 – Critical Biological Activities and Processes

Critical biological activities and processes consist of activities in which the species engages and biological processes that take place during each life stage that significantly shape the rate(s) of the outcome(s) for that life stage. Critical biological activities and processes are "rate" variables.

The CEM identifies 12 critical biological activities and processes that affect 1 or more FLSU life stages. Some of these activities or processes differ in their details among life stages. For example, FLSU of different life stages differ in their swimming agility, strength, and stamina. However, grouping activities or processes into broad types across all life stages makes it easier to compare the individual life stages to each other across the entire life cycle. Table 2 lists the 12 critical biological activities and processes and their distributions across the 5 FLSU life stages. Each critical activity or process listed in table 2 directly or indirectly affects one or more outcomes for each indicated life stage.

Table 2.—Critical biological activities and processes by life stage

Life stage ➔ / **➔ Critical biological activity or process**	**Eggs and protolarvae**	**Fry and early juveniles**	**Older juveniles and subadults**	**Adults**	**Spawning adults**
Chemical stress	X	X	X	X	X
Competition	X	X	X	X	X
Disease	X	X	X	X	X
Drifting		X			
Foraging	X	X	X	X	X
Hybridization					X
Long-distance movement			X	X	X
Mechanical stress	X	X	X	X	X
Predation	X	X	X	X	X
Resting		X	X	X	X
Swimming		X	X	X	X
Thermal stress	X	X	X	X	X

The basic sources of the information used to identify and characterize FLSU critical biological activities and processes across all life stages are Holden (1999), Bezzerides and Bestgen (2002), Mueller and Marsh (2002), Snyder and Muth (2004), Reclamation (2005, 2008), Rees et al. (2005), UDWR (2006), Carman (2007), and Minckley and Marsh (2009). Identification and characterization integrate information from both older and more recent works as well as the expert knowledge of Reclamation fish biologists. The following paragraphs discuss the 12 critical biological activities and processes in alphabetical order.

CHEMICAL STRESS

All freshwater fishes are vulnerable to stress and mortality due to an insufficient supply of dissolved oxygen (DO) and exposure to unsuitable levels of salinity and harmful dissolved contaminants. Cooke et al. (2005) summarized evidence that water pollution is a common threat to suckers (Catostomidae) in North America in general. However, few studies have specifically examined FLSU sensitivity to altered water chemistry in either laboratory or field settings (Hamilton and Buhl 1997; Canton 1999; Hamilton 1999). Studies of FLSU distribution and incidences of external evidence of stress on captured FLSU have led some investigators to propose that FLSU are sensitive to exposure to chemical pollutants, as reviewed by Hamilton and Buhl (1997), Hamilton (1999), and Rees et al. (2005). Chemical stress, whether acute or chronic, may impair a range of bodily functions, making the affected individuals less fit and therefore vulnerable to additional stress or mortality from other causes. However, as FLSU mature, they presumably become increasingly able to avoid or remove themselves from settings in which they sense chemically unsuitable conditions—if these conditions are sufficiently localized to permit such avoidance or escape.

COMPETITION

FLSU in every motile life stage must compete with other species for food and habitat, as must all animal species. For example, FLSU may prefer or require the same food materials, same types of cover, or same spawning sites as other aquatic species, and FLSU also may compete with each other for such resources. Chapters 4 and 6 discuss the range of competitors that FLSU in each life stage potentially face. For example, FLSU larvae may face competition from other fish larvae that prey on the same range of small, aquatic invertebrates or browse on the same kinds of benthic particulate matter. Every animal species evolves strategies that allow it to persist despite such competition, including behaviors that allow it to avoid or defend against competition. Avoidance behaviors may include a preference for resources other than those preferred by other species in the system (resource partitioning) or an ability to switch among alternative resources as needed. However, such behaviors may not be sufficient to afford every individual FLSU full access to all necessary resources. Chapter 6 also discusses the evidence for avoidance and defensive behaviors with which FLSU may face competition in each life stage.

DISEASE

FLSU are vulnerable to infection, as are all freshwater fishes, including that by bacteria, fungi, and parasites (Joseph et al. 1977; Brienholt and Heckmann 1980; Flagg 1982; Hamilton and Buhl 1997; Landye et al. 1999; Linder et al. 2012). Non-native fishes are often cited as potential sources of the non-native pathogens and parasites that may affect FLSU and other native fishes of the LCR (Miller 1952; Heckmann et al. 1986; Haden 1992; Mueller and Marsh 2002; Mueller 2005; Cucherousset and Olden 2011). However, FLSU may not be as susceptible to infection by some introduced parasites—e.g., the Asian fish tapeworm (*Bothriocephalus acheilognathias*)—as are other native fishes of the LCR (Brouder and Hoffnagle 1997). During several studies, FLSU have been observed that, while showing signs of infection, did not appear to be debilitated by their disease loads (Joseph et al. 1977; Flagg 1982). However, infections may make the affected individuals vulnerable to further harm or mortality from other causes.

DRIFTING

FLSU larvae relocate from their natal sites to nursery habitat by drifting, as discussed in chapter 2. Lateral and reverse currents, such as those that occur in eddies, transport drifting larvae into and out of high- versus low-velocity settings along their drift paths. Channel sections along which lateral and reverse currents draw drifting larvae out of the main line of downstream flow into low-velocity settings such as shoreline embayments may be termed "interception habitats." The term originates in a CEM developed for the endangered pallid sturgeon (*Scaphirhynchus albus*) to support species recovery along the Missouri River (W. Nelson-Stastny 2015, personal communication). Kinzli and Myrick (2010) presented a similar concept for the role of river channel shoreline features in intercepting eggs of the Rio Grande silvery minnow (*Hybognathus amarus*).

FLSU larvae also control their drifting by swimming between high- versus low-velocity and lateral versus longitudinal currents, as do other fish larvae in the LCR (Modde and Haines 2005; Valdez et al. 2011). Robinson et al. (1996, 1998) observed that FLSU proto- and mesolarvae both drift and rest in low-velocity, near-shore settings, while FLSU metalarvae drift less but do so more often mid-channel than along near-shore settings. Large runoff events, however, may radically dislocate drifting FLSU larvae. As also noted in chapter 2, the literature is divided on whether FLSU show any preference for drifting at any particular time of day (Robinson et al. 1996, 1998; Bezzerides and Bestgen 2002; Reclamation 2008; Rees et al. 2005). Robinson et al. (1998) reported an average drift distance of 8.6 km along the lower Little Colorado River, but longer drift distances are also possible (Zelasko et al. 2011). After drifting, FLSU larvae move preferentially into low-velocity (< 0.2 m/s) habitats along shorelines and in embayments, shallow near-shore pools, and backwater areas.

FORAGING

FLSU begin foraging as larvae as they finish assimilating their yolk and become able to swim, and continue through all remaining life stages. Carlson et al. (1979), Weiss (1993), Bezzerides and Bestgen (2002), Mueller and Marsh (2002), Rees et al. (2005), Reclamation (2008), Minckley and Marsh (2009), and Bestgen et al. (2011a) summarized numerous studies of the FLSU diet and its variation with life stage. FLSU larvae are omnivorous, feeding primarily on diatoms, algae, smaller insect larvae, zooplankton (e.g., cladocera, copepods, and ostracods), and POM (Joseph et al. 1977; Maddux et al. 1987 cited in Bezzerides and Bestgen 2002; Childs et al. 1998). They show a strong preference for aquatic larvae of chironomids (non-biting midges) and simuliids (black flies). They feed predominantly along the bottom of the water column (Childs et al. 1998), and their stomach contents consequently include substantial quantities of fine inorganic matter (e.g., sand). In fact, mixed organic and inorganic matter is by far the most common component of FLSU larval stomach contents. They appear to switch readily among food items depending on what is available (Minckley 1991).

As FLSU mature, they remain omnivorous and expand their diet to include larger aquatic invertebrates such as scuds (*Gammarus*) and terrestrial insects (Muth and Snyder 1995; Bezzerides and Bestgen 2002; Rees et al. 2005; Reclamation 2008; Zahn Seegert et al. 2014). Mixed organic and inorganic debris remains by far the most common component of FLSU juvenile and adult stomach contents (e.g., Snyder and Muth 1995; Zahn Seegert et al. 2014). They continue to feed preferentially in benthic habitat (≈ 1.0–1.5 m depth) (Karp and Tyus 1990; Beyers et al. 2001). FLSU adult morphology, specifically the ventral mouth position and very large, fleshy, protrusible lips, may be specifically adapted for benthic feeding (Rees et al. 2005). Juvenile and adult FLSU also continue to feed heavily on chironomid and simuliid larvae (Zahn Seegert et al. 2014). In fact, the AGFD reintroduced FLSU into the LCR below Davis Dam in 1976 specifically to help control black flies in this reach; however, the impacts were never monitored (Mueller and Wydoski 2004).

Rees et al. (2005) report that "[t]he research [on FLSU] to date reports no shift in food preference due to season, hydrological cycles, or migration, or between juvenile and adult stages." Additionally, no studies indicate that FLSU feed preferentially either during the day or night (Beyers et al. 2001).

HYBRIDIZATION

Numerous publications (e.g., Hubbs and Miller 1953; Buth et al. 1987; Douglas and Marsh 1998; Ryden 2000a; Bezzerides and Bestgen 2002; Mueller and Marsh 2002; Rees et al. 2005; Bestgen and Zelasko 2004; Bestgen et al. 2006, 2007a; Minckley and Marsh 2009; Douglas and Douglas 2010; Zelasko et al. 2011; Webber et al. 2013) presented or summarized evidence that FLSU occasionally hybridize with other catostomids, including native RASU and bluehead sucker, and the non-native white sucker. Hybridization arises because these species sometimes spawn at the same places and times. A few crosses may be fertile, as evidenced by backcrosses (Tyus and Karp 1990; Douglas and Marsh 1998; Bezzerides and Bestgen 2002; Bestgen et al. 2006; Douglas and Douglas 2010). The introduced white sucker may facilitate further hybridization among the natives because it can produce fertile hybrids with all the native catostomids in the basin (Douglas and Douglas 2010; Cucherousset and Olden 2011).

Neither bluehead sucker nor white sucker occur within the LCR, let alone specifically within the geographic range of FLSU within the LCR (Bezzerides and Bestgen 2002; Fuller 2014). However, the geographic range of FLSU within the LCR does overlap with that of RASU. FLSU occur within a single reach of the LCR, between Davis Dam and Lake Havasu, and RASU occur throughout the LCR (Reclamation 2008). Hybridization between these two species within the LCR therefore remains a possibility. However, RASU numbers remain very low throughout the LCR (Reclamation 2014), and hybridization between FLSU and RASU between Davis Dam and Lake Havasu therefore likely is rare.

As noted in chapter 2, hybridization of FLSU with other catostomids poses two kinds of threats to FLSU viability within the LCR. First, it diminishes the effective fertility of non-hybrid FLSU spawning adults because some FLSU gametes fertilize or are fertilized by another species. FLSU-RASU crosses diminish the effective fertility of both species. Second, crosses may compete with non-hybrid FLSU for food or physical habitat (Douglas and Marsh 1998; Bezzerides and Bestgen 2002; Mueller and Marsh 2002; Rees et al. 2005; Minckley and Marsh 2009; Douglas and Douglas 2010; Zelasko et al. 2011). For example, Anderson and Stewart (2007) found that, unlike FLSU and other native suckers, white sucker and its hybrids can persist in western Colorado regardless of alterations to the flow regime, giving them an adaptive advantage over the native suckers.

LONG-DISTANCE MOVEMENT

FLSU move relatively often among stream/river reaches over long distances, over timespans of weeks to months, in the absence of dams that block such movement. Bezzerides and Bestgen (2002) provided a detailed review of the topic (see also more recently Bestgen and Zelasko 2004; Rees et al. 2005; Compton et al. 2008; Budy et al. 2009; Bestgen et al. 2011a; Zelasko et al. 2011; Bottcher et al. 2013; Cathcart 2014). Long-distance movement nominally is a subset of swimming activity, as discussed below (see “Swimming,” this chapter). However, long-distance movement by FLSU is affected by some habitat elements that do not affect other aspects of FLSU swimming. For this reason, the present assessment addresses FLSU long-distance movement as a separate critical activity.

Chart and Bergersen (1992) found that, when not traveling more widely, larger FLSU (> 400 mm TL) tended to remain within home ranges spanning < 1 km of stream length, and smaller adults tended to remain within ranges spanning roughly 10 km of stream length within any single year. The present study therefore defines FLSU “long-distance movement” as movement of individual fishes over distances > 10 km in a single year.

FLSU long-distance movements have been measured to span both upstream and downstream distances exceeding 200 river km. These movements may, but do not necessarily, involve travel to or from spawning sites. Many of the studies of FLSU movement were carried out to assess the impacts of dams, where congregations in tailwater below the dams suggest that the dams blocked further upstream movement (Chart and Bergersen 1992; McKinney et al. 1999; Budy et al. 2009). Budy et al. (2009) found that the timing of FLSU long-distance movement followed the same pattern as the historic rise and fall of the annual Colorado River hydrograph even in streams with altered flow regimes. Downstream movement appears to be active rather than passive (i.e., not merely transport by river currents) and more common than upstream movement (Holden 1973; Chart and Bergersen 1992; McIvor and Thieme 1999; Compton et al. 2008; Budy et al. 2009).

MECHANICAL STRESS

FLSU are vulnerable to stress and outright physical destruction due to mechanical impacts, abrasions, burial, or exposure. In theory, native fishes in the LCR may encounter many situations that result in mechanical stress, including encounters with propeller blades, propeller wash, or a jet-ski intake; entrainment by flow velocities and turbulence in excess of tolerable ranges; burial by a rapid influx of sediment; stranding by a sudden drop in water level; inundation by water levels too deep for embryos to mature; recreational fishing catch and release; competitor (agonistic) attacks or unsuccessful predator attacks; and scientific sampling (Karp and Tyus 1990; Landye et al. 1999; Clarkson and Childs 2000; Ward 2001, 2006; Ward et al. 2002; Ward and Hilwig 2004; Montony 2008; Walters et al. 2006; UDWR 2009a; Van Haverbeke et al. 2013). However, some of these mechanical stresses may be unlikely along the single LCR reach that FLSU currently occupy, from just below Davis Dam down to the head of Lake Havasu. For example, abrupt influxes of sediment are probably rare, as water released from Davis Dam does not contain much sediment. FLSU may also cause mechanical stress to themselves (e.g., through anal fin abrasion during spawning) (Weiss et al. 1998). Mechanical stress that does not fatally injure FLSU nevertheless may leave the affected individuals vulnerable to wound infections (Landye et al. 1999) or to mortality from other causes. Younger FLSU may have lesser abilities to avoid or escape settings in which they may sense mechanically hazardous conditions, such as zones of high flow velocity (Clarkson and Childs 2000). However, as FLSU mature, their increasing strength should make it possible for them to avoid or escape such settings so long as the adverse conditions are sufficiently localized to permit avoidance or escape.

PREDATION

FLSU experience mortality due to predation during every life stage, as do all wild animals. In turn, every prey species necessarily has evolved adaptations that allow it to persist despite predation. Such adaptations may include particular behaviors, body features, or reproductive strategies that allow it to detect and avoid, escape, defend against, or demographically compensate for losses from predation. Predation on FLSU, and FLSU adaptations to predation, are topics of some interest across the Colorado River basin in general: FLSU appear less affected by the presence and abundance of numerous species of non-native predatory fishes in the Colorado River basin than do RASU and BONY, the other two large, native prey fishes of the LCR (Weiss 1993; Bezzerides and Bestgen 2002; Mueller and Marsh 2002; Paukert and Rogers 2004; Rees et al. 2005; Reclamation 2005). The historic extirpation of FLSU in the LCR also appears to have resulted from factors other than—or less dominated by—predation by non-native fishes (Mueller and Marsh 2002; Mueller and Wydoski 2004). Further, FLSU readily re-occupied the LCR between Davis Dam and Lake Havasu following their reintroduction in 1976 (Mueller and Wydoski 2004) despite an abundance of non-native predators along this river reach. This latter situation contrasts with that of RASU and BONY in the LCR, among which predation by non-native fishes appears to be a major cause of mortality, low population numbers, and tenuous persistence (Marsh and Pacey 2005; Reclamation 2008).

Piscivorous fishes demonstrably prey on FLSU (Miller 1952; Marsh and Douglas 1997; Weiss et al. 1998; Brooks et al. 2000; Ryden 2000a; Ward 2001; Ward et al. 2002; Ward and Bonar 2003; Paukert and Rogers 2004; Miller and Lamarra

2006; Johnson et al. 2008; Pilger et al. 2008; Yard et al. 2011). Chapter 4 provides further information on known and potential fish predators of FLSU. Piscivorous birds may also prey on FLSU, as suggested by wounding marks (Landye et al. 1999) and by analogy with observations of avian predation of other large, native prey fishes of the LCR (Mueller 2006). As discussed further in chapters 4 and 6, fish in each FLSU life stage may experience predation from a distinct spectrum of these species (and sometimes different life stages among these species) with differing predatory behaviors (Brooks et al. 2000; UDWR 2006, 2009a). Some predatory fishes may also consume freshly broadcast FLSU eggs (Weiss et al. 1998).

A study of trophic relationships among Colorado pikeminnow (*Ptychocheilus lucius*) and its prey in the San Juan River (Franssen et al. 2006) indirectly suggests one possible reason why FLSU experience lower overall rates of mortality from predation than do RASU and BONY. The authors noted differences in the availability of native versus non-native fish prey for the Colorado pikeminnow during early spring. They suggest that native fish larvae may appear earlier in the spring than do non-native larvae, providing an early pulse of prey for a wide spectrum of smaller age classes of predators that depend on small prey. However, FLSU larvae reportedly grow larger faster than do the larvae of either RASU or BONY (McAda and Wydoski 1985; Robinson and Childs 2001; Snyder and Muth 2004; Walters et al. 2006, 2012; Reclamation 2008; Sweet et al. 2009). This faster growth rate conceivably could help FLSU larvae and fry "run the gauntlet" of spring predators better than can RASU or BONY.

The historic, unregulated LCR supported far fewer predators than does the present-day system (Mueller and Marsh 2002). However, native predators nevertheless would have shaped the evolution of FLSU behavioral and morphological adaptations to predation. The Colorado pikeminnow was the only large, predatory fish native to the LCR (Mueller and Marsh 2002; U.S. Fish and Wildlife Service [USFWS] 2002; Portz and Tyus 2004; Franssen et al. 2007). The species lacks teeth in its jaws and instead uses pharyngeal teeth to grasp and hold its prey. Pikeminnow adults often exceed 500 mm TL and have been recorded to approach 1,800 mm TL (USFWS 2002), and they become exclusively piscivorous after reaching $\approx$ 200 mm TL. Their selection of prey is strongly gape limited (Vanicek and Kramer 1969; Portz and Tyus 2004).

Franssen et al. (2007) and Ryden (D. Ryden 2013, personal communication) estimated that pikeminnow prefer deep-bodied prey no more than 33–37% of their own body length. Based on size preferences, a 500-mm TL pikeminnow thus would prey preferentially on fishes less than 165–185 mm TL, and a 1,000-mm TL pikeminnow would prey on fishes less than 330–370 mm TL. Consequently, FLSU up to roughly age 6–8 (i.e., up to early adulthood) would have been subject to pikeminnow predation (e.g., see FLSU age-size curves for Grand Canyon presented by Walters et al. 2006, 2012). Further, pikeminnow consume primarily small-bodied, soft-rayed, cylindrical prey lacking a dorsal keel (Vanicek and Kramer 1969; USFWS 2002; D. Ryden 2013, personal communication). FLSU lack any substantial dorsal keel, particularly when young. Over evolutionary time, pikeminnow predation therefore could have shaped the evolution of FLSU body form and strategies for coping with predation, which in turn affect FLSU vulnerability to the predators in the system today (see chapters 1 and 3).

Other native fishes may also prey or have preyed on FLSU. Walters et al. (2012) noted the possibility that age-1 humpback chub (*Gila cypha*) may prey on age-0 FLSU in the Grand Canyon.

RESTING

FLSU need to rest to conserve energy during every mobile life stage. They may have specific preferences for habitat conditions in locations where they seek to rest that afford them suitable proximity to food resources and protection from predators and thermal, chemical, or mechanical stress. These preferences may differ among life stages and vary with time of day. Specifically, FLSU larvae find shelter in interstitial spaces in cobble substrates. Many native fishes of the Colorado River, as larvae following swim-up, seek shelter along shorelines during the day and drift preferentially at night. However, the literature is divided over such diel sheltering among FLSU larvae (Robinson et al. 1996, 1998; Bezzerides and Bestgen 2002; Reclamation 2008; Rees et al. 2005).

FLSU older juveniles, subadults, and adults occupy, feed, and move preferentially at greater depths than do other large fishes of the Colorado River basin, at least during the day and move into shallower waters at night (Karp and Tyus 1990; Weiss 1993; Childs et al. 1998; Beyers et al. 2001; Budy et al. 2009). Studies also suggest that FLSU of varying sizes seek cover from predators in cobble/boulder substrates, emergent vegetation, turbid water, and the shelter of large woody debris, and they may seek deeper water when turbidity is low (Beland 1953; Weiss 1993; Childs et al. 1998; Budy et al. 2009; Stone 2010; Bestgen et al. 2011a). FLSU may also seek deeper water when turbidity is low to avoid sunburn (Chart and Bergersen 1992). Older juvenile, subadult, and adult FLSU appear to actively flee or avoid lentic waters (Chart and Bergersen 1992; Bezzerides and Bestgen 2002; Mueller and Wydoski 2004; Reclamation 2008; Rees et al. 2005).

The ability of FLSU to seek suitable resting sites presumably increases as their range of mobility increases with size and age. FLSU preferences for resting habitat are a topic of ongoing investigations funded under LCR MSCP Work Task C53, Sonic Telemetry of Juvenile Flannelmouth Sucker in Reach 3 (Reclamation 2014).

SWIMMING

FLSU swim to explore, move among habitats, find and position themselves within habitats, avoid or escape hazards, feed, and move to and from spawning sites. Swimming ability first appears among larvae as they approach swim-up, and FLSU thereafter develop into stronger, more agile swimmers with greater stamina.

The present assessment identified only one study that addressed defensive or escape behaviors among FLSU. Ward and Bonar (2003) studied the susceptibility of FLSU juveniles, 51–70 mm TL, to piscivorous attacks by rainbow trout (*Oncorhynchus mykiss*) after acclimation to 20 °C and a subsequent abrupt transfer to water at 10 °C. Their report notes (p. 44):

> "Although no refuge was provided within the test tank, flannelmouth suckers often avoided detection by remaining motionless in a shadow cast by the standpipe or swimming at the edge of the tank near the surface. Flannelmouth suckers always exhibited an escape response when approached by a trout and often jumped out of the water to avoid the pursuing trout. Flannelmouth suckers showed no visible signs of abnormal swimming behavior at either temperature."

Karp and Tyus (1990) described FLSU as generally non-gregarious. Adult FLSU apparently swim together in large concentrations—described variously as "schools," "aggregations," or "congregations"—only in specific circumstances, which include spawning; movement into habitats with limited availability, including refuges from intolerable water conditions (see above); or concentration below dams that block their efforts to move upstream to historic spawning or other habitat (Carlson et al. 1979; Minckley 1991; Chart and Bergersen 1992; Weiss 1993; Thieme 1997; Douglas and Marsh 1998; Hoffnagle et al. 1999; McKinney et al. 1999; Douglas and Douglas 2000; Mueller and Wydoski 2004; Compton et al. 2008; Budy et al. 2009; Bestgen et al. 2011a; Cathcart 2014).

FLSU are not the strongest swimmers among the large, native fishes of the LCR, exhibiting lower failure velocities in laboratory experiments than either RASU or BONY (Ward and Hilwig 2004). However, FLSU share several characteristics with all the native large-river fishes of the Colorado River basin, "… including streamlined body forms, humped or keeled dorsal surfaces, leathery skins with fine or embedded scales, and large, often falcate, fins [that] provide for improved swimming performance and stability in turbulent flows, which are common in much of the Colorado River and tributaries" (Bezzerides and Bestgen 2002). Both age and water temperature affect FLSU swimming performance: Ward et al. (2002) found that, among age-0 FLSU, larger individuals had higher failure velocities, and all had greater swimming strength in warmer (20 °C) versus cooler (14 or 10 °C) water.

As noted above (see “Long-Distance Movement,” this chapter), FLSU sometimes move among relatively distant habitats both within and between stream/river reaches over timespans of weeks to months in the absence of dams that block such movement (Bezzerides and Bestgen 2002; Rees et al. 2005; Compton et al. 2008; Budy et al. 2009; Bestgen et al. 2011a; Zelasko et al. 2011; Bottcher et al. 2013; Cathcart 2014). Such movements may exceed 200 river km and may be in either the up- or downstream direction, with the latter more common. Such movements sometimes, but not always, involve travel to or from spawning sites. Budy et al. (2009) found that the timing of FLSU movement along the Green River, and in/out of its tributary San Rafael River watershed, followed the same pattern as the historic rise and fall of the annual Colorado River hydrograph, and also found evidence that “… adult flannelmouth sucker of the Green River select smaller tributaries to spawn and larger rivers to feed and overwinter.” However, such cycles of movement in the UCRB coincide with changes in water temperature that may not pertain to the LCR. FLSU appear able to control their downstream movement: they do not appear to be easily displaced by strong currents other than in canyon settings (Holden 1973; Chart and Bergersen 1992; McIvor and Thieme 1999; Compton et al. 2008; Budy et al. 2009).

Many of the studies of FLSU long-distance movement were carried out to assess the impacts of dams. The results of these studies often indicated that FLSU congregated in tailwater zones, short distances below the dams, suggesting that the dams blocked further upstream movement (Chart and Bergersen 1992; McKinney et al. 1999; Budy et al. 2009). FLSU also frequently move in and out of tributary confluences, possibly to avoid intolerable conditions arising in one or the other setting such as excessive flow velocities or turbidity or excessively high or low water temperatures (Minckley 1991; Weiss 1993; Thieme 1997; Douglas and Marsh 1998; McKinney et al. 1999; Douglas and Douglas 2000; Compton et al. 2008; Rogers et al. 2008).

When they are not moving over larger distances, FLSU adults tend to remain within limited home ranges consisting of approximately 0.8 km of stream (Chart and Bergersen 1992). However, such sedentary behavior appears to be more common among larger (> 400 mm TL) adults, with smaller adults (300–400 mm TL) moving more widely over distances of ≈ 4–8 km seasonally (Chart and Bergersen 1992).

THERMAL STRESS

All fish, including FLSU, experience thermal stress when they encounter water temperatures outside some particular range, the limits of which may vary from one life stage to the next. Depending on the duration of such exposure and the magnitude of departure from suitable water temperatures, FLSU eggs may experience lower rates of maturation and lower hatching success (Carlson et al.

1979; Haines 1995 cited in Muth et al. 2000; Ward 2001). Similarly, FLSU exposed to unsuitable temperatures may experience lower metabolic rates; lower rates of growth and maturation; and impaired abilities to engage in many types of critical biological activities, including reproduction, feeding, and hazard avoidance, with the severity of the effect depending on the duration and magnitude of departure from suitable water temperatures (Joseph et al. 1977; Valdez 1990; Weiss 1993; Robinson et al. 1998; Hoffnagle et al. 1999; Clarkson and Childs 2000; Thieme et al. 2001; Bezzerides and Bestgen 2002; Ward et al. 2002; Ward and Bonar 2003; Paukert and Rogers 2004; Rees et al. 2005).

However, as FLSU mature, they presumably become increasingly able to avoid or escape settings in which they detect thermally unsuitable conditions, provided these conditions are sufficiently localized to permit such avoidance or escape. For example, FLSU may move from the upper Colorado River main stem into tributaries to avoid excessively cold water temperatures produced by hypolimnetic releases from the large main stem dams (Minckley 1991; Weiss 1993; Thieme 1997; Douglas and Marsh 1998; McKinney et al. 1999; Douglas and Douglas 2000; Robinson and Childs 2001; Thieme et al. 2001; Compton et al. 2008; Rogers et al. 2008). FLSU blocked by dams from migrating upstream within the UCRB also congregate several kilometers downstream from each dam apparently to avoid the coldest temperatures produced by their hypolimnetic releases (Chart and Bergersen 1992; McKinney et al. 1999; Budy et al. 2009).

Chapter 4 – Habitat Elements

Habitat elements consist of specific habitat conditions that allow or prevent, or promote or inhibit, one or more critical biological activities and processes.

This chapter identifies 16 habitat elements that affect 1 or more critical biological activities or processes across the 5 FLSU life stages. Some of these habitat elements differ in their details among life stages. For example, FLSU in different life stages experience predation by different aquatic invertebrate and vertebrate taxa and sizes. However, using the same labels for the same *kinds* of habitat elements across all life stages makes it easier to compare and integrate the CEM for each life stage into a single overarching CEM. Table 3 lists the 16 habitat elements and the critical biological activities and processes that they *directly* affect across all FLSU life stages.

Table 3.—Habitat elements and the critical biological activities and processes they affect

Critical biological activity or process ➔ / **➔ Habitat element**	Chemical stress	Competition	Disease	Drifting	Foraging	Hybridization	Long-distance movement	Mechanical stress	Predation	Resting	Swimming	Thermal stress
Aquatic macrophytes					X				X	X	X	
Aquatic vertebrates		X			X	X			X			
Birds and mammals		X							X			
Fishing encounters								X				
Flow network fragmentation							X					
Infectious agents			X									
Invertebrates and POM	X	X			X				X			
Macrohabitat geometry				X							X	
Mesohabitat geometry/cover		X		X	X				X	X	X	
Scientific study								X				
Substrate texture/dynamics					X			X		X	X	
Turbidity					X				X	X	X	
Water chemistry	X									X	X	
Water depth								X				
Water flow/turbulence								X		X	X	
Water temperature										X	X	X

The diagrams and other references to habitat elements elsewhere in this document identify the habitat elements by a one-to-three-word short name. Each short name refers to a longer, complete name. For example, the habitat element label, "aquatic vertebrates," is the short name for "The taxonomic, functional, and size composition; spatial and temporal distributions; abundance; and activity level of the aquatic vertebrate assemblage." The following paragraphs provide the full name and a detailed definition for each habitat element, addressing the elements in alphabetical order.

AQUATIC MACROPHYTES

***Full name*: The taxonomic composition, size range, spatial and temporal distributions, and abundance of the aquatic macrophyte assemblage.** Aquatic macrophytes consist of submerged, emergent, and floating species, including large, plant-like algae. This element refers to the range of aquatic macrophytes that inhabit the shallows of the LCR and its connected backwaters. Table 4 lists the aquatic macrophytes known to occur along the LCR and its backwaters and ponds, following Ohmart et al. (1988), Mueller (2006, 2007), Fernandez and Madsen (2013), Marsh et al. (2013), and the National Invasive Species Information Center (NISIC) (2014).

Table 4.—Aquatic macrophytes of the LCR

Species	Origin[1]
Arundo donax, giant reed	I
Chara sp., muskgrass	N
Cladophora glomerata	N
Myriophyllum spicatum, Eurasian watermilfoil	I
Najas guadalupensis, southern naiad	N
Najas marina, spiny naiad	N
Nitella sp.	N
Phragmites australis, common reed	?
Potamogeton crispus, curlyleaf pondweed	I
Potamogeton foliosus, narrowleaf pondweed	N
Potamogeton nodosus, American pondweed	N
Ruppia maritime, widgeongrass	N
Salvinia molesta, giant salvinia	I
Schoenoplectus californicus, California bulrush	N
Schoenoplectus tabernaemontani, softstem bulrush	N
Stuckenia filiformis, fineleaf pondweed	N
Stuckenia pectinata, sago pondweed	N
Typha angustifolia, narrowleaf cattail	N
Typha latifolia, broadleaf cattail	N

[1] I = introduced, N = native, and ? = disputed.

The species listed in table 4 and the detritus from them may provide cover and food for FLSU; habitat for periphyton that FLSU may consume; habitat, including periphyton foods, for aquatic and terrestrial invertebrates that FLSU may consume; and habitat for aquatic invertebrates and vertebrates that may prey on or compete with FLSU (see "Competition," "Foraging," "Resting," and "Predation," chapter 3). On the other hand, extremely dense stands of some macrophytes could exclude FLSU. Historically, the types, abundance, and distribution of aquatic macrophytes along the LCR and its backwaters depended on the availability of at least relatively stable shoreline and backwater shallows (Johnson 1991). Aquatic macrophytes in these settings in fact may help sustain their own habitat by stabilizing substrates and slowing the movement of water (Carlson et al. 1979; Fernandez and Madsen 2013). Shallow backwaters, embayments, and tributary confluences continue to support aquatic macrophytes along the LCR (Fernandez and Madsen 2013), although river regulation and flood plain development have greatly reduced the availability of these mesohabitat types. At the same time, the highly invasive giant salvinia (*Salvinia molesta*) is spreading in the LCR ecosystem (NISIC 2014). One or more possibly non-native varieties of common reed (*Phragmites australis*) (Saltonstall 2002) also may occur, contributing to the spread of common reed throughout the LCR ecosystem. These changes to the aquatic macrophyte assemblage along the LCR will have as-yet unknown ecological consequences (McFarland et al. 2004; Rogalski and Skelly 2012). For example, overly dense stands of aquatic macrophytes such as giant salvinia may suppress aquatic invertebrate abundance by reducing light and DO levels (NISIC 2014).

Table 4 includes *Cladophora glomerata*, a species of attached filamentous algae that some authors classify as a "microphyte" (e.g., Ohmart et al. 1988). However, it can form dense benthic beds several centimeters thick with filaments up to 6 m long (National Research Council [NRC] 1991; Kennedy and Gloss 2005). As a result, it can have ecological effects similar to true macrophytes. It is more common in the Colorado River main stem upstream of the LCR, such as in the Grand Canyon, and requires clear water, but it can occur along the LCR (Ruiz 1994). It colonizes all substrate types, from soft and fine to coarse and hard (Stevens et al. 1997).

AQUATIC VERTEBRATES

***Full name*: The taxonomic, functional, and size composition; spatial and temporal distributions; abundance; and activity level of the aquatic vertebrate assemblage.** This element refers to the range of aquatic vertebrates that are known or suspected to interact with FLSU or its habitat along the present-day LCR. Interactions may include predation on or competition with FLSU. Most of these vertebrates are fishes, including both native and non-native species. However, the assemblage also includes one amphibian, bullfrog

(*Rana catesbeiana*), and its larvae (*aka* tadpoles), following Mueller (2006, 2007) and Mueller et al. (2006). Activity levels may vary in response to other habitat conditions such as water temperature (Robinson and Childs 2001; Thieme et al. 2001; Ward 2001). Table 5 lists the aquatic vertebrates known to occur in the present-day LCR (Ohmart et al. 1988; Minckley 1991; Mueller and Marsh 2002; Minckley et al. 2003; Gobalet et al. 2005; Marsh and Pacey 2005; Minckley et al. 2003; Gobalet et al. 2005) and the U.S. Geological Survey [USGS], Nonindigenous Aquatic Species Program (http://nas.er.usgs.gov/default.aspx), and it identifies whether they are native (N), introduced as sport fish (S), introduced as bait or forage for sport fish (B), or other. The "Other" category includes accidental introductions, such as the bullfrog, which arrived merely by escaping (NISIC 2014). Miller (1952), Mueller and Marsh (2002), and others listed additional species historically introduced into the LCR prior to 1975. However, more recent records do not provide evidence that these additional species continue to exist in the LCR, and Table 5 therefore omits them.

Table 5 also omits hybrids. As noted above (see "Hybridization," chapter 3), the native catostomids of the Colorado River basin occasionally hybridize with each other and with introduced non-native catostomids (Hubbs and Miller 1953; Buth et al. 1987; Douglas and Marsh 1998; Ryden 2000a; Bezzerides and Bestgen 2002; Mueller and Marsh 2002; Rees et al. 2005; Bestgen and Zelasko 2004; Bestgen et al. 2006, 2007a; Minckley and Marsh 2009; Douglas and Douglas 2010; Zelasko et al. 2011; Webber et al. 2013). Hybrids of FLSU with other catostomids conceivably may compete with pure FLSU for food, habitat, and mating opportunities.

The "Prey" column in table 5 indicates whether each species is known or suspected to prey on FLSU along the LCR or has ecological characteristics that suggest it could prey on FLSU. The sources of information on aquatic vertebrate species known or suspected to prey on FLSU (including, by analogy with predation on RASU or BONY) include Marsh and Douglas (1997), Brooks et al. (2000), Douglas and Douglas (2000), Ryden (2000a), Ward (2001), Bezzerides and Bestgen (2002), Robinson and Childes (2001), Ward et al. (2002), Christopherson et al. 2004; Rees et al. (2005), Miller and Lamarra (2006), Johnson et al. (2008), Pilger et al. (2008), Yard et al. (2011), and Walters et al. (2012). Predation by RASU, BONY, and common carp (*Cyprinus carpio*) on FLSU eggs is suspected by analogy with evidence of all three species preying on BONY eggs and BONY preying on RASU eggs (Bozek et al. 1984; Mueller 2006). Predation by bullfrogs on small FLSU is assumed based on bullfrog feeding ecology and by analogy with evidence of bullfrogs preying on small RASU (Mueller et al. 2006). Table 5 also identifies other aquatic vertebrate species that could prey on FLSU based on their ecology but for which there is no direct evidence in the literature reviewed for the present assessment. Many of the publications that do identify species known or suspected to prey on FLSU note that predation on FLSU at different life stages—including eggs—differs among the predatory species and their individual life stages.

Table 5.—Aquatic freshwater vertebrates of the LCR

Species	Origin[1]	Prey[2]	$Comp_J$[3]	$Comp_A$[3]
Ameiurus melas, black bullhead	S	X	?	?
Ameiurus natalis, yellow bullhead	S	X	?	?
Carassius auratus, goldfish	Other		?	?
Catostomus latipinnis, flannelmouth sucker	N		?	?
Ctenopharyngodon idella, grass carp	S		?	?
Cyprinella lutrensis, red shiner	B	X	X	X
Cyprinodon macularius, desert pupfish	N		?	?
Cyprinus carpio, common carp	S,B	?	X	X
Dorosoma cepedianum, gizzard shad	B		?	?
Dorosoma petenense, threadfin shad	B	?	?	?
Fundulus zebrinus, plains killifish	B		X	X
Gambusia affinis, western mosquitofish	B	?	X	X
Gila cypha, humpback chub	N	X	?	?
Gila elegans, bonytail	N	?	?	?
Gila robusta, roundtail chub	N		?	?
Ictalurus punctatus, channel catfish	S	X	X	X
Lepomis cyanellus, green sunfish	S,B	X	?	?
Lepomis gulosus, warmouth sunfish	S	?	?	?
Lepomis macrochirus, bluegill	S,B	X	X	X
Lepomis microlophus, redear sunfish	S		?	?
Micropterus dolomieui, smallmouth bass	S	X	?	?
Micropterus salmoides, largemouth bass	S	X	?	?
Morone chrysops, white bass	S	?	?	?
Morone saxatilis, striped bass	S	X	?	?
Notemigonus crysoleucas, golden shiner	B		?	?
Oncorhynchus clarkii, cutthroat trout	S	X	?	?
Oncorhynchus mykiss, rainbow trout	S,B	X	?	?
Oreochromis, Sarotherodon, or *Tilapia* spp.	S		?	?
Perca flavescens, yellow perch	Other		?	?
Pimephales promelas, fathead minnow	B		X	X
Plagopterus argentissimus, woundfin	N		?	?
Poecilia latipinna, sailfin molly	Other		?	?
Poeciliopsis occidentalis, Sonoran topminnows	N		?	?
Pomoxis annularis, white crappie	S	?	?	?
Pomoxis nigromaculatus, black crappie	S	?	?	?
Ptychocheilus lucius, Colorado pikeminnow	N	X	?	
Pylodictis olivaris, flathead catfish	S	?	?	?
Rana catesbeiana, bullfrog	Other	X	X	?
Rhinichtys osculus, speckled dace	N		X	X
Richardsonius balteatus, redside shiner	B	?	?	?
Salmo trutta, brown trout	S	X	?	?
Salvelinus fontinalis, brook trout	S	X	?	?
Sander vitreus, walleye	S	X	?	?
Tilapia mossambica, mouthbrooder	B		?	?
Xyrauchen texanus, razorback sucker	N	?	?	?

[1] S = introduced sport fish, Other = accidental introductions, N = native, and B = introduced bait or forage fish.
[2] Species known to prey on FLSU?
[3] Do juveniles (J) or adults (A) of the species compete with FLSU for food or habitat?
? = suggested by species data in Froese and Pauly (2014), NatureServe Explorer (NatureServe 2014), or the U.S. Geological Survey, Nonindigenous Aquatic Species Program (http://nas.er.usgs.gov/default.aspx), and X = reported in LCR literature.

Aquatic vertebrate predation on FLSU is widely thought to affect FLSU population numbers. However, the literature presents differing views on whether predation is a dominant cause of variation in FLSU population structure and numbers along the upper and lower Colorado River (e.g., compare Bezzerides and Bestgen 2002; Zelasko et al. 2011 *versus* Weiss 1993; Paukert and Rogers 2004; Bestgen et al. 2007a; Johnson et al. 2008; Budy et al. 2009; Walsworth et al. 2013).

Finally, the last two columns in table 5 indicate whether each species is known or suspected to compete with FLSU along the LCR or has ecological characteristics that suggest it could compete with FLSU for food items or physical habitat. Minckley (1982) and Brooks et al. (2000) summarized evidence of dietary overlaps among FLSU and several native and non-native species in the UCRB. The information in table 5 on the possibility of competition—specifically, whether each species feeds on materials upon which FLSU also feed and whether it uses habitat that FLSU also use—comes from the FishBase (Froese and Pauly 2014) and NatureServe Explorer (NatureServe 2014) databases.

The large number of entries in table 5 for possible competition reflects the fact that FLSU are omnivorous (see "Foraging," chapter 3). This puts them in potential competition with numerous aquatic omnivores, herbivores, insectivores, crustacivores, and piscivores. The search of the FishBase (Froese and Pauly 2014) and NatureServe Explorer (NatureServe 2014) databases for species that may compete with FLSU for food considered only reported ranges of food items, not feeding habitats, behaviors, or schedules.

BIRDS AND MAMMALS

***Full name*: The taxonomic, functional, and size composition; spatial and temporal distributions; abundance; and activity levels of the bird and mammal assemblages.** This element refers to the range of bird and mammal species known or suspected to interact with FLSU or its habitat along the LCR and its connected backwaters. More precisely, the list of species mostly consists of birds and mammals known or potentially able to prey on FLSU when the fish approach the water surface or shoreline.

Potential avian predators of FLSU may be identified by analogy with avian predation on RASU and BONY, to which investigators have given greater attention. Mueller (2006) observed or suspected predation on RASU and BONY at Cibola High Levee Pond by "kingfishers, osprey, cormorants, pelicans, … night herons, and great blue herons; and by "… raccoons, ringtail cats (*Bassariscus astutus*), and other fish-eating animals." Kesner et al. (2008) similarly strongly suspected double-crested cormorant (*Phalacrocorax auritus*) and American white pelican (*Pelecanus erythrorhynchos*) as significant predators of BONY at Imperial Ponds. An analogy with predation on RASU would also suggest that coyotes (*Canis latrans*) could prey on FLSU when the fish approach the shoreline (Mueller 2006). However, other than during spawning, FLSU generally use deeper waters than either RASU or BONY (see "Resting," chapter 3). This behavior may afford FLSU greater protection from predators hunting along shorelines or in the air overhead (Karp and Tyus 1990; Beyers et al. 2001).

At least one mammal may affect FLSU not through predation but by shaping habitat. Specifically, given its ecology, beaver (*Castor canadensis*) conceivably once may have helped create mesohabitat conditions beneficial to FLSU by introducing woody debris (Stevens et al. 1997) and creating pools along backwater channels (Cooke et al. 2005). Alternatively, beaver dams may have presented (and today may still present) barriers to FLSU movement in headwater drainages (Dauwalter et al. 2011a, 2011b). Beaver also eat aquatic macrophytes and thereby may shape their availability and generate POM at the same time (Henker 2009), affecting food availability and physical habitat for FLSU.

FISHING ENCOUNTERS

***Full name*: The frequency and intensity with which FLSU are caught by recreational fishers.** The literature suggests that fishing encounters are not likely a significant source of mechanical stress or mortality among FLSU. For example, Karp and Tyus (1990) found that FLSU were almost impossible to capture using standard angling methods compared to other capture methods. Bezzerides and Bestgen (2002) stated that "… flannelmouth suckers are not widely sought by anglers or known to the general public" and cite several publications as support. Mueller and Wydoski (2004) suggested that anglers historically may sometimes have captured and transported FLSU for use as bait. Similarly, Rees et al. (2005) note that "… Few, if any, anglers specifically target flannelmouth suckers, but incidental take probably does occur as fisherman attempt to catch gamefish species." Nevertheless, for completeness, the CEM recognizes that fishing encounters potentially could affect FLSU survival along the LCR.

FLOW NETWORK FRAGMENTATION

***Full name*: The abundance, distribution, and passability of artificial barriers to FLSU movement within the flow network.** As noted above (see "Long-Distance Movement," chapter 3), FLSU individuals of all life stages following swim-up may drift or swim over substantial distances. Natural barriers, such as falls, naturally fragment flow networks by limiting upstream fish passage (Stone et al. 2007). Artificial dams may further block both up- and downstream fish passage, breaking the riverflow network into additional fragments between which FLSU cannot move or can move only infrequently (Tyus and Karp 1989; Holden 1999; Bezzerides and Bestgen 2002; Rees et al. 2005; Carman 2007; UDWR 2006, 2009a; Budy et al. 2009; Melis et al. 2010; Bestgen et al. 2011b). Impoundments behind these dams may themselves present barriers to FLSU movement, such as movement between the main stem and tributaries with confluences inundated by a given reservoir. Specifically, the currents necessary for FLSU larval drift (Zelasko et al. 2011) dissipate in large impoundments. Presumably, this loss of drift currents would prevent or greatly impede further downstream movement of the larvae. However, the shallow, low-velocity environments created at the immediate confluences of rivers with impoundments may provide nursery habitat for FLSU fry arriving from these rivers—habitat similar to the pools that can form at tributary confluences with the main stem Colorado River (Robinson et al. 1998; Zelasko et al. 2011). FLSU older juveniles to adults in turn either avoid impoundments, fail to persist in them, or retreat back upstream when currents or swimming activity bring them into impoundments (Bezzerides and Bestgen 2002; Mueller and Wydoski 2004; Zelasko et al. 2011).

Downstream passage through hydroelectric turbines with relatively shallow intakes presumably would cause mortality among FLSU drawn into these intakes, should any FLSU venture that far downstream within a reservoir. Presumably, too, diversions behind dams may entrain drifting FLSU, removing them from the natural flow network. And large dams—or simply the excessively cold, high-velocity waters released by such dams—prevent upstream movement of FLSU (see “Swimming,” chapter 3). FLSU swim both up- and downstream over small dams (Compton et al. 2008; Beatty et al. 2009; Budy et al. 2009; Dauwalter et al. 2011a). However, data do not appear to be available on the heights that FLSU—a non-jumping species—can clear in the upstream direction (Dauwalter et al. 2011b). Dauwalter et al. (2011a, 2011b) suggested that some beaver dams can present barriers to FLSU in headwater drainages. Other structures, such as culverts and channel grade control structures, may also present barriers to upstream movement in headwater systems (Dauwalter et al. 2011b). River reaches with poor water quality may also limit the ranges of fish movement (Bestgen et al. 2011b).

At the same time, barriers may prevent or reduce mixing of FLSU with non-native catostomids, such as the non-native white sucker, reducing opportunities for hybridization (Beatty et al. 2009; Dauwalter et al. 2011b; Hopken et al. 2012) (see “Hybridization,” chapter 3). Barriers may prevent non-native competitor or predatory fish species from entering river or stream reaches occupied by FLSU (Mueller 2005; Rees et al. 2005; Compton et al. 2008; Zelasko et al. 2011).

Several factors determine whether an individual fragment of a flow network, bounded by barriers to fish passage, can support a self-sustaining population of a highly mobile fish species such as FLSU. These factors include the distances between the barriers that define the fragment, their effectiveness in preventing up- or downstream passage, the overall size (river miles) of the fragment, and the diversity of habitats available within the fragment, including tributary connections (Bezzerides and Bestgen 2002; Fagan et al. 2005; Budy et al. 2009; Fullerton et al. 2010). These factors also determine how genetically isolated the population in a fragment may become (Bezzerides and Bestgen 2002; Budy et al. 2009; Douglas and Douglas 2010; Hopken et al. 2012).

INFECTIOUS AGENTS

***Full name*: The types, abundance, distribution, and activity of infectious agents to which FLSU are susceptible.** As noted above (see “Disease,” chapter 3), FLSU in every life stage are vulnerable to infection. Non-lethal infections may make the affected individuals vulnerable to mortality from other causes. “Infectious agents” refers to the spectrum of viruses, bacteria, fungi, and parasites present and capable of infecting FLSU in the open environment of the LCR, including anchor worms (*Lernea* spp.) and ich (*Ichthyophthirius multifilis*) (Joseph et al. 1977; Brienholt and Heckmann 1980; Carothers et al. 1981; Flagg 1982; Heckmann et al. 1986; Hamilton and Buhl 1997; Landye et al. 1999; Linder et al. 2012). Non-native fishes are often cited as potential sources of the non-native pathogens and parasites that may affect FLSU and other native fishes of the LCR (Miller 1952; Heckmann et al. 1986; Haden 1992; Mueller and Marsh 2002; Mueller 2005; Cucherousset and Olden 2011). However, FLSU do not appear to be as susceptible to infection by some introduced parasites—e.g., the Asian fish tapeworm—as are other native fishes of the LCR (Brouder and Hoffnagle 1997; Carman 2007). Every infectious agent has a distinct life cycle with distinct requirements and limitations for intermediate carriers or hosts. Further, every native fish species along the Colorado River has different dietary and other requirements that affect its exposure to infectious agents as well as different biological responses to exposure. Consequently, it is not surprising that FLSU are susceptible to different degrees of the infectious agents that occur in the Colorado River ecosystem compared with other native fishes of the ecosystem. FLSU even differ in their susceptibilities from the closely related catostomid, bluehead sucker (Brienholt and Heckmann 1980).

INVERTEBRATES AND PARTICULATE ORGANIC MATTER

***Full name*: The taxonomic, functional, and size composition; abundance; spatial and temporal distributions; activity level of the invertebrate assemblage; and the abundance and nutritional quality of particulate organic matter (POM).** The invertebrates covered by this element consist of biofilms; phyto- and zooplankton; aquatic macroinvertebrates, including insect larvae, crayfish, and mollusks; and terrestrial insects that fall or land on the water. POM consists of plant litter and other decomposing organic matter carried into FLSU habitat from upstream, including that from river tributaries and their watersheds; litter from aquatic macrophytes and overhanging vegetation; and the decomposing remains of other aquatic organisms. FLSU feed on terrestrial and aquatic invertebrates and POM, with FLSU at different life stages preferring different sizes and types of these food items (see "Foraging," chapter 3). Other aquatic vertebrates in the Colorado River ecosystem also feed on aquatic invertebrates and POM (Minckley 1982; Benenati et al. 2002; Gido et al. 2006; Gido and Franssen 2007).

The assemblage of aquatic invertebrates also includes some species, such as crayfish and certain kinds of insect larvae, which may prey on fry and early juvenile FLSU based on evidence for their preying on a wide range of aquatic fauna in the Colorado River basin, including fry and early juvenile RASU and BONY (Horn et al. 1994; Lenon et al. 2002; Mueller 2006; Mueller et al. 2006; Martinez 2012; Moody and Sabo 2013). The non-native crayfish also may compete with FLSU in foraging for POM and smaller aquatic invertebrates (Martinez 2012; Moody and Sabo 2013) (see "Competition," chapter 3). Two species of non-native crayfish may occur in FLSU habitat: the virile crayfish (*Orconetes virilis*; *aka* northern crayfish) and the red swamp crayfish (*Procambarus clarkii*).

Three non-native mollusks, Asian clam (*Corbicula fluminea*), quagga mussel (*Dreissena rostriformis bugensis*), and zebra mussel (*Dreissena polymorpha*), also may occur in FLSU habitat (Ohmart et al. 1988; Nalepa 2010; NISIC 2014). These species are highly efficient filter feeders and therefore may compete with FLSU for aquatic invertebrates and POM, and they also form dense carpets that could interfere with FLSU browsing (NISIC 2014). They also may provide food for some non-native fishes (Ohmart et al. 1988). A fourth non-native mollusk, the New Zealand mud snail (*Potamopyrgus antipodarum*) occurs in the Colorado River and its impoundments as far south as Lake Mead (Benson 2014). It tolerates warm waters (up to 28 °C) and high salinity (up to ≈ 26%) (NISIC 2014). It is already well established in the Grand Canyon, where it has displaced much of the native benthic invertebrate assemblage and also forms dense benthic blankets (Kennedy and Gloss 2005; Hall et al. 2010). Should this species spread further into the LCR, it also would pose a threat to FLSU foraging.

The non-native golden alga (*Prymnesium parvum*) has been detected in Beal Lake, LCR (Reclamation 2014) and could expand to other slack-water settings (LCR MSCP biologists 2014, personal communications). Blooms of the species produce a toxin harmful to most fish species, although blooms occur only under special circumstances determined by water temperature and chemistry (Brooks et al. 2011; Roelke et al. 2011).

Historically, the abundance, distribution, and types of invertebrates and POM in the Colorado River and its backwaters depended on three factors: (1) natural inputs of dissolved nutrients supporting primary and secondary productivity in the river and its wetlands, constrained by turbidity (depth of light penetration); (2) the aquatic macrophytes and terrestrial vegetation of the LCR main stem, shallows, and flood plain, which provided habitat for numerous insects and inputs of plant litter into the river; and (3) organic matter carried downstream from the UCRB. Today, the LCR main stem no longer interacts with a natural suite of shallows and flood plain plant communities, and particulate matter from the UCRB now settles out of the river before reaching the LCR, altering both the nutrient dynamics and turbidity along the LCR. Further, primary productivity in the LCR and its reservoirs is likely affected by alterations to water chemistry arising from wastewater, and other contaminant inputs and from hypolimnetic discharge from dams, and by the effects of introduced species (e.g., see above). Autochthonous primary and secondary productivity along the river and natural inputs of POM and terrestrial insects to the river main stem and its reservoirs therefore are likely greatly altered (Minckley 1982).

MACROHABITAT GEOMETRY

***Full name*: The types, abundance, and spatial and temporal distributions of aquatic macrohabitats.** This element refers to the large-scale (i.e., 1–100 km scale) shape of the river channel, backwaters, other off-channel wetted areas, and the connected flood plain. (This assessment categorizes smaller-scale features such as eddies, pools, riffles, and runs as mesohabitats, although other authors may classify them as macrohabitat types [e.g., Holden 1999; Budy et al. 2009]). Macrohabitats define the overall flow path(s) for water and sediment moving through a system and establish the template for the formation of mesohabitats. Macrohabitat geometry along the LCR historically was shaped by main stem and tributary riverflows and also by their sediment transport, interacting with bedrock and surficial geology and with flood plain vegetation. Currently, the historic geometry of the LCR remains only in a few places where the channel is confined by bedrock and a few unaltered tributary confluences (Mueller and Marsh 2002). Otherwise, macrohabitat geometry along the LCR today depends more on the design and operation of the main stem water storage-delivery system, tributary inflow, and flood plain, channel, and shoreline management. All of these factors apply to the single section of the LCR currently occupied by FLSU – between Davis Dam and Lake Havasu.

Literature reviews and more recent studies (e.g., Bezzerides and Bestgen 2002; Rees et al. 2005; Budy et al. 2009; Budy and Salant 2011; Walters et al. 2012; Cathcart 2014; Franssen et al. 2014) indicated that older juvenile to adult FLSU are macrohabitat generalists. They occur in natural macrohabitats, including both confined (i.e., canyon) and unconfined channels of large rivers and streams, both braided and non-braided reaches along these channels, and backwaters at river confluences, particularly during main stem high flow pulses. However, they occur only infrequently in small headwater streams. Spawning occurs along larger tributaries and the main stem Colorado River at locations that appear to be determined by mesohabitat and finer-scale conditions rather than macrohabitat type. Fry and early juveniles use a more limited range of natural macrohabitat types, including backwaters and shoreline pools along rivers.

Major artificial features of the LCR, such as channel training and shoreline stabilization structures, diversion and return structures, and dams, also constitute macrohabitats for purposes of this model (Reclamation 2004). As discussed above (see "Swimming," chapter 3), adult FLSU mostly avoid or fail to persist in lotic environments such as reservoirs. They avoid tailwater zones below dams, although this may be due to the significantly colder temperatures found in these zones (see also Bezzerides and Bestgen 2002; Rees et al. 2005). FLSU fry and early juveniles may be found in reservoirs, where they may find suitable nursery habitat near confluences. Ongoing research under the LCR MSCP addresses the topic of FLSU macrohabitat associations through LCR MSCP Work Tasks C53, Sonic Telemetry of Juvenile Flannelmouth Sucker in Reach 3, and F5, Post-Development Monitoring of Fish at Conservation Areas (Reclamation 2014).

MESOHABITAT GEOMETRY/COVER

***Full name*: The types, abundance, and spatial and temporal distributions of aquatic mesohabitats and cover provided by these habitats.** Mesohabitats are portions of macrohabitats that vary in depth; flow velocity, direction, and turbulence; substrate size, shape, and stability; aquatic vegetation; and/or proximity to other mesohabitats. Each combination of conditions among these variables constitutes a distinct setting that fishes at different life stages may find suitable (or unsuitable) for particular critical biological activities, such as foraging, resting, or spawning (Parasiewicz et al. 2008), or that affect drift path geometry.

Examples of river mesohabitat types include bars, eddies, nearshore slackwaters, pools, riffles, and runs. Some authors alternatively refer to such features as macrohabitat types (e.g., Holden 1999; Budy et al. 2009) (see also "Macrohabitat Geometry," this chapter). As noted earlier (see "Drifting," chapter 3), channel sections along which lateral and reverse currents draw drifting larvae out of the main line of downstream flow into low-velocity settings constitute a type of mesohabitat. This document suggests referring to such settings as "interception habitat," following terminology developed for a CEM for the endangered pallid sturgeon to support species recovery along the Missouri River (W. Nelson-Stastny 2015, personal communication). However, the literature on mesohabitats and native fish ecology along the Colorado River does not yet use this term.

Mesohabitats are dynamic features of rivers and their backwaters; changes in water depth or river discharge can transform one mesohabitat type into another or eliminate them altogether. For example, a discharge pulse may cause eddies to disappear in some locations and appear in others, cause riffles to merge with runs, or change former shoreline slackwater areas into high-flow settings. Additionally, sediment erosion and deposition, and human modifications to the aquatic environment, also may change the types and distribution of mesohabitats present along a river. Reciprocally, mesohabitats may affect the distribution of local vertical and horizontal differences in flow velocities, flow directions, and turbulence along a river.

Table 6 summarizes the information presented in the literature on the mesohabitat types in which FLSU in different life stages have been observed (Joseph et al. 1977 and references therein; Muth and Nesler 1993; Thieme 1997; Robinson et al. 1998; Holden 1999 and references therein; McIvor and Thieme 1999; Douglas and Douglas 2000; Hoffnagle 2000; Beyers et al. 2001; Thieme et al. 2001; Valdez et al. 2001; Bezzerides and Bestgen 2002 and references therein; Reclamation 2005, 2008 and references therein; Rees et al. 2005 and references therein; Minckley and Marsh 2009; Budy and Salant 2011 and references therein; Best and Lantow 2012; Farrington et al. 2013).

Table 6.—Reported FLSU mesohabitat associations by life stage

Life stage ➔ **➔ Mesohabitat**	**Spawning**	**Fry and early juveniles**	**Older juveniles and subadults**	**Adults**
Backwater		X	X	X
Bar, gravel	X			
Eddy – midchannel				X
Eddy – shoreline		X	X	
Eddy – unclassified			X	X
Glide			X	X
Near-shore slackwater		X	X	X
Pool – confluence		X	X	
Pool – midchannel			X	X
Pool – shoreline		X	X	
Rapid – margins	X			
Rapid – unclassified				X
Riffle	X		X	x
Run – midchannel	X			
Run – unclassified			X	X
Shoreline – unclassified	X	X	X	
Side channel			X	
Slackwater – unclassified		X	X	X
Springs along channel				X

The findings in table 6 come with an important caveat: No single classification exists for mesohabitat types along the LCR or in the UCRB in general. Holden (1999) and Stewart and Anderson (2007) (see also Stewart et al. 2005) presented detailed classifications, but other studies use mesohabitat terms less formally. Different investigators may also use different terms to refer to essentially the same mesohabitat type, and terms may vary between the LCR and UCRB (Reclamation 2005). For example, Hoffnagle (2000) described "backwaters" along the Grand Canyon as "… pockets of water partially isolated from the main channel by a sand bar [that] usually form immediately downstream from a channel constriction, such as a debris fan." In contrast, Best and Lantow (2012) appear to classify such settings along the LCR below Davis Dam as shoreline slackwaters, shoreline pool habitats, or backwaters, all of which could also be classified as types of interception habitat for drifting larvae.

The types, distribution, and stability of mesohabitats present along the LCR historically were shaped by factors similar to those that shaped macrohabitat geometry but at a finer spatial scale: main stem and tributary riverflows and sediment transport, interacting with bedrock and surficial geology and with flood plain vegetation. The sizes and distribution of large woody debris also affected the types, distribution, and stability of mesohabitats along the LCR (Minckley and Rinne 1985; Mueller and Marsh 2002; UDWR 2009a). Stranded large woody debris diverts the flow of water and transported sediment, creating localized suites of mesohabitats, including eddies, pools, and bars, and also creates overhangs and pockets of shade.

Mesohabitat geometry similar to historic conditions currently occurs along the LCR only in a few places where the channel is confined by bedrock and at some tributary confluences (Mueller and Marsh 2002). Otherwise, mesohabitat geometry along the LCR today depends more on the design and operation of the main stem water storage-delivery system; tributary inflow; flood plain, channel, and shoreline management; and the effects of macrohabitat geometry. The design and operation of the main stem water storage-delivery system, for example, not only regulates water depth and flow and determines the locations of impoundments, it also eliminates inputs of sediment and large woody debris from upstream. All of these factors apply to the single section of the LCR currently occupied by FLSU – between Davis Dam and Lake Havasu.

Most studies report that FLSU may occur in almost any mesohabitat, although sometimes only as transients. The most common associations reported (greatest proportions of observations within individual studies) of FLSU life stages with specific mesohabitat types are: adults with pools and runs; fry and early juveniles with backwaters (including secondary channels), slackwaters, and shoreline mesohabitats; and spawning adults with gravel or cobble bars (also sometimes termed "shoals") at confluences and below riffles and pools. Studies have also reported that FLSU occur more abundantly along river reaches with greater channel complexity (i.e., with a greater diversity of mesohabitats in close proximity) (Reclamation 2005; Zelasko et al. 2011; Franssen et al. 2014). FLSU also reportedly seek mesohabitats with overhead cover. Cross (1975, cited in Reclamation 2005) reported that more than 50% of FLSU capture locations along the Virgin River included boulders, overhanging trees, or undercut banks.

Many reports of FLSU mesohabitat associations qualify their labels for mesohabitat types with information on depth and flow velocity (e.g., "moderate to deep" pools, "shallow" riffles) (Anderson and Stewart 2007; Budy and Salant 2011), or "nearshore low-velocity" habitats (Robinson et al. 1998), or they use alternative terms for the same settings, such as near-shore slackwater and nearshore low-velocity habitat. Where available, quantitative information on water depths, flow velocities, substrate size, and aquatic vegetation permit a refined qualification of mesohabitat conditions as discussed below (see "Substrate Texture/Dynamics," "Water Depth," and "Water Flow/Turbulence," this chapter). FLSU use of different mesohabitats may vary with other conditions such as water temperature and turbidity (Minckley and Marsh 2009). Ongoing research under the LCR MSCP addresses the topic of FLSU mesohabitat associations through MSCP Work Tasks C53, Sonic Telemetry of Juvenile Flannelmouth Sucker in Reach 3, and F5, Post-Development Monitoring of Fish at Conservation Areas (Best and Lantow 2012; Reclamation 2014).

SCIENTIFIC STUDY

***Full name*: The types, frequencies, and duration of scientific monitoring, capture, and handling.** This element refers to the possibility of capture, examination, tagging, removal, and experimental treatment of FLSU during scientific studies focused on the LCR and its backwaters. This element does not refer to the scientific study of FLSU larvae removed from the Colorado River inflow (to Lake Mead) to an off-river facility rearing (see chapter 2). Field and laboratory investigations always follow standard procedures during capture and handling to minimize stress (Ward 2006). Detection and capture methods and their associated sampling designs may vary in their suitability for different mesohabitats, in their likelihood of encountering FLSU of different sizes and life stages, and in their effects on captured individuals (Karp and Tyus 1990; Ward 2006; Bestgen et al. 2007a, 2007b).

There is almost no literature on even the *possible* impacts of scientific study on FLSU compared to a vast amount of literature documenting the actual impacts of scientific study on RASU and BONY. The literature reviewed for the present study contained only two brief mentions of possible deleterious impacts of handling on FLSU. Chart and Bergersen (1992) noted that handling may have caused stress to FLSU that resulted in their passive drift downstream following release; Ward (2001) noted that repeated handling of FLSU during laboratory studies may have slowed their growth. Nevertheless, FLSU along the LCR are subject to scientific study, and the CEM therefore needs to recognize this as a habitat element.

SUBSTRATE TEXTURE/DYNAMICS

***Full name*: The abundance, spatial distributions, and stability of substrate types (textures).** This element refers to the particle size distribution of benthic sediment within mesohabitats; substrate dynamics such as the frequency and magnitude of shifting, scour, and burial; and other potentially important features of the substrate. These features may affect substrate suitability for FLSU spawning, resting, or foraging during different life stages. Ongoing research under the LCR MSCP that may address the topic of FLSU substrate associations includes LCR MSCP Work Tasks C53, Sonic Telemetry of Juvenile Flannelmouth Sucker in Reach 3, and F5, Post-Development Monitoring of Fish at Conservation Areas (Reclamation 2014). Table 7 summarizes the substrate types identified in association with individual FLSU life stages.

Table 7.—Reported FLSU substrate associations by life stage

Substrate type ➔ / ➔ Life stage	Cobble	Gravel	Sand	Silt	Hard	References
Spawning	X	X	x			McAda 1977 (cited in Holden 1999; Reclamation 2005); Muth and Nesler 1993; Weiss 1993; Carlson et al. 1979; Weiss et al. 1998; Holden 1999; Douglas and Douglas 2000; Ryden 2000b; Bezzerides and Bestgen 2002; Snyder and Muth 2004; Reclamation 2005, 2008; Budy and Salant 2011; Best and Lantow 2012
Fry and early juveniles			X	X		Thieme 1997; Childs et al. 1998; Gido and Propst 1999
Older juveniles and subadults	x	X	X	X	X	McAda 1977 (cited in Holden 1999; Reclamation 2005); Gido and Propst 1999; Holden 1999; Bezzerides and Bestgen 2002; Reclamation 2005, 2008; Bestgen et al. 2011a; Budy and Salant 2011
Adults	X	X	X	x	X	Cross 1975 (cited in Reclamation 2005); Joseph et al. 1977; McAda 1977 (cited in Holden 1999; Reclamation 2005); Carlson et al. 1979; Gido and Propst 1999; Holden 1999; Bezzerides and Bestgen 2002; Reclamation 2005, 2008; Bottcher 2009; Budy et al. 2009; Bestgen et al. 2011a; Best and Lantow 2012

Key: "X" = common, and "x" = occasional.

Few of the reports listed in table 7 provided either measurement values or citations to indicate the size criteria (particle size ranges) used to distinguish “cobble,” “gravel,” “sand,” and “silt.” The absence of this information makes it difficult to compare study findings. Standard definitions of sediment particle size classes are available, typically based on the Wentworth grain size scale (Williams et al. 2006; Allan and Castillo 2007). However, only two of the reports listed in table 7—by Weiss (1993) and Best and Lantow (2012)—identified the particle size ranges used to define substrate categories, neither of which corresponds to the Wentworth scale. One study provided continuous, rather than categorical, particle size data on substrate associations for individual FLSU life stages: Muth and Nesler (1993) reported observing FLSU spawning over substrates with dominant particle sizes in the range of 0.75–1.95 inches in diameter (19–49 mm). This size range corresponds to coarse to very coarse gravel on the Wentworth scale. None of the studies identified in table 7 provide continuous data on overall particle size distributions or ratios among particle size categories.

Table 7 shows significant differences in substrate preferences among spawning, fry and early juvenile, older juvenile and subadult, and adult life stages. Older juvenile/subadult and adult preferences are very similar, but with a lower use of mesohabitats with silt substrates and a higher use of mesohabitats with cobble substrates among adults. Both older juveniles/subadults and adults also occur over hard substrates such as bedrock and compact beds of gravel and cobbles—substrates that may provide high-quality opportunities for foraging (see “Foraging,” chapter 3). Spawning sites are overwhelmingly described as having substrates of cobble and gravel. Larvae show strong associations only with fine-grained substrates, sand and silt, presumably a consequence of their selection of backwater and shoreline mesohabitats with low velocities (see “Water Flow/Turbulence,” this chapter). However, the majority of the studies identified in table 7 did not use survey methods that produced statistically representative data on substrate conditions among macro- and mesohabitat types. Without such comparative, representative sampling data or direct telemetric data (Best and Lantow 2012), it is not possible to assess statistical preferences (Hightower et al. 2012).

Several studies have noted possible direct and indirect causal relationship among flow conditions, substrate stability, and FLSU recruitment along several rivers and river reaches across the UCRB. Many of the studies cited for table 7 suggested that higher flows improved spawning habitat for FLSU and other native fishes of the Colorado River basin by removing fine sediment out of the interstices in gravel and cobble substrates at potential spawning sites (see also Pitlick et al. 1999). Additionally, Thieme and others (Thieme 1997; Thieme et al. 2001), found that successful FLSU recruitment in the lower Paria River required the seasonal formation of a gravel bar across the confluence of the Paria with the

Colorado River main stem. Together with elevated stage in the main stem, this bar helped create and protect a pool at the mouth of the Paria River that provided nursery habitat for FLSU larvae. Substrate stability thus directly can affect FLSU recruitment.

Several studies document that spring high-flow pulses in the UCRB flush fine sediments off gravel and cobble substrate surfaces along riffles and runs, improving habitat for both primary and secondary production, including chironomids and simuliids, both preferred foods for older juvenile to adult FLSU (see “Foraging,” chapter 3). Specific studies of this relationship include Osmundson et al. (2002) for the upper Colorado River above the Green River confluence, Propst and Gido (2004) for the San Juan River, Anderson and Stewart (2007) for the Dolores River, Budy et al. (2009) for the San Rafael River, Cross et al. (2011) for Glen Canyon, and Van Haverbeke et al. (2013) for the Little Colorado River. Where data are available, these changes in habitat quality for FLSU forage have been found to result in increases in FLSU recruitment and body condition (Osmundson et al. 2002; Propst and Gido 2004; Anderson and Stewart 2007; Van Haverbeke et al. 2013). Substrate stability thus can affect FLSU health and recruitment indirectly as well.

TURBIDITY

***Full name*: The magnitude and spatial and temporal distributions of turbidity.** This element refers to the turbidity at sites potentially used by FLSU in each life stage and its pattern of variation over time (i.e., the turbidity regime in different macro- and mesohabitat settings). Elevated discharge along a river or pulses of elevated discharge from tributaries may deliver pulses of suspended sediment to a river and also mobilize sediment in situ, resulting in episodes of elevated turbidity along the affected river reach. Bioturbation of benthic sediments (e.g., by carp during feeding and spawning) (Rogers et al. 2008; Cucherousset and Olden 2011) also may cause localized increases in turbidity for the duration of the disturbance. The LCR main stem and its connected backwaters experienced episodes of high turbidity year round prior to river regulation, especially during floods, and lower turbidity during low-flow conditions, especially along channel margins and in off-channel settings (Ohmart et al. 1988; Minckley 1991; NRC 1991, 1999). FLSU also occupied—and still occupy—headwater streams with naturally lower turbidity than that found along larger rivers in the basin (Sweet et al. 2009; Dauwalter et al. 2011a, 2011b). FLSU evolved in this environment, and turbidity therefore is presumed to affect—both directly and indirectly—several aspects of FLSU ecology. River regulation has drastically altered the turbidity regime of the main stem LCR, trapping most of the river’s natural sediment load in impoundments behind dams (NRC 1991).

Results of investigations on FLSU ecology showed the following direct effects—and lack of evidence of effects—of varying turbidity. The following descriptions use relative terms to describe levels of turbidity because different studies use different methods and measurement units to assess it:

- High turbidity may provide cover for fry, juvenile, and adult FLSU from predators. However, the dominant native predatory fish in the LCR, the Colorado pikeminnow (see "Predation," chapter 3) also evolved in the same turbid ecosystem, and turbidity does not limit its foraging ability (Muth et al. 2000). Consequently, FLSU likely evolved other mechanisms for avoiding predation than simply seeking turbid environments. Nevertheless, the AGFD (1996, cited in Hoffnagle 2001) reported increased catches of FLSU under turbid conditions (> 30 nephelometric turbidity units). This finding suggests that, under turbid conditions, more FLSU may move into open water settings where they become more susceptible to capture in nets (see Clark et al. 2010, for an overview of AGFD field methods). Alternatively, FLSU may simply be unable to detect nets under turbid conditions.

- High turbidity may cause disorientation among FLSU along main channels during flood events, resulting in displacement and possible mortality (Bestgen et al. 2006, 2007b). However, except under conditions of extreme flow velocities and turbidity, FLSU may simply move to shallows and backwaters to avoid disorientation and displacement (Minckley 1991; Hoffnagle et al. 1999).

- High turbidity does not appear to inhibit FLSU spawning (Weiss 1993).

- Turbidity protects FLSU from sunburn, but FLSU appear to compensate in less turbid settings by moving to deeper water (Chart and Bergersen 1992).

- Persistent differences in turbidity along different reaches of the Colorado River prior to regulation may have affected FLSU adult coloration, with lighter coloration more common in more turbid portions of the basin (Holden 1973).

Results of investigations, in turn, showed the following indirect ecological effects of varying turbidity on FLSU. The following descriptions again use relative terms to describe levels of turbidity because different studies use different methods and measurement units to assess it:

- High levels of turbidity affect the abundance and assemblage composition of algae and aquatic invertebrates along rivers inhabited by FLSU by inhibiting light penetration and interfering with filter-feeding. In general, consequently, higher levels of turbidity result in lower algal and aquatic invertebrate productivity (Angradi 1994; Stevens et al. 1997; Benenati et al. 2000; Wellard Kelly et al. 2013). More specifically, Zahn Seegert et al. (2014) found that very high levels of turbidity along the Grand Canyon resulted in lower rates of feeding on simuliids and chironomid larvae, and diatoms by older juvenile and adult FLSU, and higher rates of feeding on amorphous detritus. However, less extreme levels of turbidity do not inhibit production of chironomid or simuliid larvae, and the latter "are often abundant colonizers on firm substrata in rivers, such as recently disturbed rock surfaces and driftwood" (Stevens et al. 1997). Similarly, Cross et al. (2011) found that the production of chironomid and simuliid larvae recovered quickly following the 2008 controlled flood along the Grand Canyon. (Epilithic algae and simuliid larvae also benefit from the cleaning of hard surfaces during flood events, providing fresh, "clean" surfaces for their recolonization – see "Substrate Texture/Dynamics," this chapter). More generally, Stevens et al. (1997) found that altered temperature and turbidity below Glen Canyon together have a much stronger effect on main stem Colorado River benthos compared to the effects of dam operations on main stem geomorphology.

- High levels of turbidity may inhibit the abundance of non-native fish species. Clark et al. (2010) suggested that turbidity along the lower Little Colorado River inhibits colonization by non-native fishes. On the other hand, moderately elevated levels of turbidity in the Grand Canyon did not deter non-native rainbow trout piscivory on FLSU (Yard et al. 2011). The study authors suggested that rainbow trout simply moved to shallow channel margins where their sight-feeding would not be limited and where FLSU also move under the same conditions. However, extreme floods, with associated extreme turbidity, displaced and/or resulted in direct mortality of rainbow trout along the same river reaches (Coggins and Yard 2010; Coggins et al. 2011). Similarly, Bestgen et al. (2006, 2007b) found that pulses of extreme flow and turbidity along the Green River caused much greater displacement and mortality among smallmouth bass (*Micropterus dolomieui*) than among FLSU. However, smallmouth bass readily tolerate moderate turbidity (Bestgen et al. 2011a).

- High levels of turbidity do not inhibit the abundance of non-native mollusks (see "Invertebrates and Particulate Organic Matter," this chapter). Ohmart et al. (1988) observed that turbidity does not significantly suppress Asiatic clam along the LCR. The species can expel inorganic matter from its gills as "pseudofeces." Similarly, Nalepa (2010) noted that turbidity does not prohibit either zebra or quagga mussel colonization of a site, but extreme levels of turbidity do reduce their productivity/abundance. Osterling et al. (2007) also found that sediment turbidity produced by mayfly larval bioturbation inhibited quagga mussel colonization of sites with high densities of the larvae.

Other causal relationships are possible between turbidity and non-native species that could affect FLSU, but they have not received scientific attention (see "Nuisance Species Introductions," chapter 5). For example, introduced planktonic species could create blooms that result in elevated turbidity in the absence of suspended sediment. However, such blooms would be expected only in water with low rates of turnover, such as in isolated backwaters, which are not typical FLSU habitat during any life stage. For another example, benthic filter-feeders such as quagga and zebra mussels could filter out large amounts of plankton and POM. Under some circumstances, this could reduce turbidity.

Finally, turbidity also affects another habitat element, scientific study. Investigators have long recognized that elevated levels of turbidity have two types of effects on fish monitoring: (1) they limit detection and capture of FLSU by monitoring methods that require visual contact, including recovery of individuals stunned by electroshocking; and (2) they attenuate transponder signals (recently Bestgen et al. 2007a; Rogers et al. 2008; Stone 2010; Van Haverbeke et al. 2013). These circumstances are thought to have resulted in under-detection of FLSU in surveys carried out during high-turbidity events.

WATER CHEMISTRY

***Full name*: The magnitudes and horizontal, vertical, and temporal distributions of water chemistry properties that affect FLSU.** This element refers to the water chemistry at sites potentially used by FLSU in each life stage, including the way that water chemistry may vary over time and space. The element covers parameters such as DO, pH, salinity, naturally occurring dissolved substances, and contaminants such as added nitrate/nitrite, perchlorate, selenium, and artificial organic compounds (Ohmart et al. 1988; Seiler et al. 2003; Reclamation 2004, 2005, 2010, 2011b, 2011c).

FLSU during different life stages are suspected to be vulnerable to direct effects from altered water chemistry (Gido et al. 1997; Carman 2007; Bestgen et al. 2011a), as would be expected for any fish species. However, little information exists on direct impacts to FLSU from changes in any specific water quality properties, leading to calls for increased monitoring to look for such possible impacts (Rees et al. 2005; UDWR 2009a). The effects of variation in water chemistry on FLSU is not a topic of ongoing research among LCR MSCP Work Tasks (Reclamation 2014). However, Reclamation work tasks focused on other fish species (e.g., Work Task C32, Determination of Salinity, Temperature, pH, and Oxygen Limits for Bonytail and Razorback Sucker, and C59, Selenium Monitoring in Created Backwater and Marsh Habitat), incidentally could produce data on FLSU preferences and tolerances.

A study by Hamilton and Buhl (1997) appears to be the only laboratory assessment of larval FLSU susceptibility to contaminants, specifically mixtures of inorganic contaminants simulating water conditions recorded at different locations along the San Juan River. The watershed of this tributary to the Colorado River has a history of mining waste discharges, contaminated irrigation return flows, and incidences of infected lesions among fish. The lesions are thought to have been initiated by contact with other stressors "such as high contaminant concentrations, malnutrition, or poor water quality." The study results showed that FLSU larvae were susceptible to harmful effects of various mixtures of dissolved metals, particularly copper and zinc, at concentrations sometimes found in contaminated San Juan River backwaters and tributary reaches. In contrast, results of the study showed that FLSU larvae were relatively unaffected by arsenic, boron, molybdenum, selenate, selenite, uranium, and vanadium. The authors also noted that the biological effects of inorganic contaminants can vary with other environmental factors such water pH, salinity, DO levels, and temperature. However, such interactions were not systematically investigated.

A variation in water chemistry could also have indirect effects on FLSU. For example, a variation in dissolved nutrients could affect rates of primary (autochthonous) production in waters occupied by FLSU (Ohmart et al. 1988; NRC 1991; Melis et al. 2010), affecting the availability of food items for the species. As noted above (see "Invertebrates and Particulate Organic Matter," this chapter), toxins released by golden alga blooms could also harm FLSU in backwaters and other water bodies with limited water circulation.

WATER DEPTH

***Full name*: The spatial and temporal distributions of water depth.** This element refers to the depth of water covering the habitat sites potentially used or avoided by FLSU in each life stage and the ways in which depths vary over time and space. Depth may directly affect site suitability for FLSU spawning, resting, foraging, swimming among habitats, and avoiding predation or capture by sampling equipment. Additionally, depth may indirectly affect these conditions through its effects on other habitat elements such as water temperature or chemistry, flow velocities, or the invertebrate biological community. In turn, other factors, such as turbidity and the availability of different mesohabitat types, may affect FLSU use of settings with different depths. Field reports of FLSU in relation to water depth typically refer to the total depth of the water column at a location where FLSU were observed and only rarely indicate the vertical position of FLSU *within* the water column. However, FLSU always spawn at or near the bottom of the water column (see chapter 2). Table 8 summarizes the depths reported in association with individual FLSU life stages based on life stage identifications reported by the publication authors.

Table 8.—Reported FLSU average depth (m) associations by life stage

Life stage	Depth range	Depth	Location	Reference
Spawning adults	0.15–0.25	0.20	Paria River	Weiss 1993; Weiss et al. 1998
	0.22–0.38	0.30	Bright Angel Creek	Weiss et al. 1998
		0.66	White River	Lanigan and Berry 1981
		0.91	Not stated	Unattributed data in Holden 1999
		< 0.91	San Juan River between Lake Powell and Navajo Reservoir	Ryden 2000b
		≈ 1.0	Yampa-Green River confluence; lower Gunnison River, upper Colorado River below the Gunnison River	McAda and Wydoski 1985
	90% ≥ 1.0 and ≤ 4.0	3.0	LCR between Davis Dam and Lake Havasu	Best and Lantow 2012
	0.5–1.5		White River	Carlson et al. 1979
	< 1.14		Lower Yampa River	Muth and Nesler 1993
	< 1.2		UCRB in general	Snyder and Muth 2004
Fry and early juveniles	0.19 ± 0.13	0.19	San Juan River	Gido and Propst 1999
	< 0.5		LCR between Davis Dam and Lake Havasu	Best and Lantow 2012
Older juveniles and subadults	0.25 ± 0.17	0.25	San Juan River	Gido and Propst 1999
	0.18–0.49	0.34	Escalante River	UDWR 2009b
	0.40 ± 0.18	0.40	San Juan River	Gido and Propst 1999
	0.1–1.25	0.51	San Juan River	Archer et al. 1996
	> 0.3		Paria River	Thieme 1997; Thieme et al. 2001
	0.61–1.00	0.80	San Rafael River	Bottcher 2009
Adults	0.40–0.41	0.41	Riffles in upper Colorado River near Grand Junction, Colorado	Beyers et al. 2001
	0.59 ± 0.49	0.59	Virgin River	Cross 1975 (cited in Reclamation 2005)
	0.48–1.65	1.15	Eddies in upper Colorado River near Grand Junction, Colorado	Beyers et al. 2001
	0.6–2.15	1.16	Runs in upper Colorado River near Grand Junction, Colorado	Beyers et al. 2001
	0.15–2.4	1.27	White and Yampa Rivers	Carlson et al. 1979
	0.5–2.5	1.50	Yampa, Colorado, Gunnison, and Dolores Rivers in Colorado	Stewart and Anderson 2007 (see also Stewart et al. 2005)
	88% ≥ 1.0 and ≤ 4.0	2.4	LCR between Davis Dam and Lake Havasu	Best and Lantow 2012
	0.9–6.1	3.50	Upper Colorado River and multiple tributaries	McAda 1977; Sigler and Sigler 1996 (cited in UDWR 2006)
	> 2.0		LCR between Davis Dam and Lake Havasu	Mueller and Wydoski 2004

Table 8 compiles information across a large number of studies, which presented depth information in varying formats. The table lists average depth only when a report provided an average or presented depth data in a form (e.g., a histogram) from which it was possible to calculate or infer an average.

The following caveats apply to table 8:

- Only a few studies compare the depths of FLSU capture to the frequency of different depths available within each sampled reach (e.g., Weiss 1993; Weiss et al. 1998; Gido and Propst 1999; Stewart and Anderson 2007; Bottcher 2009). Without such comparative, representative sampling data or direct telemetric data (e.g., Beyers et al. 2001), it is not possible to assess statistical preferences in FLSU behavior (Hightower et al. 2012).

- Table 8 associates the results from Bottcher (2009) with older juvenile FLSU. The author stated more precisely that the captured fish ranged from age-0 to adults but were predominantly age-0 and juveniles. Table 8 also associates the results from UDWR (2009b) with older juvenile FLSU. The data in the report show that the captured fish included 30% age-0, 63% older juveniles, and 7% adults.

- Weiss (1993) noted for FLSU spawning depths along the Paria River that "… few areas with depths > 25 cm were present in the study area." FLSU therefore faced a limited range of options for spawning depths. Despite the limitation, spawning FLSU showed a statistically significant preference for greater depths within the range available. Nevertheless, Weiss (1993) observed FLSU "… spawning in shallow water (< 25 cm) with their dorsal fins or even backs protruding from the water." Similarly, Thieme et al. (2001) stated that the Paria River provided "… unsuitable rearing area for YOY flannelmouth sucker, possibly owing to uniformly shallow depths [< 0.3 m] and lack of submerged vegetation."

- Gido and Propst (1999) specifically studied San Juan River secondary channels rather than the main stem. They reported depth associations for "larvae," "juveniles," and "subadults" but not for adults. Their "juvenile" category fits within the "older juvenile and subadult" life stage defined for the present CEM.

- Archer et al. (1996) specifically studied backwater habitats occupied by fry and early juvenile FLSU. They sampled locations away from currents connected to the river, for which the data are summarized above, and "flow-through" locations with continuous flow connected to the river. However, the authors presented the depths for the flow-through stations only as ">" values (e.g., "> 1.0"), which cannot be averaged. All flow-through locations had depths recorded as either "> 1.0" or "> 1.25" m.

- Stewart and Anderson (2007) (see also Stewart et al. 2005) provided FLSU depth information in the form of a plot of habitat suitability along two dimensions, depth and velocity. The plot showed that FLSU preferred a narrower range of depths at higher velocities (> 0.75 m/s).

- Best and Lantow (2012) did not provide quantitative values for averages from their data on FLSU spawning and non-spawning adults. The values in table 9 are reconstructed from the histograms in Appendix C of their report.

- Mueller and Wydoski (2004) surveyed FLSU along the LCR between Davis Dam and Lake Havasu 28 times between 1999 and 2002 and found that "… electrofishing and trammel netting proved ineffective in the main channel, where less than 1% of the flannelmouth suckers were taken. The majority were captured in trammel nets set off-channel adjacent to spawning concentrations." However, they first stated, "Adult flannelmouth suckers were commonly observed in the main channel, where depths exceed 2 m." Thus, their statement concerning FLSU association with a specific range of depths refers to qualitative observations along the main channel rather than to quantitative findings at spawning sites and refers to adults away from spawning sites rather than to adults aggregated for spawning. Their publication does not provide information on depths at spawning sites.

- Additional data on FLSU use of mesohabitats with different depths exist in studies such as those by Childs et al. (1998) and Gido and Propst (1999). However, these studies focus on multivariate methods (logistic regression and discriminant function analysis, respectively), the outputs from which do not provide simple tabulations of habitat preferences or suitability. The data underlying these studies necessarily contain information potentially amenable to future analysis for such simpler purposes.

The information listed in table 8 matches the common qualitative description of FLSU as habitat generalists with no strong depth preferences. Adults generally spawn in shallower locations than they occupy at other times; juveniles, including early juveniles in nursery habitat, prefer generally shallower waters than do adults; and larvae occupy the same depths as do early juveniles but shallower depths than do older juveniles (Minckley 1991; Holden 1999; Reclamation 2005, 2008; Rees et al. 2005). However, the apparent distribution of depths used by FLSU may be a consequence of their seeking out specific mesohabitats with specific ranges of flow velocities rather than seeking out specific depths *per se* (Carlson et al. 1979; Minckley 1991; Holden 1999; UDWR 2006; Stewart and Anderson 2007; Bottcher 2009). Finally, the data listed in table 8 mostly do not come from statistically representative samples across river macro- and mesohabitat types. Such factors may make it difficult to identify strong FLSU habitat preferences based on depth.

Water depths in the rivers and connected backwaters historically occupied by FLSU depended on river discharge and channel and backwater geometry. River discharge, in turn, depended on the locations, timing, and rates of rainfall, snowfall, snowmelt, and runoff across the main stem and its various tributaries. In contrast, water depths in these rivers and connected backwaters today depend on the design and operation of the water management system. Operations to meet water demands, particularly during the irrigation season, can result in multiple abrupt changes in the rate at which dams release water over the course of any single day. Further, the patterns of release from any single dam can change from one week to the next. As a result, depths can vary widely along any single river reach by the hour, day, and week, as is the case along the sole river reach occupied by FLSU along the LCR – between Davis Dam and Lake Havasu.

Figure 2 shows the record of instantaneous variation in water depth at USGS river gage 09423000, Colorado River Below Davis Dam, AZ-NV, from February 1 to May 31, 2014. The water depth at the gage during this 4-month period during the irrigation season varied up to ± 6.5 feet (approximately 2 m) and rarely varied less than ± 1.5 feet (approximately 0.5 m) within a single day. No other substantial inputs of water take place along the river between Davis Dam and Lake Havasu, and there are only a few local agricultural and municipal diversions. Consequently, the entire river between these two locations would experience the same or a similar range and pattern of variation in water depths.

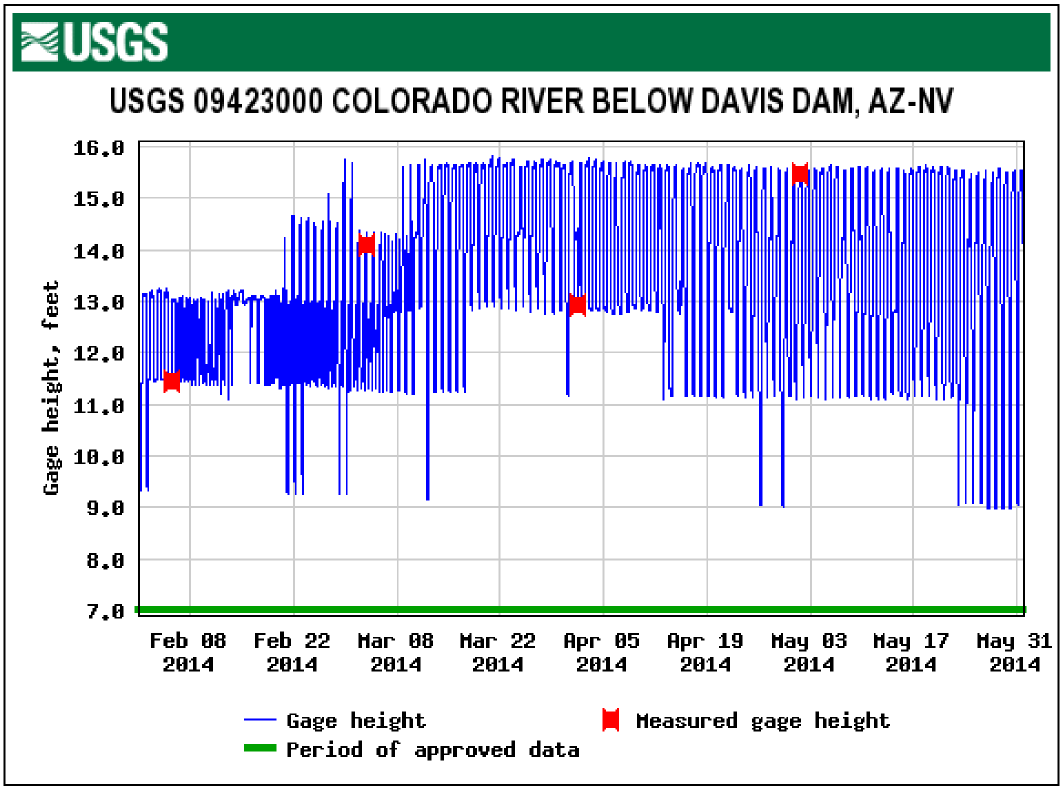

Figure 2.—Water depth at USGS river gage 09423000, Colorado River Below Davis Dam, Arizona-Nevada, February 1 to May 31, 2014.

WATER FLOW/TURBULENCE

***Full name*: The magnitudes and horizontal, vertical, and temporal distributions of water flow velocity and turbulence.** This element refers to the range of water flow velocities and turbulence encountered by FLSU in each life stage in the mesohabitats they occupy or through which they pass. Velocity fields may be large (e.g., spanning an entire inter-reservoir reach), intermediate (e.g., vertical mixing within a river run), or small (e.g., concentrated along the tailrace below a dam or at a diversion intake). Turbulence fields may be small (e.g., concentrated around a diversion or penstock intake or the downstream end of a channel training structure), or they may be very small (e.g., concentrated around an individual watercraft and its jets or propellers). Flow and turbulence at all scales along the main stem LCR depend on the design and operation of the water storage-delivery system (Reclamation 2004). Within individual macro- and mesohabitats, flow and turbulence also depend on tributary inflows, substrate, and channel geometry. At fine spatial scales, flow and turbulence depend on motorboat activity and local effects of mesohabitat geometry and substrate.

Weather—a factor outside the scope of this CEM—also affects flow and turbulence through the effects of storms on tributary runoff and wave formation.

Velocity and turbulence may directly affect site suitability for spawning, resting, foraging, swimming between habitats, and avoiding predation or capture by sampling equipment. Additionally, velocity may indirectly affect these conditions through its effects on or close interactions with other habitat elements such as mesohabitat setting, depth, water chemistry, the macroinvertebrate assemblage, the availability of POM , or the abundance of non-native fishes (Shannon et al. 1996; Hoffnagle et al. 1999; Holden 1999; Gido et al. 2006; Nalepa 2010; Kennedy et al. 2014). In turn, other factors, such as turbidity and the availability of different mesohabitat types, may affect FLSU use of settings with different flow velocities or turbulence. Finally, flow velocities can affect the scientific study of FLSU, impeding detection of radio tags and, during very high flows, limiting the ability of field staff to maneuver boats and use specific monitoring methods such as wading channel cross-sections to measure flow (Thieme 1997; Hoffnagle et al. 1999; Beyers et al. 2001). Ongoing research under the LCR MSCP that may address the topic of FLSU associations with and responses to variation in flow velocity and turbulence includes LCR MSCP Work Tasks C53, Sonic Telemetry of Juvenile Flannelmouth Sucker in Reach 3, and F5, Post-Development Monitoring of Fish at Conservation Areas (Reclamation 2014).

Table 9 summarizes the quantitative values for flow velocities reported in association with individual FLSU life stages based on life stage identifications reported by the publication authors. Spawning always occurs at or near the bottom of the water column (see chapter 2), and velocity reports for spawning sites therefore specifically refer to flows close to the substrate. Otherwise, velocities list in table 9 refer to the estimated or measured average flow velocity of the water column, not necessarily the velocity at the specific depth(s) that FLSU may occupy *within* the water column.

Table 9 is used to compile information across numerous studies. The table lists the average velocity only when a report provided an average or presented velocity data in a form (e.g., a line graph or histogram) from which it was possible to calculate or infer an average. The following additional caveats apply to table 9:

- Gido and Propst (1999) sampled only secondary channels of the San Juan River, a setting which the authors noted had lower flow velocities than present along the main channel. They reported values for "larvae," "juveniles," and "subadults" but not for adults. Their "juvenile" category fits within the "older juveniles and subadults" life stage defined for the present CEM.

Table 9.—Reported FLSU velocity (m/s) associations by life stage

Life stage	Velocity range	Average velocity	Location	Reference
Spawning adults	97% < 1.0	0.6	LCR between Davis Dam and Lake Havasu	Best and Lantow 2012
		≈ 1.0	Yampa and upper Colorado Rivers	McAda and Wydoski 1985
	0.15–1.0		Paria River	Weiss 1993; Weiss et al. 1998
	0.23–0.89		Bright Angel Creek	Weiss et al. 1998
Fry and early juveniles		0.086 ± 0.109	San Juan River	Gido and Propst 1999
		< 0.2	Nearshore Grand Canyon	Childs et al. 1998
Older juveniles and subadults		0.041 ± 0.186	San Juan River	Gido and Propst 1999
		0.12 ± 0.24	San Juan River	Gido and Propst 1999
	< 0.2 – > 0.81	0.49	San Rafael	Bottcher 2009
Adults	0.02–0.15	0.13	Eddies on Colorado River near Grand Junction	Beyers et al. 2001
	0–1.0	0.44	Virgin River	Cross 1975 (cited in Reclamation 2005)
	0.22–1.10	0.54	Runs on Colorado River near Grand Junction	Beyers et al. 2001
	0.61–0.81	0.71	Riffles on Colorado River near Grand Junction	Beyers et al. 2001
	0.25–1.25	0.75	Yampa, Colorado, Gunnison, and Dolores Rivers in Colorado	Stewart and Anderson 2007
	95% < 1.5	0.8	LCR between Davis Dam and Lake Havasu	Best and Lantow 2012
	0.5–1.0		LCR between Davis Dam and Lake Havasu	Mueller and Wydoski 2004
	< 1.22		White River	Carlson et al. 1979

- Childs et al. (1998) sampled only near-shore habitats selected specifically for their low flow velocities based on knowledge that FLSU larvae prefer such mesohabitats. The average velocity from that study listed in table 9 is simply the velocity criterion used to define near-shore, low-velocity habitats. In fact, many studies routinely mention the strong association of FLSU larvae with such habitats (see "Mesohabitat Geometry/Cover," this chapter) and concentrate surveys of FLSU larvae in such settings (e.g., Best and Lantow 2012). Only a few studies have measured velocity at representative samples of locations (e.g., Weiss 1993; Weiss et al. 1998; Gido and Propst 1999; Stewart and Anderson 2007; Bottcher 2009). Without such comparative, representative sampling data or direct telemetric data (e.g., Beyers et al. 2001; Best and Lantow 2012), it is not possible to assess statistical preferences (Hightower et al. 2012).

- Beyers et al. (2001) did not analyze the velocity data collected along with their telemetry. The authors stated that mean water-column velocity "… has little relevance to the velocity at the point where fish actually resided in the water column." However, none of the other reports cited in table 9 distinguishes between velocity at the depths occupied by fishes and the average velocity of the water column at the occupied locations. The velocity values listed in table 9 from Beyers et al. (2001) were calculated from their Appendix A2, which includes only measurements with high certainty.

- Best and Lantow (2012) did not provide quantitative values for averages from their data on FLSU spawning and non-spawning adults. The values in table 9 are reconstructed from the histograms in their Appendix C.

- Table 9 associates the results from Bottcher (2009) with older juvenile FLSU. The author stated more precisely that the captured fish ranged from age-0 to adults but were predominantly age-0 and juveniles.

- Stewart and Anderson (2007) (see also Stewart et al. 2005) provided FLSU velocity information in the form of a plot of habitat suitability along two dimensions, depth and velocity. The plot showed that FLSU preferred a narrower range of velocities at smaller depth velocities (< 0.5 m).

- As noted above (see "Water Depth," this chapter), Mueller and Wydoski (2004) surveyed FLSU along the LCR between Davis Dam and Lake Havasu 28 times between 1999 and 2002 and found that "… electrofishing and trammel netting proved ineffective in the main channel, where less than one percent of the flannelmouth suckers were taken. The majority were captured in trammel nets set off-channel adjacent to spawning concentrations." However, the authors first stated, "Adult flannelmouth suckers were commonly observed in the main channel, where … velocities were swift (0.5–1 m/s)." Thus, their statement concerning FLSU association with a specific range of velocities refers to qualitative observations along the main channel rather than to quantitative findings at spawning sites and refers to adults away from spawning sites rather than to adults aggregated for spawning. Their publication does not provide information on velocities at spawning sites.

- Additional occurrence-velocity data on FLSU exist in studies such as by Childs et al. (1998) and Gido and Propst (1999). However, these studies focus on multivariate methods (logistic regression and discriminant function analysis, respectively), the outputs from which do not provide simple tabulations of habitat preferences or suitability. The data underlying these studies necessarily contain information potentially amenable to future analysis for such simpler purposes.

- Other studies have assessed FLSU relationships to flow conditions but report flow in terms of volumetric discharge (e.g., cubic meters per second [m^3/s]) rather than velocity (e.g., Holden 1999). These data cannot be converted to velocity without detailed data on channel geometry at the study locations.

Reports by Ward and others (Ward 2001; Ward et al. 2002; Ward and Hilwig 2004) provided additional information about FLSU relationships to flow velocities in the form of laboratory findings concerning the maximum velocities against which FLSU can swim without failure. "Failure" in these studies occurs when an individual fish ceases swimming against the current and allows itself to be swept down-current. The first two studies only looked at age-0 FLSU and included the effects of water temperature and prior strength conditioning on swimming performance. Based on the velocity at which 50% of fish failed within 30 minutes (designated the fatigue velocity, FV_{50}), the first two studies found that wild-caught age-0 FLSU, average 50.3 mm TL, achieved a mean FV_{50} of 0.457 m/s (95% confidence interval [CI] = 0.443–0.471 m/s) at 20 °C. Laboratory-reared, age-0 FLSU achieved a mean FV_{50} of 0.663 m/s (95% CI = (0.641–0.681) among larger individuals, average 114.1 mm TL at 20 °C. The third study assessed the mean failure velocity among all individuals, with and without prior strength conditioning, and compared the results to those of BONY, RASU, and spikedace (*Meda fulgida*). Among captive, conditioned, age-0 FLSU, mean 93.4 mm TL (range 91.9–94.8), mean failure velocity was 0.667 m/s (95% CI = 0.631–0.703). These studies indicate that older (larger) juveniles are capable of swimming in environments with much greater velocities than those listed in table 9 for younger (smaller) juveniles.

The information listed in table 9 matches the common qualitative description of FLSU as habitat generalists with no strong velocity preferences other than a pattern of adult avoidance of settings with near-0 flow such as in reservoirs (see

"Swimming," chapter 3). Adults generally spawn in locations with lower flow velocities than those that occur in locations they occupy at other times; adults cope well with high-flow pulses; juveniles, including those in nursery habitat, prefer lower-velocity waters than do adults; and larvae prefer even lower-velocity waters than do early or older juveniles (Minckley 1991; Muth and Nesler 1993; Hoffnagle et al. 1999; Bezzerides and Bestgen 2002; Reclamation 2005, 2008; Carman 2007; Franssen et al. 2014). However, as noted above (see "Water Depth," this chapter), the apparent distribution of velocities at locations used by FLSU may be a consequence of their seeking out specific mesohabitats rather than seeking out specific velocities *per se* (Carlson et al. 1979; Minckley 1991; Holden 1999; UDWR 2006; Stewart and Anderson 2007; Bottcher 2009). Such factors may make it difficult to identify strong FLSU habitat preferences based on velocity.

Few studies specifically refer to or include information on flow turbulence other than to indicate whether a location contains eddies. As noted above (see "Mesohabitat Geometry/Cover," this chapter), older juvenile or subadult to adult FLSU often occur in mid-channel and shoreline eddies, and FLSU larvae often occur in shoreline eddies. However, as indicated in table 9, Beyers et al. (2001) recorded much lower flow velocities in eddies than in runs and riffles visited by adult FLSU along the Colorado River near Grand Junction, Colorado. These results suggest either that FLSU cannot tolerate turbulent water unless they exhibit relatively low velocities or that eddies naturally exhibit low *average* velocities because of the mixing of currents that takes place in such hydraulic settings.

River discharge (the volume of water moving at any given time) in the rivers and connected backwaters historically occupied by FLSU depended on the locations, timing, and rates of rainfall, snowfall, snowmelt, and runoff across the main stem and its various tributaries. Flow velocities, in turn, depended on the interaction of discharge with channel geometry. In contrast, water discharges and velocities in these rivers and connected backwaters today depend on the design and operation of the water management system. Operations to meet water demands, particularly during the irrigation season, can result in multiple abrupt changes in the rate at which water is released over the course of any single day, and the patterns of release from any single dam can change from one week to the next. As a result, flow velocities can vary widely along any single river reach by the hour, day, and week, as is the case along the sole river reach occupied by FLSU along the LCR – between Davis Dam and Lake Havasu.

Figure 3 shows the record of instantaneous variation in water discharge at USGS river gage 09423000, Colorado River Below Davis Dam, AZ-NV, from February 1 to May 31, 2014. Discharge at the gage during this 4-month period during the irrigation season varied up to ± 20,000 cubic feet per second [cfs] (approximately 570 m^3/s) and rarely varied less than ± 6,000 cfs (approximately 170 m^3/s) within a single day. With no substantial inputs and only a few agricultural and municipal

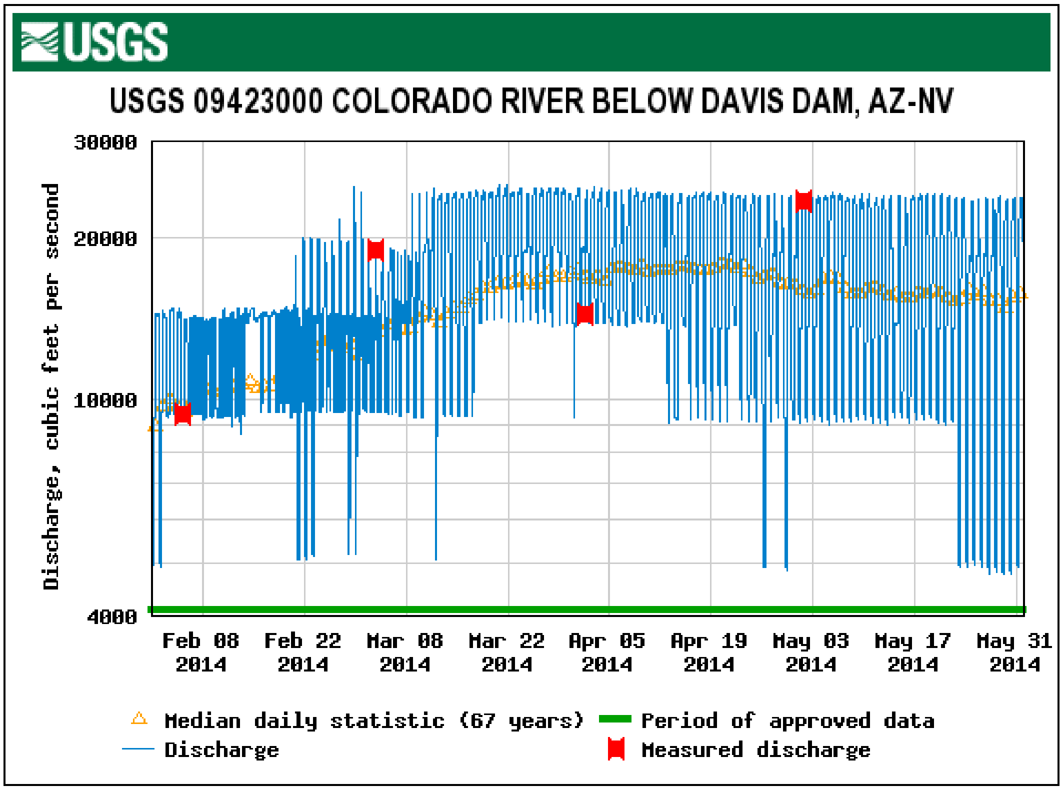

Figure 3.—Water discharge at USGS river gage 09423000, Colorado River Below Davis Dam, Arizona-Nevada, February 1 to May 31, 2014.

diversions between Davis Dam and Lake Havasu, the entire river between these two locations would experience the same or a similar range and pattern of variation in discharge.

WATER TEMPERATURE

***Full name*: The magnitudes and horizontal, vertical, and temporal abundance and distributions of water temperatures.** This element refers to the water temperature along river reaches and at individual sites used or avoided by FLSU in each life stage and the ways in which temperature varies over time and space along these reaches and at individual sites. Water temperature may vary spatially in three dimensions: up/downstream, laterally among mesohabitats across the wetted area of a channel, and vertically from top to bottom of the water column.

Water temperatures affect FLSU directly by affecting the timing of spawning, embryo development, growth and development following hatching, and activity levels (e.g., swimming performance):

- FLSU spawn in water over a wide range of temperatures, reported from 6–23 °C across the UCRB down to the Grand Canyon (Joseph et al. 1977; McAda 1977; Weiss et al. 1998; Carlson et al. 1979; Carothers and Minckley 1981; AGFD 2001; Bezzerides and Bestgen 2002; Zelasko et al. 2011). Spawning occurs between March and July, with the earliest and peak spawning times (as indicated by subsequent larval drift densities) occurring in the first few (6 or more) weeks of the potential spawning season in any given year (Joseph et al. 1977; McAda 1977; Carothers and Minckley 1981; Carlson et al. 1982; Muth and Nesler 1993; Sigler and Sigler 1996; Gido and Propst 1999; AGFD 2001; Bezzerides and Bestgen 2002; Zelasko et al. 2011). These reports consistently indicate that earliest and peak spawning occur during the time of year when water temperatures begin to warm following the winter minimum but prior to the rise in discharge due to snowmelt across the higher elevations of the Colorado River basin. This timing suggests that the seasonal change in water temperature provides the most important cue for FLSU spawning, possibly together with the seasonal change in photoperiod (Robinson et al. 1998; Hoffnagle et al. 1999), with change in discharge playing little or no role. One consequence of this cueing behavior is that FLSU begin to spawn earlier than any other native large-river fish in the Colorado River basin except for bluehead sucker (Gido and Propst 1999; Valdez et al. 2000; Bezzerides and Bestgen 2002; Farrington et al. 2013).

- FLSU that move in and out of tributaries, such as along the Grand Canyon, appear to take their temperature cue for spawning from the main stem rather than from the tributaries, resulting in synchronized spawning among tributaries (Minckley 1991; Bezzerides and Bestgen 2002). Scattered individual instances of FLSU spawning in tributaries to the Grand Canyon in mid- to late fall (Douglas and Douglas 2000; AGFD 2001) remain unexplained.

- Living in cooler water may reduce FLSU fecundity (Zelasko et al. 2011), as it does fecundity in bluehead suckers (McAda 1977; McAda and Wydoski 1983).

  Water temperatures affect the rate of maturation of FLSU embryos. McAda (1977) reported egg incubation times of 6–7 days at 15.6–17.8 °C, Haines (1995) found that the mean timespan between fertilization and peak hatch varied from 16.5 days at 12 °C down to 6.0 days at 20 °C, and Ward (2001) reported that FLSU eggs at 20 °C began hatching 5 days following fertilization. Haines (1995) also found that the percentage of FLSU eggs that hatched (83–91%) did not vary with temperature between 12 and 20 °C. (These results contrasted with those for RASU in the same study for which the percentage of eggs that hatched was lower [48–67%] and did vary with temperature.)

- The rate of maturation of larvae from hatching to swim-up appears to vary with water temperature. Thieme (1997) stated that swim-up occurs 20–28 days following hatching along the Paria River in water averaging 12 °C, while Ward (2001) observed swim-up as early as 5 days following hatching at 20 °C in a laboratory setting.

- FLSU larval (post-swim-up) and juvenile rates of growth and development also vary with water temperature. Larvae and juveniles in cooler streams (e.g., Wyoming headwaters versus Grand Canyon main stem) and in cooler waters in laboratory studies (e.g., 10 °C and 14 versus 20 °C) show slower rates of increase in weight and length and later transformations from larval to juvenile morphology (Clarkson and Childs 2000; Robinson and Childs 2001; Sweet et al. 2009; Walters et al. 2012). Robinson and Childs (2001), using length and temperature data for juveniles in the lower Little Colorado River, estimated that their growth would cease in water < 10.8 °C. The low-velocity, shallow mesohabitats selected by FLSU fry and early juveniles (e.g., backwaters and shoreline slackwaters) (see "Mesohabitat Geometry/Cover" and "Water Flow/Turbulence," this chapter) also are often reported as naturally warmer than adjacent open channel waters during the rearing season (Thieme 1997; Holden 1999; Muth et al. 2000; Walters et al. 2000; Reclamation 2005).

- As discussed above (see "Water Flow/Turbulence," this chapter), FLSU juveniles also show weaker swimming abilities in cooler water. FLSU juveniles rapidly introduced from warm (e.g., 20 °C) water into cold (e.g., 10 °C) water—such as could occur when juveniles are flushed by a runoff pulse from a warm tributary into the colder main stem (Angradi et al. 1992)—also exhibit poor swimming performance and disorientation (Clarkson and Childs 2000). However, FLSU juveniles also showed improved swimming abilities in colder water after acclimation (Ward et al. 2002; Ward and Hilwig 2004).

- In fact, FLSU can acclimate to a wide range of water temperatures, from 6–9 °C in tributary headwaters in Wyoming at 2,052–2,225 m elevation (Sweet et al. 2009) to 35 °C in the LCRB (Deacon et al. 1987; Sublette et al. 1990; Brooks et al. 2000; Bezzerides and Bestgen 2002; Reclamation 2005; Rees et al. 2005).

Several authors have noted the possibility that colder water temperatures below dams along the modern Colorado River and its tributaries—a consequence of hypolimnetic discharges—have negative effects on native large-river fishes in general (e.g., Minckley 1991; Sabo et al. 2012) and FLSU in particular (Childs et al. 1998; Bezzerides and Bestgen 2002; Paukert and Rogers 2004; Rees et al.

2005). The possible impacts noted by these authors include altered metabolism and foraging success, altered reproductive output, altered spawning timing, and altered larval and juvenile survival and growth.

Several studies specifically have noted reduced FLSU numbers downstream from some dams (see Rees et al. 2005). However, these studies have not verified that these reductions in abundance resulted from altered temperatures rather than from other factors, such as altered flow turbulence, turbidity, chemistry, or benthic productivity, or from the effects of non-native fishes that prosper in these settings (see below). In fact, water temperature may not have a strong or consistent effect on FLSU occurrence close to the bases of dams. FLSU have been observed residing in habitat close to the base of Flaming Gorge Dam (Vanicek et al. 1970 cited in Rees et al. 2005; Bestgen et al. 2006; UDWR 2009b) and both residing and spawning in the 20 km immediately below Davis Dam (Best and Lantow 2012). Paukert and Rogers (2004) also found that FLSU experience no impairment in condition even in the coldest waters immediately below Glen Canyon Dam. As noted above, FLSU are able to acclimate to or tolerate a very wide range of water temperatures, although with slower growth and development in cooler settings. However, even if FLSU "… apparently are able to tolerate the highly regulated, stenothermic conditions in the Colorado River below Glen Canyon Dam" (Paukert and Rogers 2004) and other large dams in the basin, one might hypothesize that FLSU will not spawn in the artificially most stenothermic waters if these waters experience no seasonal rise in water temperature.

Variation in water temperature also has several indirect effects on FLSU:

- Colder water temperatures (e.g., associated with winter and early spring, higher-elevation headwaters, or hypolimnetic discharges from dams) are known or proposed to support lower rates of primary productivity, and lower densities and different taxonomic mixes of benthic invertebrates, thus potentially affecting the FLSU diet (Carothers and Minckley 1981; Angradi 1994; Stevens et al. 1997; Benenati et al. 2000, 2002; Hoffnagle 2001; Wellard Kelly et al. 2013).

- Warmer water temperatures may support higher abundances, activity levels, or reproductive activity among several non-native micro- and macroinvertebrates known to occur in the Colorado River basin, the activities of which could affect FLSU (see "Infectious Agents" and "Invertebrates and Particulate Organic Matter," this chapter). These non-native species include virile crayfish (Martinez 2012), quagga mussel (Nalepa 2010), golden alga (Baker et al. 2009; Brooks et al. 2011), and some parasites (Carothers et al. 1981; Heckmann et al. 1986; Brouder and Hoffnagle 1997; Landye et al. 1999; Linder et al. 2012).

- Giant salvinia, a non-native aquatic macrophyte with the potential to alter FLSU habitat (see "Aquatic Macrophytes," this chapter) prefers warm waters (McFarland et al. 2004), with optimum growth at 30 °C, but tolerates temperatures from 5 to 40 °C.

- Water temperatures are known or suspected to affect the activity of cold-intolerant, non-native fishes that prey on or compete with FLSU. Cold hypolimnetic releases from dams may drive these non-native species further downstream year round (e.g., smallmouth bass) or at least seasonally (e.g., channel catfish [*Ictalurus punctatus*]), but periods of warmer water during droughts may allow these non-natives back into these same waters (Joseph et al. 1977; Hoffnagle 2001; Anderson and Stewart 2007; Bestgen et al. 2007a, 2007b). Influxes of naturally cold waters similarly can reduce non-native predation on FLSU in some reaches of the Yampa River (Holden and Stalnaker 1975; Johnson et al. 2008). In turn, Martinez (2012) noted that climate change may favor expansion of cold-water intolerant species such as smallmouth bass, a known predator on FLSU (see "Aquatic Vertebrates," this chapter).

- Water temperatures may also affect predatory behavior among non-native cold-tolerant fishes. Ward and Bonar (2003) studied the predatory behavior of rainbow trout in the presence of fry, and early juvenile ("age-0") FLSU transferred rapidly from water at 20 °C to water at 10 °C. The purpose of the experiment was to investigate the effects of cold-shock on the vulnerability of age-0 FLSU to predation as could occur when runoff pulses flush age-0 FLSU out of warmer tributaries into the cold main stem below Glen Canyon Dam. The study found that the trout attacked age-0 FLSU more in 20 °C water (FLSU not cold-shocked) but were more successful at catching age-0 that had been cold-shocked. In a related study, Yard et al. (2011) found that rainbow trout piscivory on natives fishes in general along the main stem Colorado River in the Grand Canyon did not vary with temperature, while brown trout piscivory did. However, water temperatures along the main stem during the study varied only between 7.9 and 15.6 °C and therefore do not indicate whether higher temperatures might affect trout piscivory rates, given that both strongly prefer cold water habitats.

Water temperature along the river and its lakes depends strongly on operational decisions at the dams along the LCR main stem (Reclamation 2004). Ongoing research under LCR MSCP Work Task C53, Sonic Telemetry of Juvenile Flannelmouth Sucker in Reach 3 (Best and Lantow 2012; Reclamation 2014) may provide further information on FLSU responses to varying water temperatures between Davis Dam and Lake Havasu. This is the only portion of the LCR in which FLSU currently reliably occur.

Chapter 5 – Controlling Factors

Controlling factors consist of environmental conditions and dynamics, both natural and anthropogenic, which significantly affect the abundance, spatial and temporal distributions, and quality of critical habitat elements. They may also significantly directly affect some critical biological activities or processes. A hierarchy of such factors exists, with long-term dynamics of climate and geology at the top. However, this CEM focuses on seven immediate controlling factors that lie within the scope of potential human manipulation. The seven controlling factors identified in this CEM do not constitute individual variables; rather, each identifies a category of variables (including human activities) that share specific features that make it useful to treat them together. Table 10 lists the seven controlling factors and the habitat elements they *directly* affect.

Table 10.—Controlling factors and the habitat elements they directly affect

Controlling factor ➔ **➔ Habitat element**	Channel and off-channel engineering	Fishing activity and fisheries management	Motorboat activity	Nuisance species introduction and management	Tributary inflows	Wastewater and other contaminant inflows	Water storage-delivery system design and operation
Aquatic macrophytes				X			
Aquatic vertebrates		X		X			
Birds and mammals							
Fishing encounters		X					
Flow network fragmentation							X
Infectious agents		X		X		X	
Invertebrates and POM				X	X	X	
Macrohabitat geometry	X				X		X
Mesohabitat geometry/cover	X				X		
Scientific study							
Substrate texture/dynamics			X		X		X
Turbidity	X				X	X	X
Water chemistry					X	X	X
Water depth	X						X
Water flow/turbulence			X		X	X	X
Water temperature					X	X	X

Two habitat elements listed in table 10 are not directly shaped by any of the controlling factors included in the CEM: birds and mammals and scientific study. The taxonomic, functional, and size composition; spatial and temporal distributions; abundance; and activity levels of the bird and mammal assemblages along the LCR depend on a wide range of factors beyond the scope of the present CEM. In turn, the types, frequencies, and duration of scientific monitoring, capture, and handling experienced by FLSU along the LCR depend on the activities of numerous governmental agencies, independent scientific institutions, and investigators under contract to these agencies and institutions. The activities and methods of these agencies, institutions, and contractors similarly lie outside the scope of the present CEM.

CHANNEL AND OFF-CHANNEL ENGINEERING

This factor addresses the activities of Reclamation, the USFWS, and the States and Tribes in managing the geomorphology of the river channel and off-channel habitats, including depth profiles, shorelines, and substrates. It covers activities such as dredging, shoreline armoring, construction and maintenance of river levees and training structures, construction and maintenance of connected backwater environments, and other modifications in areas of intense development (Reclamation 2004). These activities strongly shape macro- and mesohabitat geometry and moderately shape depth profiles throughout the system. However, areas of active mechanical shaping along channel and off-channel habitats are spatially limited, with relatively infrequent (less often than annual) maintenance or alteration (LCR MSCP biologists 2013, personal communications). Channel, shoreline, and backwater management activities such as dredging and bank and training structure maintenance can disturb sediment in ways that also may produce localized turbidity that disperses with distance from the activity. The LCR MSCP Habitat Conservation Plan specifically recognizes this as one of the ways in which Federal actions may routinely affect FLSU (Reclamation 2004). However, the effects will be localized and brief due to the limited flow velocities present in the regulated LCR.

FISHING ACTIVITY AND FISHERIES MANAGEMENT

This factor addresses State management of fisheries along the LCR, including management of sport fishes and species covered under the LCR MSCP Habitat Conservation Plan, including FLSU following their release. The States bordering the LCR recognize and oversee the sport fisheries for introduced fishes along the river, its reservoirs and connected backwaters, and its tributaries. The fishes recognized by these States as sport fishes include intentionally introduced and/or stocked species and accidental introductions. The States and recreational fishers have also introduced forage species to support the sport fisheries. These forage species may be caught as sport fish and may also be considered (by the States) to be nuisance species. Arizona lists the official sport fishes for the State (http://www.azgfd.gov/h_f/sport_fish.shtml) and State records for any caught along the LCR (http://www.azgfd.gov/h_f/state_records.shtml).

Management of sport fisheries includes regulating fishing activities and introducing and/or stocking sport species as well as bait and forage species for the sport fisheries. These management activities and the legacies of past such activities may affect the LCR ecosystem in several ways, including introducing infectious agents, shaping public perceptions of the relative value of sport fisheries versus native species recovery programs, shaping the spectrum of species that prey on or compete with FLSU, and altering physical habitat. The potential for conflicts between sport fishery management and the conservation of native fishes along the Colorado River in fact is a longstanding concern (Holden 1991; Minckley 1991; NRC 1991; Rolston 1991; Mueller and Marsh 2002; Minckley et al. 2003; Marsh and Pacey 2005; Clarkson et al. 2005). Table 5, above, lists non-native sport species introduced into the LCR and species introduced as bait or forage for the sport fisheries, and indicates whether they are known to prey on or compete with FLSU or could be proposed as competitors based on their feeding ecology. Infectious (including parasitic) organisms that are known to infect FLSU and likely introduced with non-native sport fishes include *Lerneae* spp. and *Myxobolus* spp. (Flagg 1982).

The States of the LCR and Federal agencies overseeing the LCR also manage the populations of several native species other than FLSU. Three of these are covered under the LCR MSCP Habitat Conservation Plan (Reclamation 2004)—RASU, humpback chub, and BONY—and one, roundtail chub (*Gila robusta*), is managed as a non-threatened sport fish. The Colorado pikeminnow is managed as an endangered species in the UCRB but not along the LCR. As mentioned earlier, it was almost certainly a native predator on FLSU.

Recreational fishers also could have effects on FLSU. However, as noted above (see "Fishing Encounters," chapter 4), anglers do not specifically target FLSU. On the other hand, anglers also are known to transplant desired sport or forage/bait fishes to water bodies where they appear to be absent. Mueller and Wydoski (2004) hypothesized that this was the source of FLSU observed spottily along the LCR prior to 1976.

MOTORBOAT ACTIVITY

This factor addresses motorboat activity, which occurs along the LCR main stem, its reservoirs, and its connected backwaters. It can cause boat wakes and propeller turbulence that damage habitat or disturb eggs embedded in substrates, or it can harm individual fish (larvae to larger individuals) entrained in the vortex from a spinning propeller or water jet. Boating regulations and signage (http://www.azgfd.gov/outdoor_recreation/boating_rules.shtml) enforce no-wake zones along the LCR river reach currently occupied by FLSU and in river-connected refuges. Turbulence from intensive boat passage through areas of shallow depths, and boat groundings in such settings, also could disturb substrate sediments. Such impacts would be highly localized and infrequent for any single location, although boaters conceivably may find some shoreline areas more attractive than others for anchoring or tying up.

NUISANCE SPECIES INTRODUCTION AND MANAGEMENT

This factor addresses animals and plants introduced into LCR waters and wetlands that affect FLSU survival or reproduction *but are not officially managed by the States for recreation or as bait or forage for a sport fishery*. The introductions may have occurred intentionally or not. The potential list of species in this group includes microbes (e.g., viruses or invasive plankton). Nuisance species have the potential to poison, infect, prey on, compete with, or present alternative food resources for FLSU during one or more life stages; cause other alterations to the aquatic food web that affect FLSU; alter water chemistry; or affect physical habitat features such as cover, substrate stability, or turbidity. As noted (see “Aquatic Macrophytes,” “Aquatic Vertebrates,” “Invertebrates and Particulate Organic Matter,” chapter 4), introduced nuisance species along the LCR include plants, amphibians, crustaceans, and fishes. Interactions of nuisance species with FLSU may include the following (see also “Aquatic Vertebrates,” chapter 4):

- Non-native varieties (haplotypes) of the common reed alter shoreline and wetland cover, and giant salvinia forms dense mats along shorelines that block sunlight and reduce DO levels (McFarland et al. 2004; NISIC 2014).

- When it forms blooms, the golden alga produces a toxin potentially harmful to FLSU and many other fishes (Brooks et al. 2011; Roelke et al. 2011).

- Asian clam, quagga mussel, and zebra mussel can blanket benthic habitat. They also filter out large quantities of plankton, increasing water clarity, and may provide food for non-native fishes (Ohmart et al. 1988; Nalepa 2010). Increased water clarity potentially could allow more growth of emergent macrophytes across a given shallow water setting as suggested by LCR MSCP biologists (September 2013, personal communications).

- Bullfrog larvae prey on small fishes (Mueller 2006). Rogalski and Skelly (2012) also reported a possible positive relationship between common reed expansion and non-native American bullfrog productivity.

- Northern crayfish and red swamp crayfish may prey on small FLSU, as they do on small RASU (Horn et al. 1994; Mueller 2006; Mueller et al. 2006), and also may compete with FLSU for food (POM and smaller aquatic invertebrates).

- Threadfin shad (*Dorosoma petenense*), red shiner (*Notropis lutrensis*), western mosquitofish (*Gambusia affinis*), and fathead minnow (*Pimephales promelas*) likely prey on and/or compete with FLSU (see table 5, above).

State and Federal actions to control nuisance species (e.g., common reed, giant salvinia, tamarisk (*Tamarix* spp.), golden alga, and quagga and zebra mussels) also fall under this factor. These actions have the potential to alter habitat for FLSU as well. Water temperature and salinity may affect the activity of individual nuisance species, for example, by affecting the likelihood of toxic algal blooms (Brooks et al. 2011; Roelke et al. 2011).

TRIBUTARY INFLOWS

The vast majority of the water flowing through the LCR originates upstream in the UCRB. However, the LCR also receives water from its own natural tributaries, including the Virgin, Muddy, Bill Williams, and Gila Rivers. The first two flow into Lake Mead, the Bill Williams into Lake Havasu, and the Gila River into the Colorado at Yuma, Arizona. All four tributaries are themselves highly regulated but nevertheless contribute both water and sediment to their respective confluence reaches. Lake Mead also receives water from Las Vegas Wash, which delivers wastewater and stormwater from the Las Vegas, Nevada, metropolitan area. However, the present CEM recognizes that FLSU in the LCR currently occupy only along Reach 3 between Davis Dam and Lake Havasu, which has only intermittent seasonal tributaries.

Tributary inflow confluences can constitute distinctive zones of flow variation, turbidity, water chemistry and temperature, and geomorphology—i.e., distinctive macrohabitats—with distinct assemblages of mesohabitat types. Prior to regulation, the major source of sediment inputs and the major shaper of substrate types and their stability was the LCR itself. However, tributaries are probably the largest external sources of sediment under the present regulated condition, and their confluences are among the most geologically active sites along the river.

Tributary inflows may also include suspended POM. For these reasons, FLSU may interact with or use even scattered, intermittent tributary confluences as distinct habitat settings.

WASTEWATER AND OTHER CONTAMINANT INFLOWS

This factor addresses the management of regulated discharges, irrigation practices, and management of contaminated sites across the watershed as well as the chemical contributions these sources make to river chemistry. The LCR receives inputs directly from large municipal wastewater systems, most notably from Las Vegas via the Las Vegas Wash. Reach 3 between Davis Dam and Lake Havasu receives municipal wastewater from Laughlin, Nevada, from the Clark County (Nevada) Water Reclamation District, Laughlin Wastewater Reclamation Facility. Bullhead City, Arizona, and Needles, California, also operate municipal wastewater facilities, but they discharge their effluent to infiltration ponds rather than directly to the river. Otherwise, Reach 3 receives storm runoff from developed areas of Laughlin, Nevada, Bullhead City, Arizona, Needles, California, and scattered residential developments in between; and Lake Havasu itself receives diffuse wastewater input from the septic systems of Lake Havasu City, Arizona. Finally, non-point source pollution from irrigation return flows and storm runoff from individual sites of chemical contamination bring additional contaminants into the river upstream of Davis Dam (Seiler et al. 2003; Reclamation 2004, 2005, 2010, 2011b, 2011c; Hamilton et al. 2005a, 2005b; Sanchez et al. 2005; Acharya and Adhikari 2010a, 2010b; Adhikari et al. 2011; Turner et al. 2011; Stolberg 2009, 2012). Reach 3 between Davis Dam and Lake Havasu has several large areas of flow-irrigated agriculture with pump intakes, gravity-flow distributions systems, and small return flows. Their points of return flow are probably too small for FLSU to use as distinct habitat settings.

Theoretically, municipal and rural wastewater could also contain pathogens that affect FLSU, although no studies have specifically investigated this topic for the LCR. Unregulated discharges may carry pathogens directly into the LCR, and regulated wastewater treatment facilities may sometimes release pathogens due to limits to the operational capabilities of these facilities (including any associated treatment wetlands). Recreational users of the LCR waters and shores presumably also leave waste that possibly also could contain pathogens able to affect FLSU.

WATER STORAGE-DELIVERY SYSTEM DESIGN AND OPERATION

The LCR main stem consists of a chain of reservoirs separated by flowing reaches. The water moving through this system is highly regulated for storage and delivery (diversion) to numerous international, Federal, State, Tribal, municipal, and agricultural users as well as for hydropower generation. In addition, the dams along and above the LCR trap essentially all of the sediment and both coarse and fine organic matter that would have flowed past their locations prior to their construction. This combination of flow regulation, impoundments, diversions, and trapping of matter creates a river in which water management and the infrastructure built for that management together comprise almost the only factor affecting the hydraulic and hydrogeomorphic dynamics along the LCR (Reclamation 2004). Water management along the system balances demand against the amount of water that enters the system from the upper basin within limits set by law.

The present CEM also encompasses the other protected areas along the LCR managed under the auspices of the LCR MSCP Habitat Conservation Plan. Water depths and flows in these areas depend on the regulated conditions along the river and the reservoirs and/or on site-level management decisions, including management of gates and surface and groundwater pumping to deliver water. However, FLSU currently occur along the LCR only between Davis Dam and Lake Havasu and, in fact, occur almost entirely within only the uppermost 20 km of this river segment. Further, older juvenile and adult FLSU appear to avoid or fail to thrive in the lentic waters of reservoirs. Presumably they similarly would not thrive in isolated ponds either. The FLSU conceptual ecological model addresses the water storage-delivery system design and operation only in terms of their implications for riverine and connected backwater habitat conditions along the LCR in general and along Reach 3 in particular.

Water releases from Davis Dam, water-use intakes and return flows between the dam and Lake Havasu, and slackwater environments (e.g., coves and backwaters) between the dam and the lake create locally distinct velocity fields. In addition, releases from Davis Dam control the amount of water flowing between the dam and the lake, and reservoir operations along the Colorado River as a whole determine Davis Dam operations (Reclamation 2004). Davis Dam releases hypolimnetic water from Lake Mohave, resulting in tailwater flows with a unique chemistry and thermal range that affect the water chemistry and temperature for some distance downstream (Reclamation 2004).

Chapter 6 – Conceptual Ecological Model by Life Stage

This chapter contains five sections, each presenting the CEM for a single FLSU life stage. For each life stage, the text and diagrams identify its life-stage outcomes; its critical biological activities and processes; the habitat elements that support or limit the success of its critical biological activities and processes; the controlling factors that determine the abundance, distribution, and other important qualities of these habitat elements; and the causal links among them.

The model for each life stage assesses the character and direction, magnitude, predictability, and scientific understanding of each causal link based on the following definitions (see attachment 1 for further details):

- **Character and direction** categorizes a causal relationship as positive, negative, or complex. "Positive" means that an increase in the causal node results in an increase in the affected node, while a decrease in the causal node results in a decrease in the affected node. "Negative" means that an increase in the causal node results in a decrease in the affected element, while a decrease in the causal node results in an increase in the affected node. Thus "positive" or "negative" here do ***not*** mean that a relationship is beneficial or detrimental. The terms instead provide information analogous to the sign of a correlation coefficient. "Complex" means that there is more going on than a simple positive or negative relationship. Positive and negative relationships are further categorized based on whether they involve any response threshold in which the causal agent must cross some value before producing an effect. In addition, the "character and direction" attribute categorizes a causal relationship as uni- or bi-directional. Bi-directional relationships involve a reciprocal relationship in which each node affects the other.

- **Magnitude** refers to "… the degree to which a linkage controls the outcome *relative to other drivers*" (DiGennaro et al. 2012). Magnitude takes into account the spatial and temporal scale of the causal relationship as well as the strength (intensity) of the relationship at any single place and time. The present methodology separately rates the intensity, spatial scale, and temporal scale of each link on a three-part scale from "Low" to "High" and assesses overall link magnitude by averaging the ratings for these three. If it is not possible to estimate the intensity, spatial scale, or temporal scale of a link, the subattribute is rated as "Unknown" and ignored in the averaging. If all three subattributes are "Unknown," however, the overall link magnitude is rated as "Unknown." Just as the terms for link character provide information analogous to the sign of a correlation coefficient, the terms for link magnitude provide information analogous to the size of a correlation coefficient.

- **Predictability** refers to "… the degree to which current understanding of the system can be used to predict the role of the driver in influencing the outcome. Predictability … captures variability… [and recognizes that] effects may vary so much that properly measuring and statistically characterizing inputs to the model are difficult" (DiGennaro et al. 2012). A causal relationship may be unpredictable because of natural variability in the system or because its effects depend on the interaction of other factors with independent sources for their own variability. Just as the terms for link character provide information analogous to the sign of a correlation coefficient, the terms for link predictability provide information analogous to the size of the range of error for a correlation coefficient. The present methodology rates the predictability of each link on a three-part scale from "Low" to "High." If it is not possible to rate predictability due to a lack of information, then the link is given a rating of "Unknown" for predictability.

- **Scientific understanding** refers to the degree of agreement represented in the scientific literature and among experts in understanding how each causal relationship works—its character, magnitude, and predictability. Link predictability and understanding are independent attributes. A link may be highly predictable but poorly understood or poorly predictable but well understood. The present methodology rates the state of scientific understanding of each link on a three-part scale from "Low" to "High."

The CEM for each life stage thus identifies the causal relationships that most strongly support or limit life-stage outcomes, support or limit the rate of each critical biological activity or process, and support or limit the quality of each habitat element, as that element affects other habitat elements or affects critical biological activities or processes.

A separate spreadsheet is used to record the assessment of the character and direction, magnitude, predictability, and scientific understanding for each causal link along with the underlying rationale and citations for each life stage. The CEM for each life stage, as cataloged in its spreadsheet, is illustrated with diagrams showing the controlling factors, habitat elements, critical biological activities and processes, and causal links identified for that life stage. A diagram may also visually display information on the character and direction, magnitude, predictability, and/or scientific understanding of every link. The diagrams use a common set of conventions for identifying the controlling factors, habitat elements, critical biological activities and processes, and life-stage outcomes as well as for displaying information about the causal links. Figure 4 illustrates these conventions.

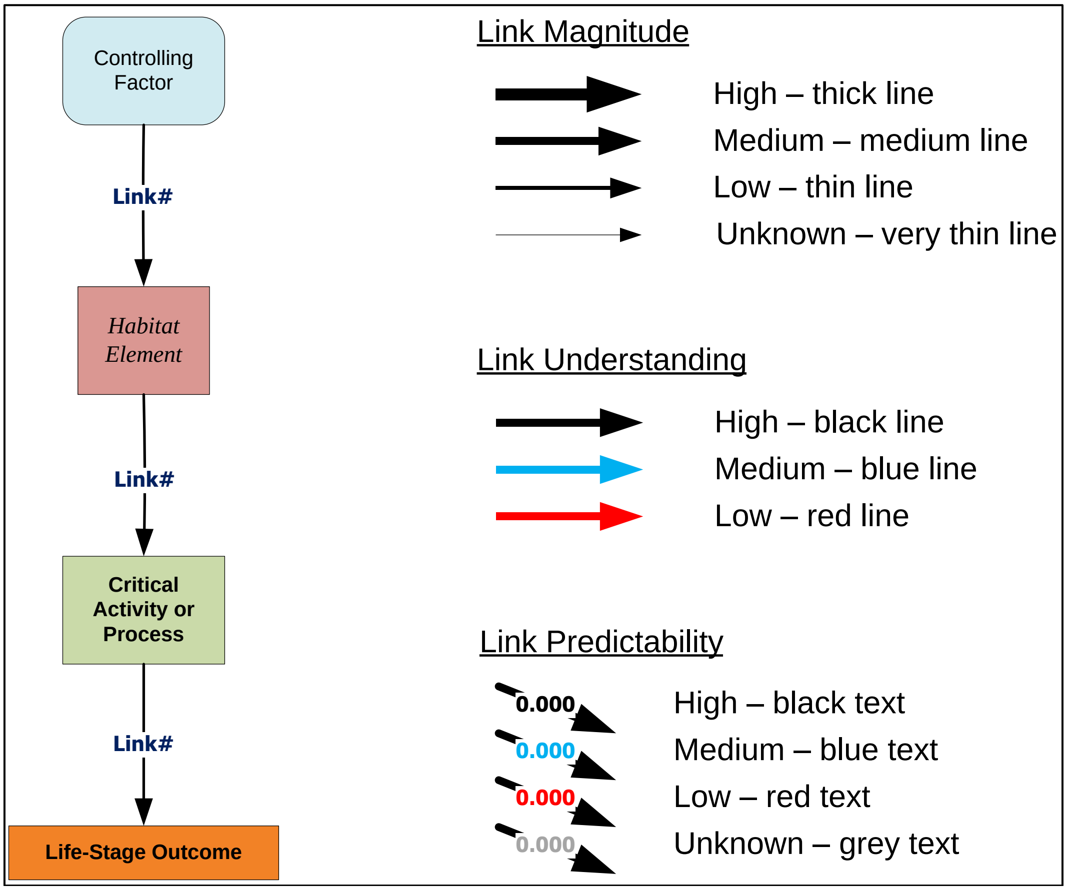

Figure 4.—Diagram conventions for LCR MSCP species conceptual ecological models.

The discussions of each life stage in this chapter and of all five life stages considered together in chapter 7 include analyses of the information contained in the spreadsheet. The analyses highlight causal chains that strongly affect the outcomes for each life stage and identify important causal relationships with high scientific uncertainty. The latter constitutes topics of potential importance for adaptive management investigation.

FLSU LIFE STAGE 1 – EGGS AND PROTOLARVAE

As described in chapter 2, this life stage begins when spawning adults release their gametes and depart the scene of individual spawning events. The stage then continues through egg incubation and hatching and ends with larval morphological transition from protolarval to flexion mesolarval morphology and swim-up at approximately 13–14 mm TL. This life stage has a single life-stage outcome, designated S_{EM}, the rate of survival of (recruitment from) the life stage (figure 1).

The information reviewed for the CEM identifies 7 (of 12) critical biological activities or processes affecting the single outcome for this life stage as shown on figure 5. However, this information identifies only one of these, predation, as a significant factor in the single outcome of this life stage, egg and protolarval survival rate. That is, the literature identifies only the rate of predation as a likely factor affecting survivorship in this life stage along the single section of the LCR currently occupied by FLSU – between Davis Dam and Lake Havasu.

Figure 5 also shows that the literature suggests only two habitat elements significantly affect the rate of predation on FLSU eggs and protolarvae in this section of the LCR: (1) the taxonomic, functional, and size composition; spatial and temporal distributions; abundance; and activity level of the aquatic vertebrate assemblage; and (2) the magnitude and spatial and temporal distributions of turbidity. Specifically, the CEM proposes that the diversity and abundance of potential predators on FLSU eggs and protolarvae in the occupied section of the LCR, and the lack of natural turbidity, result in an elevated rate of predation.

However, the information reviewed for the CEM for this life stage (figure 5), concerning the effects of predation on egg and protolarval survivorship and the effects of the aquatic vertebrate assemblage and turbidity on the rate of predation, suggests a low level of understanding for both relationships. That is, the literature provides little firm evidence concerning predation on FLSU eggs and protolarvae in this section of the LCR. The ratings for magnitude instead rest on observations across the Colorado River basin as a whole and inferences supported by established ecological principles.

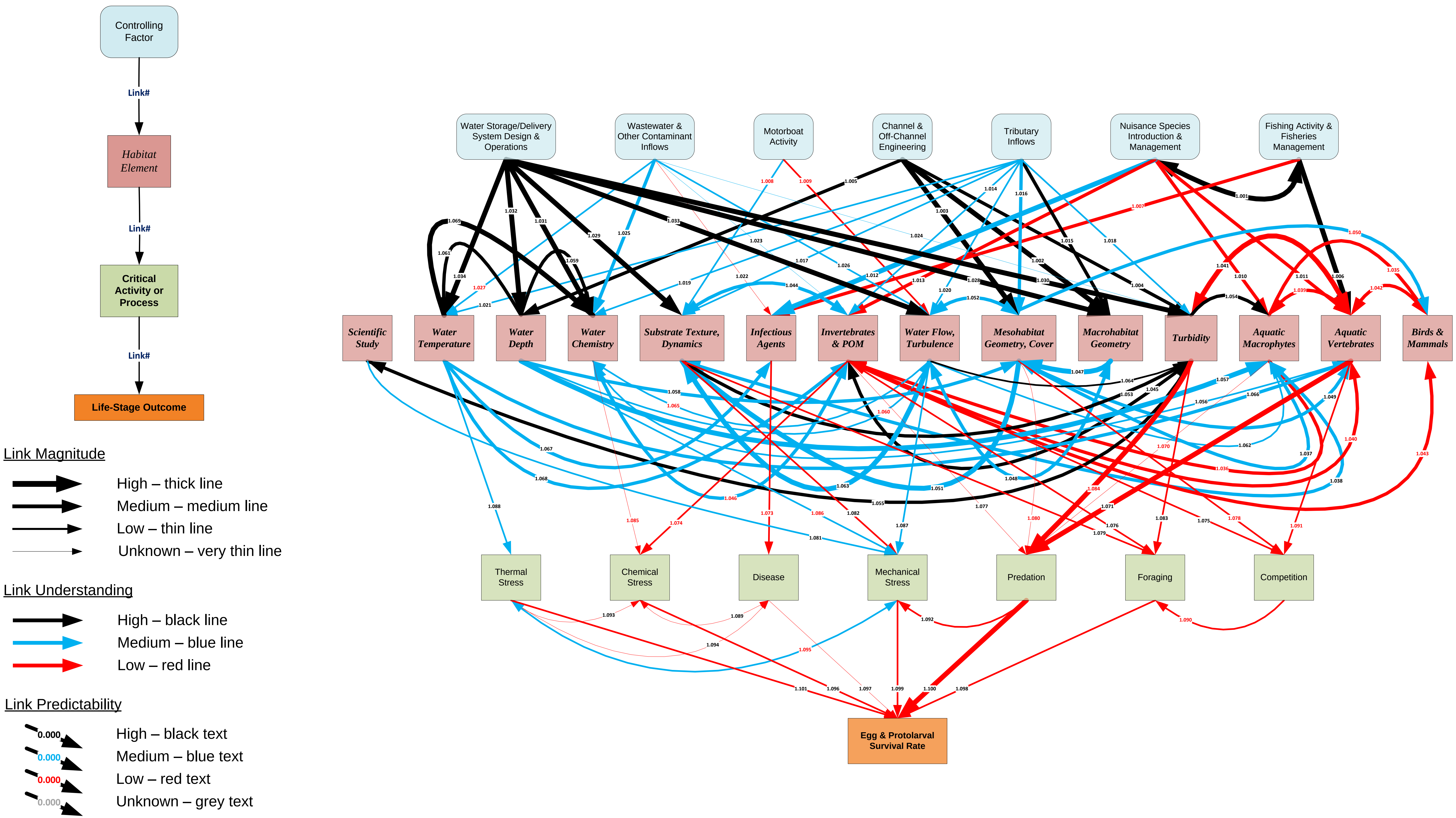

Figure 5.—FLSU life stage 1 – eggs and protolarvae.

FLSU LIFE STAGE 2 – FRY AND EARLY JUVENILES

As described in chapter 2, this life stage begins with larval swim-up and dispersal to nursery habitat, includes the transformation from metalarval to juvenile body morphology, and ends with the dispersal of the transformed juveniles beyond their nursery habitat. This life stage spans approximately the first 4–5 months of life following swim-up, with growth to approximately 50 mm TL. Some juveniles may remain in their nursery habitat longer than others. FLSU larvae disperse from their natal sites and navigate to nursery habitat primarily through drifting, controlled by limited swimming abilities. Little is known about the locations or properties of FLSU nursery sites prior to river regulation. This life stage has a single life-stage outcome, designated S_{FJ}, the rate of survival of (recruitment from) the life stage (figure 1).

As also noted in chapter 2, LCR MSCP staff also capture limited numbers of FLSU fry at the Colorado River inflow to Lake Mead and remove them to a rearing facility for use in research (Reclamation 2014). Under the program, approximately 100 reared juveniles are repatriated annually to the river below Davis Dam, where they constitute an additional source of recruits to the next life stage. The present CEM does not address this rearing program.

The information reviewed for the CEM, summarized on figure 6, identifies 10 (of 12) critical biological activities or processes affecting the single outcome for this life stage, fry and early juvenile survival rate. However, the literature suggests that only three of these critical biological activities or processes have direct, high- or medium-magnitude effects on the single outcome: foraging (high magnitude), predation, and mechanical stress (both medium magnitude). This finding specifically refers to the section of the LCR currently occupied by FLSU – between Davis Dam and Lake Havasu.

Foraging has a significant effect on survivorship of FLSU in this life stage because FLSU fry and early juveniles grow rapidly in their nursery habitat, physical environmental conditions permitting, and such growth requires a substantial diet. However, the literature reflects a low level of understanding of this causal relationship. Rather, the CEM posits the relationship based on basic ecological principles and the evidence for substantial growth and development during this life stage. However, there do not appear to be any studies assessing whether low rates of foraging success among FLSU fry and early juveniles reduce survivorship *per se*.

The CEM rates the effect of predation on survivorship in this life stage as moderate only because the literature commonly proposes predation as a major cause of mortality among FLSU of all life stages (Bezzerides and Bestgen 2002; Rees et al. 2005). In fact, no data specifically address predation on FLSU fry and juveniles along the LCR, let alone elsewhere in the Colorado River basin, resulting in a low rating for link understanding. However, an analogy with RASU and BONY would suggest that FLSU fry and early juveniles in off-channel nursery habitats would be subject to predation by a wide range of mostly non-native vertebrates and invertebrates, including juvenile and adult fishes, crayfish, odonate larvae, and bullfrog larvae and adults (Christopherson et al. 2004; Mueller 2006). Piscivorous wading birds could also prey on FLSU fry and early juveniles in the shallow waters of their nursery habitat. On the other hand, the availability of cover in nursery habitat, and avoidance behaviors among FLSU there, could offset their vulnerability to predation in these settings.

The CEM rates the effects of mechanical stress on survivorship in this life stage as moderate based on a hypothesis suggested by ecological principles. In principle, the wide range of daily fluctuation in water depth along the LCR during the rearing season, along the section of Reach 3 occupied by FLSU (see "Water Depth," chapter 4, and Best and Lantow 2012), could cause mechanical disturbance in shoreline and connected off-channel nursery habitat. However, the literature does not indicate whether these fluctuations are sufficient to cause mechanical stress to FLSU fry and early juveniles. Consequently, the CEM gives a low rating to the understanding of this hypothesized relationship.

The literature suggests that three other critical biological activities or processes—resting, drifting, and swimming—strongly indirectly affect survivorship in this life stage. These three links are rated as having medium understanding because they propose relationships that are well understood in aquatic ecology in general but are not well documented specifically for FLSU along the LCR. Resting behavior affects foraging, predation, and mechanical stress: the greater the ability of FLSU fry and early juveniles to find resting sites that provide adequate food, adequate cover, and shelter from mechanical disturbance, the greater their ability to successfully forage, avoid predation, and avoid mechanical stress. Drifting occurs only at the beginning of this life stage but is crucial to overall life-stage success. Any failure of drifting to bring FLSU fry into suitable resting habitat terminates the life stage for those fry. Swimming abilities, in turn, are crucial for FLSU fry moving in and out of drift pathways as they attempt to control (navigate) their movement from natal to nursery habitat. Swimming abilities also are crucial for foraging and for avoiding and escaping predation.

The literature suggests that seven habitat elements affect these four salient critical biological activities or processes for this life stage with high magnitude (figure 6):

- The taxonomic composition, size range, spatial and temporal distributions, and abundance of the aquatic macrophyte assemblage (aquatic macrophytes). Aquatic macrophytes at appropriate densities directly affect FLSU fry and early juveniles by providing foraging cover and POM on which FLSU feed (chapter 3). Aquatic macrophytes also may provide resting sites for avoiding predators and habitat for invertebrates that may, in turn, become food for FLSU. Finally, the distances between aquatic macrophyte patches along the drift path from natal site to nursery habitat, and within individual FLSU nursery sites along the LCR, presumably affect the distances across which FLSU fry and early juveniles must swim without adequate vegetative cover. However, these relationships are not well studied along the LCR.

- The taxonomic, functional, and size composition; spatial and temporal distributions; abundance; and activity level of the aquatic vertebrate assemblage (aquatic vertebrates). Specifically, the literature suggests a hypothesis that the diversity and abundance of potential predators on FLSU fry and early juveniles in this section of the LCR results in an elevated rate of predation. The CEM assigns a low rating for understanding this relationship.

- The taxonomic, functional, and size composition; abundance; spatial and temporal distributions; activity level of the invertebrate assemblage; and the abundance and nutritional quality of POM (invertebrates and POM). This habitat element strongly affects FLSU foraging during this life stage, with high understanding, as FLSU fry and early juveniles feed overwhelmingly on small invertebrates and POM. In turn, the invertebrate assemblage in FLSU nursery habitat may include non-native crayfish that may prey on FLSU fry. This relationship has been observed with RASU, and the CEM rates it as moderately well understood for FLSU based on an analogy with RASU.

- The types, abundance, and spatial and temporal distributions of aquatic mesohabitats and cover provided by these habitats (mesohabitat geometry/cover). As discussed in chapters 2 and 3, FLSU fry following swim-up drift downstream, seeking suitable rearing habitat. Their movement between higher- versus lower-velocity settings along their drift pathway depends in part on the distribution of "interception habitat," an aspect of channel mesohabitat geometry. A lack of interception habitat with suitable proximities along present-day LCR Reach 3 may strongly negatively impact drifting success. At the same time, the spatial distribution of interception habitat and other mesohabitat types along the channel defines the distances across which FLSU fry must swim in and out of drift pathways. However, these relationships are not well understood. Mesohabitat geometry/cover also strongly affect the distribution of cover for FLSU within nursery habitats, thereby also affecting rates of foraging and predation, but again with low understanding along the LCR.

- The abundance, spatial distributions, and stability of substrate types (substrate texture/dynamics). This habitat element helps determine the availability and distribution of suitable resting habitat in FLSU nursery sites. The relationship is moderately well understood.

- The spatial and temporal distributions of water depth (water depth). Changes in water depth in nursery sites along the LCR during this life stage can cause mechanical stress to FLSU fry and early juveniles.

- The magnitudes and horizontal, vertical, and temporal distributions of water flow velocity and turbulence (water flow/turbulence). FLSU demonstrably seek locations with low velocities as nursery habitat. The literature clearly indicates that FLSU fry use velocity cues to guide their movements during their period of drift from natal to nursery sites. However, it is not known whether the altered range and pattern of flow velocities along Reach 3 has altered the intensity of this relationship. Additionally, abrupt and/or large changes in flow velocities within nursery habitat hypothetically can also cause mechanical stress to FLSU fry and early juveniles. The latter relationship has not been studied along the LCR.

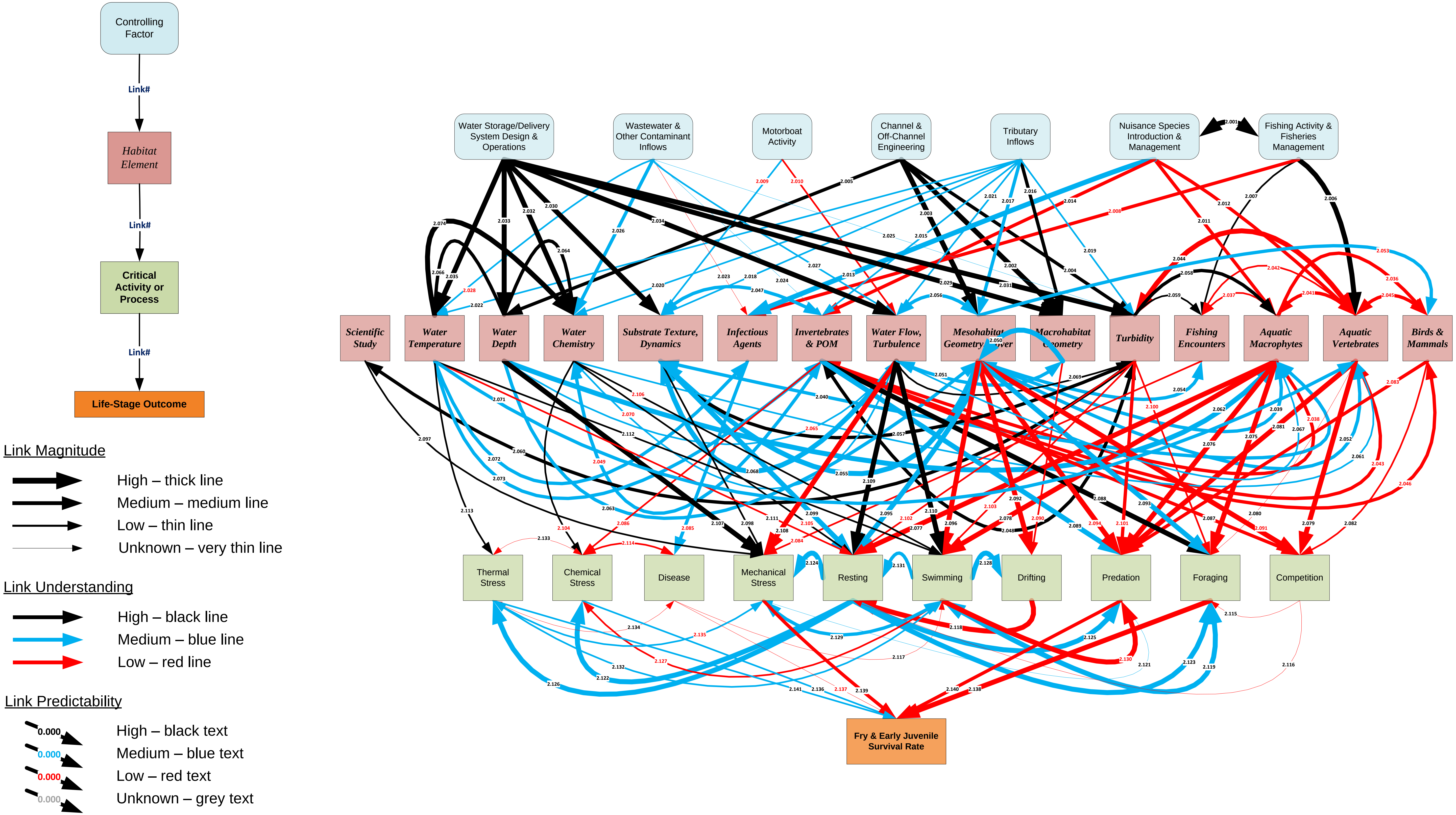

Figure 6.—FLSU life stage 2 – fry and early juveniles.

FLSU LIFE STAGE 3 – OLDER JUVENILES AND SUBADULTS

As described in chapter 2, this life stage begins after FLSU juveniles disperse from their nursery habitat, roughly around the middle of their first year. They grow from roughly 50 to 350 mm TL. This life stage ends when they reach sexual maturity, usually during their fourth to sixth year of life. This life stage has a single life-stage outcome, designated S_{JA}, the rate of survival of (recruitment from) the life stage (figure 1).

The literature identifies 10 (of 12) critical biological activities or processes that affect the single outcome for this life stage, older juvenile and subadult survival rate (figure 7). However, the literature suggests that only 2 of these 10 critical biological activities or processes have direct, high-magnitude effects on this outcome: foraging and predation. This finding refers to the section of the LCR currently occupied by FLSU – between Davis Dam and Lake Havasu.

The CEM proposes that foraging has a significant effect on survivorship in this life stage because FLSU older juveniles and subadults grow substantially before reaching maturity, and such growth requires a substantial diet. However, the CEM rates the causal relationship as having low understanding. The CEM posits the relationship based on basic ecological principles and the evidence for substantial growth and development during this life stage. At the same time, there do not appear to be any studies assessing whether low rates of foraging success among FLSU older juveniles and subadults in fact do reduce their survivorship.

The literature frequently proposes predation as a major cause of mortality among all FLSU life stages (Bezzerides and Bestgen 2002; Rees et al. 2005). Aquatic, avian, and terrestrial fauna able or known to prey on FLSU are abundant, widespread, and active year round in the LCR ecosystem and include non-native predator fishes with different gape-size limitations and/or different predatory behaviors than those present among the native aquatic predators alongside which FLSU evolved (see “Predation,” chapter 3). FLSU remains have been observed in the stomach contents of several non-native predatory fishes in the UCRB (see “Predation,” chapter 3).

However, much uncertainty remains about the impacts of predation on FLSU survivorship. FLSU numbers have not fallen drastically in synchrony with the increasing abundance of non-native predatory fishes along the LCR (or basin-wide) since the 1930s, as have RASU and BONY numbers. Bezzerides and Bestgen (2002) noted that FLSU circa 2000 occupied approximately only 45% of their original river miles of distribution within the entire Colorado River basin. Yet, they also note that reservoirs today cover approximately 22% of the river miles across the Colorado River basin and that FLSU avoid reservoir habitat.

Additionally, a significant fraction of the Gila River and its tributaries formerly occupied by FLSU today no longer experience perennial flow and therefore also provide no habitat for FLSU. Consequently, half or more of the collapse of the geographic distribution of FLSU basin-wide may be attributed simply to losses of perennial riverine habitat rather than to increased predation. Further, FLSU today appear to be common and healthy along many (although certainly not all) remaining flowing reaches within their historic range despite the abundance of non-native predators along these same reaches, and they readily became re-established between Davis Dam and Lake Havasu following their repatriation in these waters—again despite the ubiquity of non-native predatory fishes there (Bezzerides and Bestgen 2002; Mueller and Wydoski 2004; Best and Lantow 2012). The magnitude of the impacts of predation on FLSU older juveniles and subadults in the LCR therefore remains poorly documented and poorly understood.

The literature suggests that three other critical biological activities or processes—resting, swimming, and competition—strongly *indirectly* affect survivorship in this life stage. Resting behavior affects survivorship indirectly through its direct effects on predation, mechanical stress, and foraging. FLSU older juveniles and subadults able to find resting sites with adequate cover are better able to avoid predation and mechanical stress and to forage successfully. Swimming abilities are crucial for FLSU older juveniles and subadults foraging and for avoiding and escaping predation. In turn, competition for habitat, particularly cover, conceivably could constrain FLSU older juvenile and subadult success in finding suitable resting habitat. These effects are rated mostly as having medium understanding because they propose relationships well understood in aquatic ecology in general but not well documented specifically for FLSU along the LCR. However, the effect of swimming on predation is poorly documented and therefore given a low rating for understanding.

The literature suggests that four habitat elements affect these five salient critical biological activities or processes for this life stage with high magnitude (figure 7):

- Many aquatic vertebrate species in the LCR and its off-channel habitats, during at least one of their life stages, are potential competitors with older juvenile and subadult FLSU for food and/or habitat (see chapters 3–4). The taxonomic, functional, and size composition; spatial and temporal distributions; abundance; and activity levels of the aquatic vertebrate assemblage thus likely affect the rate of competition that FLSU older juveniles and subadults face for both food and physical habitat. The assemblage conceivably could include hybrids of FLSU with other catostomids, which may compete with pure FLSU for food and habitat, because the crosses will likely have food and habitat requirements and preferences similar to those of pure FLSU. However, this relationship is not well studied along the LCR and therefore receives a low rating for understanding.

Each FLSU life stage experiences predation from a distinct spectrum of aquatic vertebrate species (and different life stages among these species) with differing predatory behaviors (see "Predation," chapter 3, and "Aquatic Vertebrates," chapter 4). The taxonomic, functional, and size composition; spatial and temporal distributions; abundance; and activity levels of the aquatic vertebrate assemblage therefore strongly shape the rate of predation on FLSU older juveniles and subadults. However, this relationship is not well studied along the LCR and therefore receives a low rating for understanding.

- Aquatic macrophyte patches at appropriate densities provide resting cover for older juvenile and subadult FLSU (see "Resting," chapter 3, and "Mesohabitat Geometry/Cover," chapter 4). However, aquatic macrophyte patches are no longer widely distributed across the LCR compared to conditions prior to regulation (see "Aquatic Macrophytes," chapter 4). Their contribution to older juvenile and subadult FLSU resting habitat availability is limited to those locations where they do occur, but the intensity may be high at those locations (Karam et al. 2011, 2012, 2013) and possibly persist year round depending on seasonal growth patterns among the macrophytes. However, again, this relationship is not well studied along the LCR and therefore receives a low rating for understanding.

- The availability of resting cover for FLSU older juveniles and subadults presumably varies among mesohabitat types (chapters 3–4). Consequently, the abundance and spatial distribution of mesohabitat types defines the geography of where FLSU older juveniles and subadults will find suitable resting habitat. However, little is known about how much time FLSU older juveniles and subadults spend in different mesohabitats along LCR Reach 3.

- FLSU older juveniles and subadults are omnivorous, feeding on diatoms, algae, insect larvae, mature insects, zooplankton (e.g., cladocera, copepods, and ostracods), and POM (see "Foraging," chapter 3). Prey size increases as FLSU increase in size. The taxonomic, functional, and size composition; abundance; spatial and temporal distributions; and activity level of the invertebrate assemblage; and the abundance and nutritional quality of POM therefore affect FLSU older juvenile and subadult foraging success. This relationship is moderately well understood in the literature on FLSU across the Colorado River basin as a whole (see "Foraging," chapter 3) although not well studied along LCR Reach 3 in particular.

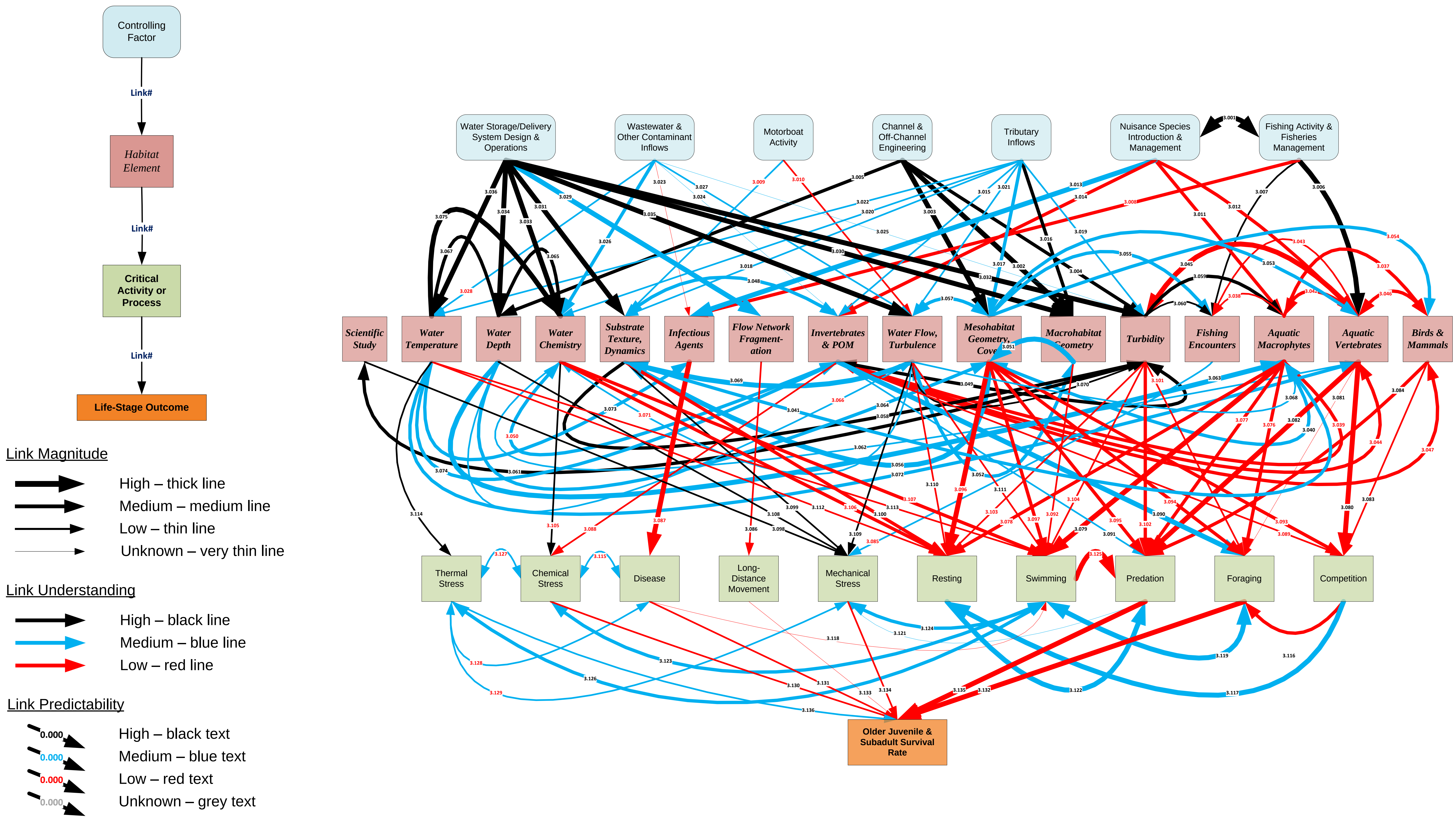

Figure 7.—FLSU life stage 3 – older juveniles and subadults.

FLSU LIFE STAGE 4 – ADULTS

As described in chapter 2, this life stage covers all age classes of sexually mature FLSU, which may achieve lifespans approaching 30 years. Individuals range in length from roughly 350 to more than 600 mm TL. This life stage has two life-stage outcomes: (1) S_{AA}, the rate of survival of adults from year to year so that they remain part of the adult population (Rees et al. 2005), and (2) P_{SA}, the percentage of adult females that participate in and contribute gametes to spawning per year.

The literature identifies 10 (of 12) critical biological activities or processes that affect 1 or both of the 2 outcomes for this life stage: 7 that affect the adult survival rate and 6 that affect the adult reproductive participation rate (figure 8). However, the literature suggests that only two of these critical biological activities or processes have direct, high-magnitude effects on the two outcomes: foraging and predation. This finding refers to the section of the LCR currently occupied by FLSU – between Davis Dam and Lake Havasu.

The CEM (figure 8) proposes that foraging has a significant effect on survivorship in this life stage because FLSU adults that do not forage effectively presumably simply die or suffer higher levels of predation. However, evidence for this relationship is limited. FLSU individuals that die as direct or indirect consequences of poor foraging presumably would not be detected as underfed individuals in field surveys. In only one study has capturing living FLSU in poor condition been reported, specifically along the Green River below Flaming Gorge Dam (Bestgen et al. 2006). The CEM posits the relationship based on basic ecological principles. There do not appear to be any studies assessing whether low rates of foraging success among FLSU adults in fact do reduce their survivorship along LCR Reach 3. In turn, the CEM proposes that foraging has a significant effect on the adult reproductive participation rate simply by an analogy with the rating for the effects of foraging on survivorship overall.

The literature frequently proposes predation as a major cause of mortality among all FLSU life stages (Bezzerides and Bestgen 2002; Rees et al. 2005). Aquatic, avian, and terrestrial fauna able or known to prey on FLSU are abundant, widespread, and active year round in the LCR ecosystem and include non-native predator fishes with different gape-size limitations and/or different predatory behaviors than those present among the native aquatic predators alongside which FLSU evolved (see "Predation," chapter 3). FLSU remains have been observed in the stomach contents of several non-native predatory fishes in the UCRB (see "Predation," chapter 3).

However, as noted above (see "FLSU Life Stage 3 – Older Juveniles and Subadults"), much uncertainty remains about the impacts of predation on FLSU survivorship. FLSU numbers have not fallen drastically in synchrony with the increasing abundance of non-native predatory fishes along the LCR (or basin-wide) since the 1930s, as have RASU and BONY numbers. Bezzerides and Bestgen (2002) noted that FLSU circa 2000 occupied approximately only 45% of their original river miles of distribution within the entire Colorado River basin. Yet, they also noted that reservoirs today cover approximately 22% of the river miles across the Colorado River basin and that FLSU avoid reservoir habitat. Additionally, a significant fraction of the Gila River and its tributaries formerly occupied by FLSU today no longer experience perennial flow and therefore also provide no habitat for FLSU. Consequently, half or more of the collapse of the geographic distribution of FLSU basin-wide may be attributed simply to losses of perennial riverine habitat rather than to increased predation. Further, FLSU today appear to be common and healthy along many (although certainly not all) remaining flowing reaches within their historic range despite the abundance of non-native predators along these same reaches and readily became re-established between Davis Dam and Lake Havasu following their repatriation in these waters again despite the ubiquity of non-native predatory fishes there (Bezzerides and Bestgen 2002; Mueller and Wydoski 2004; Best and Lantow 2012). The magnitude of the impacts of predation on FLSU adults in the LCR therefore remains poorly documented and poorly understood (figure 8).

The literature again suggests that three other critical biological activities or processes—resting, swimming, and competition—strongly *indirectly* affect survivorship in this life stage (figure 8). Resting behavior affects predation, as the greater the ability of FLSU adults to find resting sites that provide adequate cover, the greater their ability to avoid predation. Swimming abilities are crucial for FLSU adult foraging and for avoiding and escaping predation. In turn, competition for foods and for habitat, particularly cover, conceivably could constrain FLSU adult success in finding suitable resting habitat. These effects are rated mostly as having medium understanding because they propose relationships well understood in aquatic ecology in general but not well documented specifically for FLSU along the LCR. However, the effects of swimming on predation and of competition on foraging are poorly documented and therefore given low ratings for understanding.

The literature suggests that four habitat elements affect these five salient critical biological activities or processes for this life stage with high magnitude (figure 8):

- Many aquatic vertebrate species in the LCR and its off-channel habitats, during at least one of their life stages, are potential competitors with adult FLSU for food and/or habitat (see chapters 3–4). The taxonomic, functional, and size composition; spatial and temporal distributions; abundance; and activity levels of the aquatic vertebrate assemblage thus likely affect the rate of competition that FLSU adults face for both food and physical habitat. The assemblage conceivably could include hybrids of FLSU with other catostomids, which may compete with pure FLSU for food and habitat, because the crosses will likely have food and habitat requirements and preferences similar to those of pure FLSU. However, this relationship is not well studied along the LCR and therefore receives a low rating for understanding.

FLSU in each life stage experience predation from a distinct spectrum of aquatic vertebrate species (and different life stages among these species) with differing predatory behaviors (see “Predation,” chapter 3, and “Aquatic Vertebrates,” chapter 4). The taxonomic, functional, and size composition; spatial and temporal distributions; abundance; and activity levels of the aquatic vertebrate assemblage therefore strongly shape the rate of predation on FLSU adults. However, this relationship is not well studied along the LCR and therefore receives a low rating for understanding.

- Aquatic macrophytes provide food and cover for adult FLSU and also cover for predators. The CEM assigns low to moderate magnitudes to these three relationships because they are contingent on other factors. However, the CEM proposes that the distances between aquatic macrophyte patches along the LCR would affect the distances across which adult FLSU must swim without adequate vegetative cover, with high magnitude. Adult FLSU range more widely than do younger FLSU, but aquatic macrophyte patches are no longer widely distributed across the LCR compared to conditions prior to regulation (see “Aquatic Macrophytes,” chapter 4). However, this relationship is not well studied along the LCR and therefore receives a low rating for understanding.

- The availability of resting cover for FLSU adults presumably varies among mesohabitat types, as presumably also do the availability of habitat for FLSU prey and cover for predators and competitors (chapters 3–4). Consequently, the abundance and spatial distribution of mesohabitat types defines the geography of where FLSU adults will find suitable resting habitat, encounter suitable foods, and encounter potential predators and competitors. However, little is known about how much time FLSU adults spend in different mesohabitats along LCR Reach 3.

- FLSU adults are omnivorous, feeding on diatoms, algae, insect larvae, mature insects, zooplankton (e.g., cladocera, copepods, and ostracods), and POM (see “Foraging,” chapter 3). Prey size increases as FLSU increase in size. The taxonomic, functional, and size composition; abundance; spatial and temporal distributions; activity level of the invertebrate assemblage; and the abundance and nutritional quality of POM therefore affect FLSU adult foraging success. This relationship is well understood in the literature on FLSU across the Colorado River basin as a whole (see “Foraging,” chapter 3) although not well studied along LCR Reach 3 in particular.

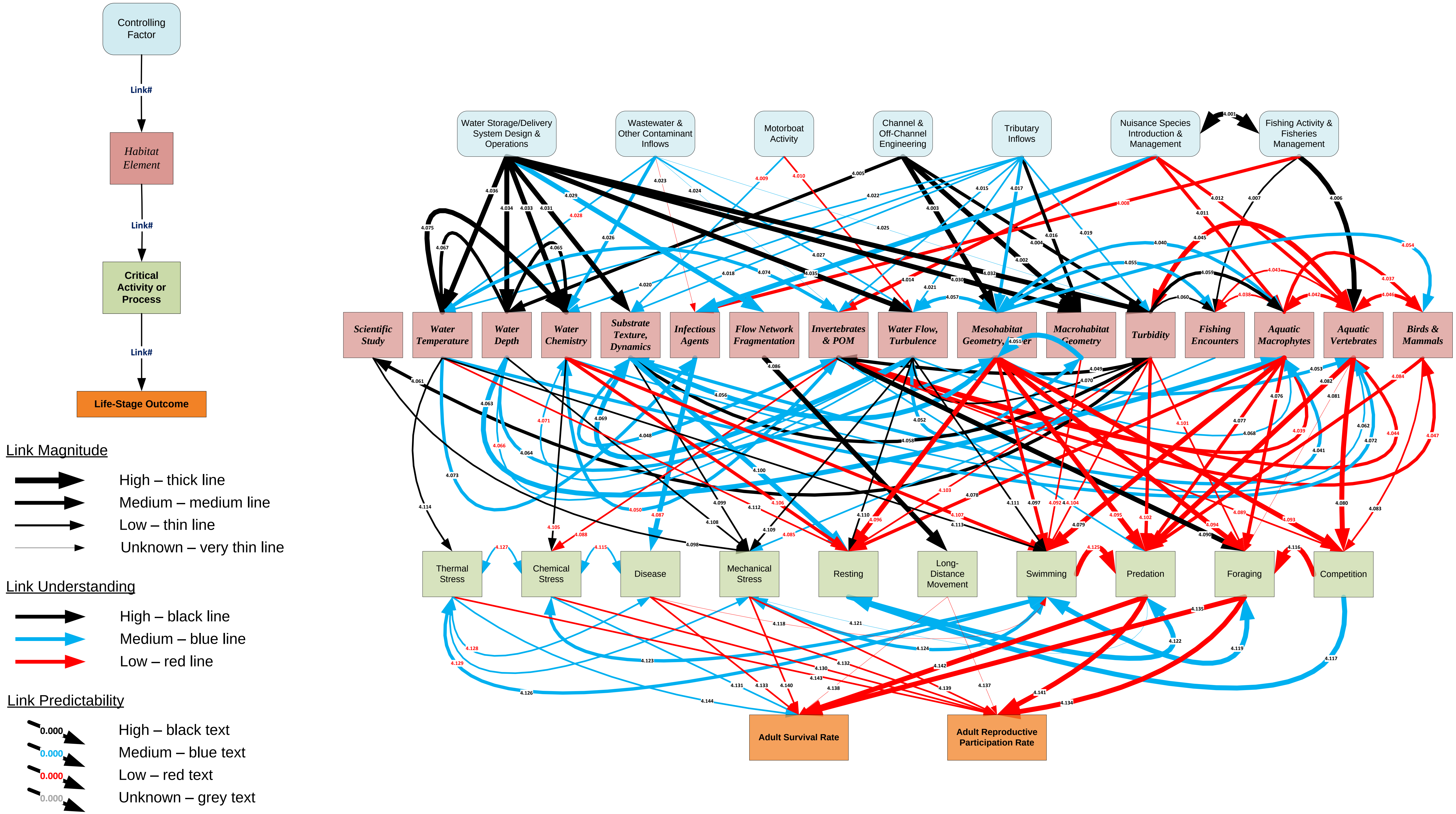

Figure 8.—FLSU life stage 4 – adults.

FLSU LIFE STAGE 5 – SPAWNING ADULTS

As described in chapter 2, this life stage covers adult FLSU during the times in which they participate in spawning. This life stage begins when would-be spawners leave their home territories to move toward spawning sites and ends when these individuals return to their home territories. This life stage thus encompasses the time FLSU spend at spawning sites and the time they spend traveling to and from these sites. This life stage has two life-stage outcomes: (1) S_{SA}, the rate of survival of spawning adults to return to the adult population following spawning, and (2) R_{SP}, the rate of production of fertilized eggs (fertility rate) at spawning sites.

The literature identifies 11 (of 12) critical biological activities or processes that affect one or both of the two outcomes for this life stage: 7 that affect the adult survival rate and 8 that affect the fertility rate (figure 9). However, the literature suggests that only three of these critical biological activities or processes have direct, high-magnitude effects on survivorship, and only four have direct, high-magnitude effects on the fertility rate. The three critical biological activities or processes with direct, high-magnitude effects on survivorship are swimming, predation, and foraging. The four critical biological activities or processes with direct, high-magnitude effects on fertility are thermal stress, mechanical stress, swimming, and foraging. These findings refer to the section of the LCR currently occupied by FLSU – between Davis Dam and Lake Havasu.

The CEM (figure 9) proposes that foraging significantly affects survivorship in this life stage because FLSU spawning adults that do not forage presumably either simply fail to spawn, die of starvation, or suffer higher levels of predation and so are not detected as underfed spawning individuals. Logically, this relationship should be significant and apply to spawning at all spawning locations in the LCR system. The CEM posits the relationship based only on basic ecological principles. There do not appear to be any studies on assessing whether low rates of foraging success among FLSU adults in fact do reduce their survivorship during the spawning cycle along LCR Reach 3.

The literature frequently proposes predation as a major cause of mortality among all FLSU life stages, as discussed for FLSU adults, above (Bezzerides and Bestgen 2002; Rees et al. 2005). Aquatic, avian, and terrestrial fauna able or known to prey on FLSU are abundant, widespread, and active year round in the LCR ecosystem and include non-native predator fishes with different gape-size limitations and/or different predatory behaviors than those present among the native aquatic predators alongside which FLSU evolved (see "Predation," chapter 3). FLSU remains have been observed in the stomach contents of several non-native predatory fishes in the UCRB (see "Predation," chapter 3).

However, as noted above (see "FLSU Life Stage 4 – Adults"), much uncertainty remains about the impacts of predation on FLSU survivorship in any life stage. FLSU numbers have not fallen drastically in synchrony with the increasing abundance of non-native predatory fishes along the LCR (or basin-wide) since the 1930s, as have RASU and BONY numbers. Bezzerides and Bestgen (2002) noted that FLSU circa 2000 occupied approximately only 45% of their original river miles of distribution within the entire Colorado River basin. Yet, they also note that reservoirs today cover approximately 22% of the river miles across the Colorado River basin and that FLSU avoid reservoir habitat. Additionally, a significant fraction of the Gila River and its tributaries formerly occupied by FLSU today no longer experience perennial flow and therefore also provide no habitat for FLSU. Consequently, half or more of the collapse of the geographic distribution of FLSU basin-wide may be attributed simply to losses of perennial riverine habitat rather than to increased predation. Further, FLSU today appear to be common and healthy along many (although certainly not all) remaining flowing reaches within their historic range despite the abundance of non-native predators along these same reaches and readily became re-established between Davis Dam and Lake Havasu following their repatriation in these waters again despite the ubiquity of non-native predatory fishes there (Bezzerides and Bestgen 2002; Mueller and Wydoski 2004; Best and Lantow 2012). The magnitude of the impacts of predation on FLSU spawning adult survivorship in the LCR remains poorly documented and poorly understood (figure 9).

FLSU adults must navigate to sites for spawning, swim to engage in spawning, swim back to other habitat following spawning, and avoid predation at the same time. However, the relationship between swimming abilities and survivorship among FLSU spawning adults is not documented in the literature and is therefore poorly understood.

FLSU experience lower rates of growth when they are thermally stressed, and fecundity varies with body size (see chapter 2). Therefore, in principle, FLSU would be expected to experience lower fecundity when thermally stressed. However, the literature does not assess this relationship. On the other hand, any thermal anomalies during spawning could disrupt spawning activity altogether, thereby reducing effective fertility without affecting fecundity. Further, because thermal anomalies would likely be products of water delivery decisions at Davis Dam, the anomalies would likely simultaneously affect the entire section of LCR Reach 3 occupied by FLSU today. The CEM hypothesizes that thermal stress could reduce fertility along Reach 3 but indicates a low level of understanding of this possibility.

FLSU that experience mechanical stress prior to spawning conceivably would experience lower rates of growth, and fecundity varies with body size (see chapter 2). Therefore, in principle, FLSU would be expected to experience lower fecundity when persistently mechanically stressed. However, the literature does not assess this relationship. On the other hand, any episodes of mechanical stress during spawning, such as would occur during an unusually intense high-flow pulse, could disrupt spawning activity altogether. Such episodes would reduce fertility without reducing fecundity. Further, because such episodes would likely be products of water delivery decisions at Davis Dam, the disturbances would likely simultaneously affect the entire section of LCR Reach 3 occupied by FLSU today. The CEM hypothesizes that mechanical stress could reduce fertility along Reach 3 but indicates a low level of understanding of this possibility.

The CEM proposes that swimming abilities among FLSU spawning adults significantly affect their fertility rate because FLSU adults must sense and respond to triggers for participating in spawning activity, determine the locations of and swim to sites for spawning, swim to engage in specific spawning events, and swim back to other habitat following spawning. However, the literature does not assess this relationship. The CEM therefore hypothesizes that swimming abilities affect fertility along Reach 3 but indicates a low level of understanding of this possibility.

The CEM proposes that foraging success among FLSU spawning adults significantly affects their fertility rate simply by analogy with the rating for the effects of foraging on survivorship among spawning adults overall. There do not appear to be any studies on assessing rates of foraging success among FLSU adults along LCR Reach 3 let alone whether the rate of foraging success affects their fertility.

The literature again suggests that three other critical biological activities or processes strongly *indirectly* affect survivorship in this life stage (figure 9)—resting, swimming, and competition. Resting behavior affects predation, as the greater the ability of FLSU spawning adults to find resting sites that provide adequate cover during the spawning cycle, the greater their ability to avoid predation. Additionally, the CEM recognizes spawning sites as a type of "resting" site. The simple availability of sites physically suitable for spawning presumably affects FLSU fertility. Swimming abilities are crucial for FLSU spawning adult foraging and for avoiding and escaping predation. In turn, competition for cover during the spawning cycle conceivably could constrain FLSU spawning adult success in finding suitable resting habitat, and competition for food conceivably could constrain their foraging success. These effects are rated mostly as having medium understanding because they propose relationships well understood in aquatic ecology in general but not well documented specifically for FLSU along the LCR. However, the effects of swimming on predation and of competition on foraging are poorly documented and are therefore given a low rating for understanding.

The literature suggests that six habitat elements affect five salient critical biological activities or processes for this life stage – competition, predation, swimming, resting, and foraging – with high magnitude (figure 9):

- Many aquatic vertebrate species in the LCR, during at least one of their life stages, are potential competitors with spawning FLSU for food and/or habitat (see chapters 3–4). The taxonomic, functional, and size composition; spatial and temporal distributions; abundance; and activity levels of the aquatic vertebrate assemblage thus likely affect the rate of competition that FLSU spawning adults face for both food and physical habitat. The assemblage conceivably could include hybrids of FLSU with other catostomids, which may compete with pure FLSU for food and habitat, because the crosses will likely have food and habitat requirements and preferences similar to those of pure FLSU. However, this relationship is not well studied along the LCR and therefore receives a low rating for understanding. The CEM assumes that the abundance of hybrids of FLSU with other catostomids along LCR Reach 3 is too low to affect FLSU fertility.

- FLSU in each life stage experiences predation from a distinct spectrum of aquatic vertebrate species (and different life stages among these species) with differing predatory behaviors (see "Predation," chapter 3, and "Aquatic Vertebrates," chapter 4). The taxonomic, functional, and size composition; spatial and temporal distributions; abundance; and activity levels of the aquatic vertebrate assemblage therefore strongly shape the rate of predation on FLSU spawning adults. However, this relationship is not well studied along the LCR and therefore receives a low rating for understanding.

- Aquatic macrophytes provide food and cover for spawning FLSU and also cover for predators. The CEM assigns low to moderate magnitudes to these three relationships because they are contingent on other factors. However, the CEM proposes that the distances between aquatic macrophyte patches along the LCR would affect the distances without adequate vegetative cover across which spawning FLSU must swim during their travels to and from spawning sites, with high magnitude. Spawning FLSU travel widely to reach spawning sites, but aquatic macrophyte patches are no longer widely distributed across the LCR compared to conditions prior to regulation (see "Aquatic Macrophytes," chapter 4). However, this relationship is not well studied along the LCR and therefore receives a low rating for understanding.

- The CEM hypothesizes that turbidity may affect the ability of spawning FLSU to navigate to and from spawning sites. FLSU evolved in a natural system with frequent, widespread, persistent turbidity. Consequently, their repertoire must include behaviors that take turbidity into account, including when spawning and when navigating to and from spawning sites. On the other hand, occasionally unsuitable turbidity during a spawning cycle in the natural system could simply have disrupted spawning on those occasions. The regulated river of course does not experience a natural range of turbidities to which FLSU spawning adults can respond (see "Turbidity," chapter 4,). However, FLSU spawn prior to the spring rise in river discharge, and the river historically would have experienced its major surge in turbidity during that spring rise rather than beforehand. Consequently, it seems likely that FLSU spawned in relatively non-turbid water, a condition provided consistently today by river regulation. The persistent reduction in turbidity therefore may benefit spawning FLSU. However, the literature provides no evidence on whether or how turbidity affects FLSU spawning site selection or spawning activity.

- The availability of resting cover for FLSU spawning adults presumably varies among mesohabitat types, as presumably also do the availability of habitat for FLSU prey and cover for predators and competitors (chapters 3–4). Consequently, the abundance and spatial distribution of mesohabitat types defines the geography of where spawning FLSU will find suitable resting habitat, encounter suitable foods, and encounter potential predators and competitors. However, little is known about how much time FLSU adults spend in different mesohabitats along LCR Reach 3.

- FLSU adults, including spawning adults, are omnivorous, feeding on diatoms, algae, insect larvae, mature insects, zooplankton (e.g., cladocera, copepods, and ostracods), and POM (see "Foraging," chapter 3). Prey size increases as FLSU increase in size. The taxonomic, functional, and size composition; abundance; spatial and temporal distributions; activity level of the invertebrate assemblage; and the abundance and nutritional quality of POM therefore affect FLSU adult foraging success. This relationship is well understood in the literature on FLSU across the Colorado River basin as a whole (see "Foraging," chapter 3) although not well studied along LCR Reach 3 in particular.

FLSU spawn only at sites that meet species preferences for a limited range of self-stabilizing substrates consisting of large pebbles and cobbles (see "Substrate Texture/Dynamics," chapter 3). Additionally, FLSU adults, in general, use crevices, cavities, and overhangs as cover. Sites with such cover conditions will likely be highly stable since they also will have self-stabilizing substrates consisting of large pebbles, cobbles, boulders, and/or bedrock exposures or will have significant densities of aquatic macrophytes, which themselves contribute to substrate stability. However, spawning FLSU may not always rest in habitats with cover, even in the daytime, given reports of their aggregating in daytime for spawning (see "Mesohabitat Geometry/Cover," "Substrate Texture/Dynamics," and "Water Depth," chapter 3).

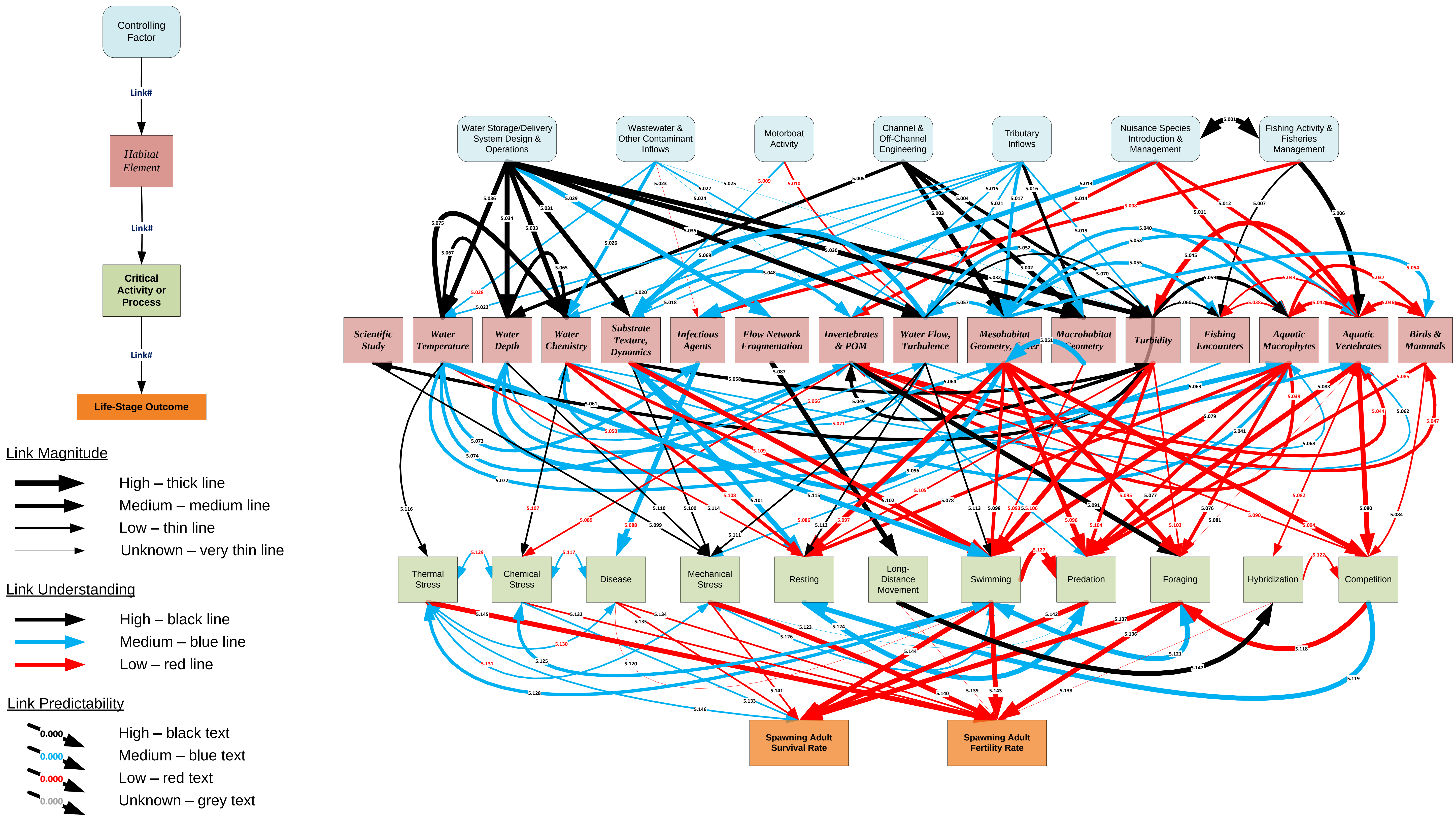

Figure 9.—FLSU life stage 5 – spawning adults.

Chapter 7 – Causal Relationships Across All Life Stages

This chapter examines the information assembled for the CEM across all life stages to assess the following:

- Which critical biological activities and processes most strongly affect the life-stage outcomes across all life stages?
- Which critical biological activities and processes strongly affect other critical biological activities and processes across all life stages?
- Which habitat elements, through their abundance, distribution, and/or quality, most strongly affect the most influential activities and processes across all life stages?
- Which habitat elements, through their abundance, distribution, and/or quality, most strongly affect the abundance, distribution, and/or quality of other habitat elements across all life stages?
- Which controlling factors most strongly affect the most influential habitat elements across all life stages?
- Which of the most influential causal relationships appear to be the least understood in ways that could affect their management?

EFFECTS OF CRITICAL BIOLOGICAL ACTIVITIES AND PROCESSES ON LIFE-STAGE OUTCOMES

Most of the 12 critical biological activities and processes identified in the CEM (chapter 3) have similar direct influences on all 7 life-stage outcomes across the 5 FLSU life stages. Table 11 shows which critical biological activities and processes directly affect each life-stage outcome. Each relationship between a critical biological activity or process and a life-stage outcome is color coded to indicate the magnitude (High, Medium, Low, Unknown) of the relationship. Three critical biological activities or processes have no direct effect on any life-stage outcomes.

Table 11.—Direct effects of critical biological activities and processes on life-stage outcomes (number of life stages in which relationship occurs)

Life-stage outcomes → / ↓ Critical biological activities and processes	Egg and protolarval survival rate	Fry and early juvenile survival rate	Older juvenile and subadult survival rate	Adult reproductive participation rate	Adult survival rate	Spawning adult fertility rate	Spawning adult survival rate
Chemical stress	1	1	1	1	1	1	1
Competition							
Disease	1	1	1	1	1	1	1
Drifting							
Foraging	1	1	1	1	1	1	1
Hybridization				1		1	
Long-distance movement			1	1	1	1	
Mechanical stress	1	1	1	1	1	1	1
Predation	1	1	1	1	1		1
Resting							
Swimming						1	1
Thermal stress	1	1	1	1	1	1	1

Table 11 indicates the following important (medium- or high-magnitude) direct effects of critical biological activities or processes on life-stage outcomes:

- Foraging activities and their rates of success along LCR Reach 3 are proposed to directly affect survivorship during all but one of the life-stage outcomes with high magnitude and to affect fertility. Foraging is proposed to play only a small role in promoting survivorship in the egg and protolarval stage.

- Mechanical stress during drifting is proposed to directly affect survivorship among FLSU fry and early juveniles with medium magnitude. Additionally, mechanical stress in the form of physical disturbance during spawning is proposed to affect fertility during spawning with high magnitude.

- Predation is proposed to directly affect survivorship during all life stages, except one, with high magnitude. The model proposes that there is insufficient information to make even a simple guess as to the potential intensity of predation on FLSU fry and early juveniles. A rating of "Unknown" for link intensity reduces the rating of overall link magnitude to "Medium" in the CEM methodology.

- Swimming is proposed to directly affect both survivorship and fertility during the spawning cycle with high magnitude because FLSU must navigate to and from, remain properly positioned, and carry out specific spawning acts at specific locations along LCR Reach 3.

- Thermal stress is proposed to directly affect fertility during the spawning cycle with high magnitude because a lack of suitable thermal spawning cues can diminish overall reproductive activity and output.

EFFECTS OF CRITICAL BIOLOGICAL ACTIVITIES AND PROCESSES ON EACH OTHER

Several critical biological activities and processes help shape other critical biological activities and processes, thereby influencing life-stage outcomes indirectly across the five FLSU life stages. Table 12 shows the number of life stages in which each critical biological activity or process directly affects one or more other critical biological activities or processes and the average magnitudes of these effects. Each relationship between one critical activity or process and another is again color coded to indicate the average magnitude (High, Medium, Low, Unknown) of the relationship. Bi-directional relationships are noted in table 12. One critical activity, long-distance movement, has no effect on any other critical activity or process. The effects of other critical biological activities and processes on mechanical stress are indicated as bi-directional relationships.

Table 12.—Direct effects of critical biological activities and processes on other critical biological activities and processes (number of life stages in which relationship occurs)

Affected critical biological activity or process ➔ **➔ Causal critical biological activity or process**	Chemical stress	Competition	Disease	Drifting	Foraging	Hybridization	Long-distance movement	Mechanical stress	Predation	Resting	Swimming	Thermal stress
Chemical stress			5*									
Competition					5					4		
Disease											4	
Drifting										1		
Foraging											4*	
Hybridization		1										
Long-distance movement						1						
Mechanical stress												
Predation								5				
Resting	1				1			1	4			1
Swimming	4*			1				4*	4	1		4*
Thermal stress	5*		5*					5*				

* Indicates that a relationship is bi-directional.

Table 12 indicates the following important (medium- or high-magnitude) direct effects of critical biological activities or processes on other critical biological activities or processes:

- Competition is proposed to affect FLSU foraging along LCR Reach 3 with medium magnitude because the types and abundances of feeding competitors that FLSU face affects foraging success. Competition is also proposed to affect FLSU resting behavior along LCR Reach 3 with medium magnitude because the types and abundances of the habitat competitors that FLSU face affects their ability to find and occupy suitable resting habitat.

- Drifting activity is proposed to affect the ability of FLSU fry to find and move into suitable nursery habitat along LCR Reach 3 with high magnitude because drifting is a crucial mechanism by which FLSU fry find their way to nursery habitat.

- Foraging and swimming activities are proposed to affect each other with high magnitude along LCR Reach 3. FLSU must swim effectively to forage, and the foraging provides the fuel that FLSU need for swimming.

- The range of their long-distance movement is proposed to affect the rate at which FLSU hybridize with other sucker species along the LCR with high magnitude. At present, Davis Dam and Lake Havasu greatly restrict the range of FLSU long-distance movement along the LCR which, in turn, greatly limits the opportunities for the mixing of FLSU with other sucker species during spawning.

- FLSU resting behaviors are proposed to affect rates of chemical stress, foraging, mechanical stress, predation, and thermal stress along LCR Reach 3 with consistently high magnitude. FLSU selection of resting location(s) affects exposure to potentially chemically, mechanically, or thermally stressful conditions. Similarly, FLSU selection of cover types and locations affects their foraging success and their ability to avoid or escape predators.

- FLSU swimming abilities are proposed to affect drifting success and predation rates along LCR Reach 3 with high magnitude. FLSU fry must control their movement in and out of drift currents by swimming, and swimming abilities help determine the ability of FLSU to avoid or escape predators.

EFFECTS OF HABITAT ELEMENTS ON CRITICAL BIOLOGICAL ACTIVITIES AND PROCESSES

The 16 habitat elements identified in the CEM (chapter 4) have similar direct influences on the 12 critical biological activities and processes (chapter 3) across all FLSU life stages. Table 13 shows the number of life stages in which each habitat element directly affects one or more critical biological activities or processes. Each relationship between a habitat element and a critical biological activity or process is color coded to indicate the average magnitude (High, Medium, Low, Unknown) of the relationship. Bi-directional relationships are noted in table 13.

Table 13.—Direct effects of habitat elements on critical biological activities and processes (number of life stages in which relationship occurs)

Critical biological activities and processes → / **↓ Habitat element**	Chemical stress	Competition	Disease	Drifting	Foraging	Hybridization	Long-distance movement	Mechanical stress	Predation	Resting	Swimming	Thermal stress	Overall
Aquatic macrophytes					4				5	4	4		17
Aquatic vertebrates		5			4	1 *			5				15
Birds and mammals		4							4				8
Fishing encounters								4					4
Flow network fragmentation							3						3
Infectious agents			5										5
Invertebrates and POM	5	5			5				5				20
Macrohabitat geometry				1							3		4
Mesohabitat geometry/cover		5		1	4				5	4	4		23
Scientific study								5					5
Substrate texture/dynamics					1			5		4	1		11
Turbidity					5				5	4	4		18
Water chemistry	5									4	4		13
Water depth								5					5
Water flow/turbulence								5		4	4		13
Water temperature										4	4	5	13

* Indicates that a relationship is bi-directional.

Table 13 indicates the following important (medium- or high-magnitude) effects of habitat elements on critical biological activities or processes:

- Aquatic macrophytes—the taxonomic composition, size range, spatial and temporal distributions, and abundance of the aquatic macrophyte assemblage—are proposed to have a medium-magnitude effect on three critical biological activities or processes in four to five life stages and a high-magnitude effect on a fourth critical biological activity or process, swimming, in four life stages. The effect on swimming arises because FLSU seek cover in aquatic macrophytes in all mobile life stages, but patches of aquatic macrophytes in LCR Reach 3 today are thought to be far more widely separated than prior to river regulation. This change in spatial distribution results in greater swimming distances between patches.

- Aquatic vertebrates—the taxonomic, functional, and size composition; spatial and temporal distributions; abundance; and activity level of the aquatic vertebrate assemblage—are proposed to affect (1) the likelihood predation on FLSU and (2) the likelihood that FLSU will experience competition for food or habitat in all five life stages, with high- and medium-magnitude impacts, respectively. (The presence of sucker hybrids in the aquatic vertebrate assemblage affects the likelihood of hybridization during FLSU reproduction and vice versa. However, these reciprocal effects have only low magnitude given the low likelihood of such hybrids occurring in LCR Reach 3).

- Birds and mammals—the taxonomic, functional, and size composition; spatial and temporal distributions; abundance; and activity levels of the bird and mammal assemblages—are proposed to affect two critical biological activities or processes across four life stages but only one with medium or high magnitude. Specifically, the CEM proposes that birds and mammals potentially can prey on FLSU in all life stages, with medium-magnitude effect.

- Flow network fragmentation—the abundance, distribution, and passability of artificial barriers to FLSU movement within the flow network—is proposed to interfere with long-distance movement by FLSU older juveniles, subadults, and adults, including spawning adults. This relationship is rated as having a consistent medium magnitude across all the affected life stages. Davis Dam and Lake Havasu limit the range of FLSU long-distance movement within the LCR, but the occupied reach between the two barriers still appears to provide the most needed habitat resources.

- Infectious agents—the types, abundance, distribution, and activity of infectious agents—are proposed to affect only one critical biological activity or process, disease, across all five life stages, with consistently medium magnitude. While several agents are known to infect FLSU in the river, the literature indicates that they do not necessarily impair FLSU health.

- Invertebrates and POM—the taxonomic, functional, and size composition; abundance; spatial and temporal distributions; activity level of the invertebrate assemblage; and the abundance and nutritional quality of POM—are proposed to affect four critical biological activities or processes across all five life stages but only one with medium or high magnitude. Specifically, invertebrates and POM affect foraging with high magnitude in all life stages except eggs and protolarvae, for which they have only a low impact, resulting in a medium average magnitude across all life stages.

- Mesohabitat geometry/cover—the types, abundance, and spatial and temporal distributions of aquatic mesohabitats and cover provided by these habitats—is proposed to affect six critical biological activities or processes across one to five life stages with a mix of medium and high average magnitudes. It affects drifting by FLSU fry, and foraging and resting by all FLSU life stages except the eggs and protolarvae stage, with high magnitude. With medium magnitude, it affects competition (for food and/or habitat) in all five life stages, predation in all five life stages, and swimming activities in all FLSU life stages except the eggs and protolarvae stage.

- Substrate texture/dynamics—the abundance, spatial distribution, and stability of substrate types (textures)—is proposed to affect four critical biological activities or processes in one to five life stages, but only two with medium or high magnitude. Specifically, substrate texture/dynamics affect FLSU resting with medium magnitude in all life stages, except the eggs and protolarvae stage, and swimming activities among FLSU spawning adults with high magnitude.

- Turbidity—the magnitude and spatial and temporal distributions of turbidity—is proposed to affect four critical biological activities or processes in four to five life stages but only one with medium or high magnitude. Specifically, turbidity is proposed to affect the predation rate in all five life stages with medium magnitude.

- Water flow/turbulence—the magnitudes and horizontal, vertical, and temporal distributions of water flow velocity and turbulence—is proposed to affect three critical biological activities or processes across four to five life stages, including two with medium magnitude. Specifically, it affects resting and swimming activities in all life stages except the eggs and protolarvae stage, all with medium magnitude.

EFFECTS OF HABITAT ELEMENTS ON EACH OTHER

Several habitat elements help shape other habitat elements, thereby influencing critical biological activities and processes indirectly across all FLSU life stages. Table 14 shows the number of life stages in which each habitat element directly affects one or more other habitat elements and the average magnitudes of these effects. Each relationship between a habitat element and another is again color coded to indicate the average magnitude (High, Medium, Low, Unknown) of the relationship. Bi-directional relationships are noted in table 14. Four habitat elements have no direct effect on any other habitat elements included in the CEM.

Table 14.—Direct effects of habitat element on other habitat elements (number of life stages in which relationship occurs)

Affected habitat element → / ↓ Driver habitat element	Aquatic macrophytes	Aquatic vertebrates	Birds and mammals	Fishing encounters	Infectious agents	Invertebrates and POM	Mesohabitat geometry/cover	Scientific study	Substrate texture/dynamics	Turbidity	Water chemistry	Water flow/turbulence	Water temperature	Overall
Aquatic macrophytes			5	4		5	5*		5*					24
Aquatic vertebrates	5*			4		5*				5*				19
Birds and mammals		5*				5*								10
Fishing encounters														0
Flow network fragmentation														0
Infectious agents														0
Invertebrates and POM									5*	5*	5*			15
Macrohabitat geometry							5					5*		10
Mesohabitat geometry/cover		5	5	4					5			5		24
Scientific study														0
Substrate texture/dynamics										5				5
Turbidity	5			4				5						14
Water chemistry		5												5
Water depth	5						5				5	5	5	25
Water flow/turbulence	5								5	5	5			20
Water temperature		5			5	5					5			20

* Indicates that a relationship is bi-directional.

Table 14 indicates the following important (medium- or high-magnitude) effects of habitat elements on other habitat elements proposed in the CEM:

- Aquatic macrophytes—the taxonomic composition, size range, spatial and temporal distributions, and abundance of the aquatic macrophyte assemblage—along LCR Reach 3 are proposed to have a medium-magnitude effect on birds and mammals and invertebrates and POM. Additionally, aquatic macrophytes reciprocally both affect and are affected by mesohabitat geometry/cover and substrate texture along LCR Reach 3, also with medium magnitude.

- Aquatic vertebrates—the taxonomic, functional, and size composition; spatial and temporal distributions; abundance; and activity level of the aquatic vertebrate assemblage—along LCR Reach 3 are proposed to have medium-magnitude effects on aquatic macrophytes and invertebrates and POM, and high-magnitude effects on turbidity. The relationship between aquatic vertebrates and turbidity is reciprocal. Turbidity affects aquatic vertebrate abundances and distributions, and some aquatic vertebrates, such as the common carp, disturb benthic sediments as they feed. The relationship between aquatic vertebrates and both aquatic macrophytes and invertebrates and POM also are reciprocal, as aquatic vertebrate assemblage composition and abundance are affected by the availability of macrophytes, invertebrates and POM foods, and the availability of macrophytes as cover.

- Birds and mammals—the taxonomic, functional, and size composition; spatial and temporal distributions; abundance; and activity levels of the bird and mammal assemblages—are proposed to have medium-magnitude effects on aquatic vertebrates and on invertebrates and POM by feeding on these classes of organisms along LCR Reach 3. Both relationships are reciprocal: bird and mammal activity is affected by the density of aquatic macrophytes, and both may feed on aquatic invertebrates.

- Invertebrates and POM—the taxonomic, functional, and size composition; abundance; spatial and temporal distributions; activity level of the invertebrate assemblage; and the abundance and nutritional quality of POM—along LCR Reach 3 are proposed to affect and reciprocally be affected by substrate texture/dynamics, turbidity, and water chemistry with medium magnitude.

- Macrohabitat geometry—the types, abundance, and spatial and temporal distributions of aquatic macrohabitats—along LCR Reach 3 affects mesohabitat geometry/cover with high magnitude. Additionally, macrohabitat geometry and water flow/turbulence along LCR Reach 3 reciprocally affect each other with medium magnitude.

- Mesohabitat geometry/cover—the types, abundance, and spatial and temporal distributions of aquatic mesohabitats and cover provided by these habitats—along LCR Reach 3 affects aquatic vertebrates, birds, and mammals, and fishing encounters with medium magnitude. As noted above (see "Aquatic macrophytes" in table 14), mesohabitat geometry/cover and aquatic macrophytes along LCR Reach 3 reciprocally affect each other with medium magnitude. Mesohabitat geometry/cover also affects substrate texture/dynamics with high magnitude. Finally, mesohabitat geometry/cover along LCR Reach 3 both affects and is affected by water flow/turbulence, with medium magnitude.

- Substrate texture/dynamics—the abundance, spatial distributions, and stability of substrate types (textures)—along LCR Reach 3 affects turbidity with medium magnitude.

- Turbidity—the magnitude and spatial and temporal distributions of turbidity—along LCR Reach 3 affects both aquatic macrophytes and scientific study with medium magnitude.

- Water depth—the spatial and temporal distributions of water depth—along LCR Reach 3 affects aquatic macrophytes with high magnitude and affects mesohabitat geometry/cover and water chemistry with medium magnitude.

- Water flow/turbulence—the magnitudes and horizontal, vertical, and temporal distributions of water flow velocity and turbulence—along LCR Reach 3 affects substrate texture/dynamics with high magnitude. Additionally, as noted above (see "Macrohabitat geometry in table 14), water flow/turbulence and macrohabitat geometry along LCR Reach 3 reciprocally affect each other with medium magnitude.

- Water temperature—the magnitudes and horizontal, vertical, and temporal abundance and distributions of water temperatures—along LCR Reach 3 affects water chemistry with high magnitude. Additionally, water temperatures along LCR Reach 3 affect aquatic vertebrates, infectious agents, and invertebrates and POM with medium magnitude.

A comparison of tables 13 and 14 shows that 10 habitat elements have overall average medium- or high-magnitude direct effects on 1 or more critical biological activities or processes: aquatic macrophytes, aquatic vertebrates, birds and mammals, flow network fragmentation, infectious agents, invertebrates and POM, mesohabitat geometry/cover, substrate texture/dynamics, turbidity, and water flow/turbulence. Tables 13 and 14 also indicate the following concerning these 10 pivotal habitat elements with medium- or high-magnitude direct effects on 1 or more critical biological activities or processes:

- All are constrained by medium- or high-magnitude interactions with at least one other habitat element.

- Six are constrained by medium- or high-magnitude interactions with 3 or more other habitat elements among the listed 10. These six are aquatic macrophytes, aquatic vertebrates, invertebrates and POM, mesohabitat geometry/cover, substrate texture/dynamics, and turbidity.

- Two are constrained with medium or high magnitude by an additional habitat element, macrohabitat geometry, which therefore significantly indirectly affects one or more critical biological activities or processes.

- One, flow network fragmentation, is unaffected by any other habitat element. It is shaped exclusively by controlling factors (see chapter 8).

EFFECTS OF CONTROLLING FACTORS ON HABITAT ELEMENTS

The seven controlling factors discussed in chapter 5 have the same direct effects on the same habitat elements across all life stages. Table 15 shows the magnitudes of direct influence of the 7 controlling factors on the 16 habitat elements identified in the CEM. Each relationship indicated in table 15 is color coded to indicate the average magnitude (High, Medium, Low, Unknown) of the relationship. None of the relationships in table 15 are reciprocal.

Two habitat elements are unaffected by any of the controlling factors included in the CEM. Flow network fragmentation affects only three life stages, and fishing encounters affect only four life stages. Otherwise, all seven controlling factors affect the indicated habitat elements in all five life stages.

Table 15.—Habitat elements directly affected by controlling factors (number of life stages in which relationship occurs)

Controlling factor → / ↓ Habitat element	Channel and off-channel engineering	Fishing activity and fisheries management	Motorboat activity	Nuisance species introduction and management	Tributary inflows	Wastewater and other contaminant inflows	Water storage-delivery system design and operation
Aquatic macrophytes				5			
Aquatic vertebrates		5		5			
Birds and mammals							
Fishing encounters		4					
Flow network fragmentation							3
Infectious agents		5		5		5	
Invertebrates and POM				5	5	5	
Macrohabitat geometry	5				5		5
Mesohabitat geometry/cover	5				5		
Scientific study							
Substrate texture/dynamics			5		5		5
Turbidity	5				5	5	5
Water chemistry					5	5	5
Water depth	5						5
Water flow/turbulence			5		5	5	5
Water temperature					5	5	5

Table 15 indicates the following important (medium- or high-magnitude) direct effects of controlling factors on habitat elements along LCR Reach 3 proposed in the CEM:

- Channel and off-channel engineering shapes macrohabitat geometry and mesohabitat geometry/cover with high magnitude, and it shapes turbidity and water depth with medium magnitude.
- Fishing activity and fisheries management shapes aquatic vertebrates with high magnitude, and it shapes infectious agents with medium magnitude.
- Nuisance species introduction and management shapes infectious agents with high magnitude, and it shapes aquatic macrophytes, aquatic vertebrates, and invertebrates and POM with medium magnitude.

- Tributary inflows shape macrohabitat geometry and mesohabitat geometry/cover with medium magnitude.

- Wastewater and other contaminant inflows shape water chemistry with medium magnitude.

- Water storage-delivery system design and operation shapes flow network fragmentation, macrohabitat geometry, substrate texture/dynamics, turbidity, water chemistry, water depth, water flow/turbulence, and water temperature with high magnitude.

The CEM also proposes that two controlling factors—fishing activity and fisheries management, and nuisance species introduction and management—reciprocally affect each other along the LCR with high magnitude. Specifically, fisheries managers and sport fishermen have intentionally introduced some non-native species into LCR Reach 3 that subsequently have become nuisance species. Recreational fishing and State agency fishery management activities also unintentionally have provided and may again provide opportunities for introductions of nuisance species. For example, quagga and zebra mussels are assumed to have arrived in the LCR on boating and fishing equipment and/or in containers used to transport sport, forage, or bait species. Further, fisheries managers and sport fishermen may respond to the presence of particular nuisance species in the system by introducing other species to control them.

POTENTIALLY INFLUENTIAL CAUSAL RELATIONSHIPS WITH LOW UNDERSTANDING

Many causal relationships proposed in the CEM (see chapter 6) are rated as having low understanding. The CEM proposes these relationships based on established ecological principles and suggestions in the literature on FLSU. However, few or no studies directly address or assess these relationships. As a result, the relationships are poorly understood across the Colorado River basin in general and/or along the LCR in particular.

Tables 16 and 17 identify those relationships that the CEM proposes have high magnitude but low understanding. Table 16 identifies such relationships specifically in which the causal agent is a habitat element, and table 17 identifies such relationships specifically in which the causal agent is a critical biological activity or process. No high-magnitude but low-understanding relationships exist in which the causal agent is a controlling factor. Tables 16 and 17 indicate the number of life stages for which the CEM proposes the relationship. Bi-directional relationships are noted in table 16.

Table 16.—High-magnitude but poorly understood relationships between habitat elements and other variables (number of life stages in which relationship occurs)

Affected condition ➔ **🡣 Causal agent: habitat element**	Competition	Disease	Drifting	Foraging	Mechanical stress	Predation	Resting	Swimming	Turbidity
Aquatic macrophytes				1		1	1	4	
Aquatic vertebrates	4					5			5*
Infectious agents		1							
Mesohabitat geometry/cover	3		1	2		3	3	1	
Substrate texture/dynamics								1	
Turbidity						1		1	
Water flow/turbulence					1				

* Indicates that a relationship is bi-directional.

Table 16 indicates consistently low levels of understanding of the ways in which three habitat elements affect multiple critical biological activities and processes across the five FLSU life stages:

- Aquatic macrophytes—the taxonomic composition, size range, spatial and temporal distributions, and abundance of the aquatic macrophytes assemblage.

- Aquatic vertebrates—the taxonomic, functional, and size composition; spatial and temporal distributions; abundance; and activity level of the aquatic vertebrate assemblage.

- Mesohabitat geometry/cover—the types, abundance, and spatial and temporal distributions of aquatic mesohabitats and cover provided by these habitats.

Table 17 indicates consistently low levels of understanding of the ways in which two critical biological activities or processes, foraging and predation, affect multiple life-stage outcomes across the five FLSU life stages. Table 17 also indicates that understanding of the survival rate of FLSU spawning adults suffers from low levels of understanding of more critical biological activities or processes than does any other life-stage outcome.

Table 17.—High-magnitude but poorly understood relationships between critical biological activities or processes and other variables (number of life stages in which relationship occurs)

Affected condition ➔ / **🡻 Causal agent: critical activity or process**	Adult reproductive participation rate	Adult survival rate	Egg and protolarval survival rate	Foraging	Fry and early juvenile survival rate	Older juvenile and subadult survival rate	Predation	Resting	Spawning adult fertility rate	Spawning adult survival rate
Competition				2						
Drifting								1		
Foraging	1	1			1	1				1
Mechanical stress										1
Predation	1	1	1			1				
Swimming							4			1
Thermal stress										1

Chapter 8 – Discussion and Conclusions

This document presents a CEM for FLSU. The purpose of this model is to help Reclamation, LCR MSCP, identify areas of scientific certainty versus uncertainty concerning FLSU ecology, the effects of specific stressors, the effects of specific management actions aimed at species habitat restoration, and the indicators used to measure FLSU habitat and population conditions. The CEM addresses the FLSU population along the river and the lakes of the LCR, including protected areas that currently provide or could provide FLSU habitat under the auspices of the LCR MSCP Habitat Conservation Plan. However, FLSU currently consistently occupy only the single section of the river, specifically the section of Reach 3 between Davis Dam and Lake Havasu. The assessment of causal relationships in the CEM consequently focuses on this section of the river wherever possible.

The CEM methodology involves six core steps:

1. For each species, identify the life stages that need to be distinguished, each with its own suite of ecological processes and environmental constraints.

2. For each life stage, identify the life-stage outcomes of concern, generally survivorship and also reproductive output where appropriate.

3. For each life-stage outcome, identify the critical biological activities and processes, the rates of which shape the rates for the life-stage outcomes. These critical biological activities and processes include basic ecological processes such as competition and predation as well as life-stage-specific activities such as drifting or spawning.

4. For each critical biological activity or process, identify the habitat elements, abundance, composition, or other properties that shape the rates of these activities or processes. Habitat elements are features of the physical and biological environment. Examples can include the abundance and composition of the assemblages of potential predators or competitors.

5. Identify controlling factors, human activities, and environmental drivers that shape the abundance and/or condition of each habitat element. The model omits factors outside the geographic or temporal scope of control of the LCR MSCP, such as climate change.

6. Identify potential causal relationships among these model components and rate these proposed relationships in terms of their apparent or likely magnitude, predictability, and level of understanding in the scientific literature. The identification and rating of the causal relationships rests on established ecological principles, studies of Colorado River ecology and hydrology in general, studies of FLSU ecology across the Colorado River basin in general, and studies of FLSU within the LCR in particular.

The FLSU conceptual ecological model identifies five life stages: eggs and protolarvae, fry and early juveniles, older juveniles and subadults, adults, and spawning adults. Life-stage outcomes consist of the survival rate for each life stage, the adult reproductive participation rate, and the spawning adult fertility rate. The FLSU conceptual ecological model identifies 12 critical biological activities and processes that affect one or more of these life-stage outcomes: chemical stress, competition, disease, drifting, foraging, hybridization, long-distance movement, mechanical stress, predation, resting, swimming, and thermal stress.

In turn, the CEM identifies 16 habitat elements, the abundance, composition, or other properties of which affect one or more critical biological activities or processes: aquatic macrophytes, aquatic vertebrates, birds and mammals, fishing encounters, flow network fragmentation, infectious agents, invertebrates and POM, macrohabitat geometry, mesohabitat geometry/cover, scientific study, substrate texture/dynamics, turbidity, water chemistry, water depth, water flow/turbulence, and water temperature. Finally, the CEM identifies seven controlling factors, the dynamics of which affect the abundance, composition, or other properties of one or more habitat elements: channel and off-channel engineering, fishing activity and fisheries management, motorboat activity, nuisance species introduction and management, tributary inflows, wastewater and other contaminant inflows, and water storage-delivery system design and operation.

The assessment of the causal relationships among these controlling factors, habitat elements, critical biological activities and processes, and life-stage outcomes indicates the following strong (high-magnitude) causal relationships. These results specifically refer to LCR Reach 3:

- Two controlling factors consistently have high-magnitude direct effects on multiple habitat elements across all FLSU life stages, listed here in order of impact: water storage-delivery system design and operation and channel and off-channel engineering.

- Five habitat elements consistently have high-magnitude direct effects on multiple critical biological activities and processes across all FLSU life stages, listed here in order of impact: mesohabitat geometry/cover, aquatic vertebrates, aquatic macrophytes, invertebrates and POM, and substrate texture/dynamics.

- Six habitat elements consistently have high-magnitude direct effects on other habitat elements and thereby have strong *indirect* effects on one or more critical biological activities or processes across all FLSU life stages. These 6 are listed here in order of impact: aquatic vertebrates, macrohabitat geometry, mesohabitat geometry/cover, water depth, water flow/turbulence, and water temperature. Two habitat elements, aquatic vertebrates and mesohabitat geometry/cover, thus have high-magnitude direct *and indirect* effects on one or more critical biological activities or processes across all FLSU life stages.

- Two critical biological activities or processes consistently have high-magnitude direct effects on multiple life-stage outcomes across all FLSU life stages, listed here in order of impact: foraging and predation. Four critical biological activities or processes consistently have high-magnitude direct effects on other critical biological activities or processes and thereby have strong *indirect* effects on one or more life-stage outcomes across all FLSU life stages. These four are listed here in order of impact: resting, competition, swimming, and foraging. One critical biological activity or process, foraging, thus has high-magnitude direct *and indirect* effects on one or more life-stage outcomes across all FLSU life stages.

The assessment of causal relationships also identified those with high magnitude but low understanding. Seven habitat elements have high-magnitude but poorly understood direct effects either on one or more other habitat elements or on one or more critical biological activities or processes. Five of these seven habitat elements with poorly understood impacts affect more than one other habitat element or more than one critical biological activity or process: aquatic macrophytes, aquatic vertebrates, mesohabitat geometry/cover, substrate texture/dynamics, and water flow/turbulence.

Seven critical biological activities or processes also have high-magnitude but poorly understood direct effects either on one or more other critical biological activities or processes or one or more life-stage outcomes. Four of these seven critical biological activities or processes with poorly understood impacts affect more than one other critical biological activity or process or more than one life-stage outcomes: competition, foraging, predation, and swimming. Additionally, drifting, another of these seven critical biological activities or processes with poorly understood impacts, strongly indirectly affects survivorship of FLSU fry. Drifting affects only a single life stage, but it has a strong—even though indirect—effect on that life stage. The low level of understanding of this relationship therefore warrants special recognition along with the habitat elements proposed to affect drifting itself.

FLSU differ from other native fishes of the LCR in their apparent ability to persist along the river and even re-establish themselves in reaches from which they had disappeared. Reviews of the status of the species across the Colorado River basin in general consistently propose that, as with the other native species of the basin, it has suffered from the combined impacts of habitat loss and fragmentation, predation by non-native species, water pollution, altered turbidity, and altered hydrology and water temperatures. However, development of the CEM did not turn up clear evidence that water pollution currently affects the overall distribution or health of the species. Similarly, FLSU appear to be able to spawn in river sections with highly altered temperature and flow regimes, although the present assessment did not evaluate the possible limits of this range of tolerance. Further, development of the CEM did not turn up clear evidence that predation by non-native species threatens the persistence of FLSU in the basin or in any individual river reach. A broad spectrum of non-native vertebrates and possibly also invertebrates (e.g., crayfish) undoubtedly do prey on FLSU. However, the CEM suggests that FLSU numbers and distribution may be more sensitive to other constraints, specifically the abundance and quality of food materials; the availability of hydrologically and geomorphically suitable spawning, drifting, nursery, and other resting habitat, including habitat with aquatic macrophytes cover; and the presence of barriers to long-distance movement.

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ATTACHMENT 1

Species Conceptual Ecological Model Methodology for the Lower Colorado River Multi-Species Conservation Program

OVERVIEW OF METHODOLOGY

The conceptual ecological models (CEMs) for species covered by the Lower Colorado River Multi-Species Conservation Program (LCR MSCP) Habitat Conservation Plan expand on a methodology developed by the Sacramento-San Joaquin Delta Ecosystem Restoration Program (ERP): https://www.dfg.ca.gov/ERP/conceptual_models.asp. The ERP is jointly implemented by the California Department of Fish and Wildlife, U.S. Fish and Wildlife Service, and National Marine Fisheries Service. The Bureau of Reclamation participates in this program.

The ERP methodology incorporates common best practices for constructing CEMs for individual species (Wildhaber et al. 2007; Fischenich 2008; DiGennaro et al. 2012). It has the following key features:

- It focuses on the *major life stages or events* through which each species passes and the *output(s)* of each life stage or event. Outputs typically consist of survivorship or the production of offspring.

- It identifies the *major drivers* that affect the likelihood (rate) of each output. Drivers are physical, chemical, or biological factors – both natural and anthropogenic – that affect output rates and therefore control the viability of the species in a given ecosystem.

- It characterizes these interrelationships using a "*driver-linkage-outcomes*" approach. Outcomes are the output rates. Linkages are cause-effect relationships between drivers and outcomes.

- It *characterizes each causal linkage* along four dimensions: (1) the character and direction of the effect, (2) the magnitude of the effect, (3) the predictability (consistency) of the effect, and (4) the certainty of present scientific understanding of the effect (DiGennaro et al. 2012).

The CEM methodology used for species covered by the LCR MSCP Habitat Conservation Plan species expands this ERP methodology. Specifically, the present methodology incorporates the recommendations and examples of Wildhaber et al. (2007, 2011), Kondolf et al. (2008), and Burke et al. (2009) for a more hierarchical approach and adds explicit demographic notation for the characterization of life-stage outcomes (McDonald and Caswell 1993). This expanded approach provides greater detail on causal linkages and outcomes. The expansion specifically calls for identifying **four** types of model components for each life stage, and the causal linkages among them, as follows:

- **Life-stage outcomes** are outcomes of an individual life stage, including the recruitment of individuals to the next succeeding life stage (e.g., juvenile to adult). For some life stages, the outcomes, alternatively or additionally, may include the survival of individuals to an older age class within the same life stage or the production of offspring. The rates of life-stage outcomes depend on the rates of the critical biological activities and processes for that life stage.

- **Critical biological activities and processes** are activities in which a species engages and the biological processes that must take place during each life stage that significantly affect life-stage outcomes. They include activities and processes that may benefit or degrade life-stage outcomes. Examples of critical activities and processes include mating, foraging, avoiding predators, avoiding other specific hazards, gamete production, egg maturation, leaf production, and seed germination. Critical activities and processes are "rate" variables. Taken together, the rate (intensity) of these activities and processes determine the rates of different life-stage outcomes.

- **Habitat elements** are specific habitat conditions that significantly ensure, allow, or interfere with critical biological activities and processes. The full suite of natural habitat elements constitutes the natural habitat template for a given life stage. Human activities may introduce habitat elements not present in the natural habitat template. Defining a habitat element may involve estimating the specific ranges of quantifiable properties of that element *whenever the state of knowledge supports such estimates*. These properties concern the abundance, spatial and temporal distributions, and other qualities of the habitat element that significantly affect the ways in which it ensures, allows, or interferes with critical activities and processes.

- **Controlling factors** are environmental conditions and dynamics – both natural and anthropogenic – that determine the quality, abundance, and spatial and temporal distributions of one or more habitat elements. In some instances, a controlling factor alternatively or additionally may directly affect a critical biological activity or process. Controlling factors are also called "drivers." A hierarchy of controlling factors will exist, affecting the system at different temporal and spatial scales. Long-term dynamics of climate and geology define the domain of this hierarchy (Burke et al. 2009). For example, the availability of suitable nest sites for a riparian nesting bird may depend on factors such as canopy cover, community type, humidity, and intermediate structure which, in turn, may depend on factors such as water storage-delivery system design and operation (dam design, reservoir morphology, and dam operations) which, in turn, is shaped by watershed geology, vegetation, climate, land use, and water demand. *The LCR MSCP conceptual ecological models focus* *on controlling factors that are within the scope of potential human manipulation, including management actions directed toward the species of interest.*

The present CEM methodology also explicitly defines a "life stage" as a biologically distinct portion of the life cycle of a species. The individuals in each life stage undergo distinct developments in body form and function; engage in distinct types behaviors, including reproduction; use different sets of habitats or the same habitats in different ways; interact differently with their larger ecosystems; and/or experience different types and sources of stress. A single life stage may include multiple age classes. A CEM focused on life stages is not a demographic model *per se* (e.g., McDonald and Caswell 1993). Instead, it is a complementary model focused on the ecological factors (drivers) that shape population dynamics.

This expanded approach permits the consideration of **six** possible types of causal relationships, on which management actions may focus, for each life stage of a species:

(1) The effect of one controlling factor on another

(2) The effect of a controlling factor on the abundance, spatial and temporal distributions, and other qualities of a habitat element

(3) The effect of the abundance, spatial and temporal distributions, and other qualities of one habitat element on those of another

(4) The effect of the abundance, spatial and temporal distributions, and other qualities of a habitat element on a critical biological activity or process

(5) The effect of one critical biological activity or process on another

(6) The effect of a critical biological activity or process on a specific life-stage outcome

Each controlling factor may affect the abundance, spatial and temporal distributions, and other qualities of more than one habitat element and several controlling factors may affect the abundance, spatial or temporal distributions, or other qualities of each habitat element. Similarly, the abundance, spatial and temporal distributions, and other qualities of each habitat element may affect more than one biological activity or process, and the abundances, spatial or temporal distributions, or other qualities of several habitat elements may affect each biological activity or process. Finally, the rate of each critical biological activity or process may contribute to the rates of more than one life-stage outcome.

Integrating this information across all life stages for a species provides a detailed picture of: (1) what is known, with what certainty, and the sources of this information; (2) critical areas of uncertain or conflicting science that demand resolution to better guide LCR MSCP management planning and action; (3) crucial attributes to use to monitor system conditions and predict the effects of experiments, management actions, and other potential agents of change; and (4) how managers may expect the characteristics of a resource to change as a result of changes to controlling factors, including changes in management actions.

Conceptual Ecological Models as Hypotheses

The CEM for each species produced with this methodology constitutes a collection of hypotheses for that species. These hypotheses concern: (1) the species' life history; (2) the species' habitat requirements and constraints; (3) the factors that control the quality, abundance, and spatial and temporal distributions of these habitat conditions; and (4) the causal relationships among these. Knowledge about these model components and relationships may vary, ranging from well settled to very tentative. Such variation in the certainty of current knowledge always arises as a consequence of variation in the types and amount of evidence available and in the ecological assumptions applied by different experts.

Wherever possible, the information assembled for the LCR MSCP species CEMs documents the degree of certainty of current knowledge concerning each component and linkage in the model. This certainty is indicated by the quality, abundance, and consistency of the available evidence and by the degree of agreement/disagreement among the experts. Differences in the interpretations or arguments offered by different experts may be represented as alternative hypotheses. Categorizing the degree of agreement/disagreement concerning the components and linkages in a CEM makes it easier to identify topics of greater uncertainty or controversy.

Characterizing Causal Relationships

A causal relationship exists when a change in one condition or property of a system results in a change in some other condition or property. A change in the first condition is said to cause a change in the second condition. The present CEM methodology includes methods for assessing causal relationships (links) along four dimensions (attributes) adapted from the ERP methodology (DiGennaro et al. 2012):

(1) The character and direction of the effect

(2) The magnitude of the effect

(3) The predictability (consistency) of the effect

(4) The certainty of present scientific understanding of the effect

The present and ERP methodologies for assessing causal linkages differ in three ways. First, the ERP methodology assesses these four attributes for the *cumulative* effect of the entire causal chain leading up to each outcome. However, the LCR MSCP methodology recognizes six different types of causal linkages as described above. This added level of detail and complexity makes it difficult in a single step to assess the cumulative effects of all causal relationships that lead up to any one individual causal link. For example, in the present methodology, the effect of a given critical biological activity or process on a particular life-stage outcome may depend on the effects of several habitat elements on that critical biological activity or process which, in turn, may depend on the effects of several controlling factors. For this reason, the present methodology assesses the four attributes separately for each causal link *by itself* rather than attempting to assess cumulative effects of all causal linkages leading to the linkage of interest. The present methodology assesses cumulative effects instead through analyses of the data assembled on all individual linkages. The analyses are made possible by assembling the data on all individual linkages in a spreadsheet as described below.

Second, the present CEM methodology explicitly divides link magnitude into three separate subattributes and provides a specific methodology for integrating their rankings into an overall ranking for link magnitude: (1) link intensity, (2) link spatial scale, and (3) link temporal scale. In contrast, the ERP methodology treats spatial and temporal scale together and does not separately evaluate link intensity. The present methodology defines link intensity as the relative strength of the effect of the causal node on the affected node *at the places and times where the effect occurs*. Link spatial scale is the relative spatial extent of the effect of the causal node on the affected node. Link temporal scale is the relative temporal extent of the effect of the causal node on the affected node. The present methodology defines link magnitude as the average of the separate rankings of link intensity, spatial scale, and temporal scale as described below.

Third, the ERP methodology addresses a single, large landscape, while the present methodology needed the flexibility to generate models applicable to a variety of spatial scopes. For example, the present methodology needed to support modeling of a single restoration site, the LCR main stem and flood plain, or the entire Lower Colorado River Basin. Consequently, the present methodology assesses the spatial scale of cause-effect relationships only relative to the spatial scope of the model.

The LCR MSCP conceptual ecological model methodology thus defines the four attributes for a causal link as follows:

- **Link character** – This attribute categorizes a causal relationship as positive, negative, involving a threshold response, or "complex." "Positive" means that an increase in the causal node results in an increase in the affected node, while a decrease in the causal node results in a decrease in the affected node. "Negative" means that an increase in the causal node results in a decrease in the affected element, while a decrease in the causal node results in an increase in the affected node. Thus, "positive" or "negative" here do ***not*** mean that a relationship is beneficial or detrimental. The terms instead provide information analogous to the sign of a correlation coefficient. "Threshold" means that a change in the causal agent must cross some value before producing an effect. "Complex" means that there is more going on than a simple positive, negative, or threshold effect. In addition, this attribute categorizes a causal relationship as uni- or bi-directional. Bi-directional relationships involve a reciprocal relationship in which each node affects the other.

- **Link magnitude** – This attribute refers to "… the degree to which a linkage controls the outcome *relative to other drivers*" (DiGennaro et al. 2012). Magnitude takes into account the spatial and temporal scale of the causal relationship as well as the strength (intensity) of the relationship in individual locations. The present methodology provides separate ratings for the intensity, spatial scale, and temporal scale of each link, as defined above, and assesses overall link magnitude by averaging these three elements. Just as the terms for link character provide information analogous to the sign of a correlation coefficient, the terms for link magnitude provide information analogous to the size of a correlation coefficient. Tables 1-1 through 1-4 present the rating framework for link magnitude.

- **Link predictability** – This attribute refers to "… the degree to which the current understanding of the system can be used to predict the role of the driver in influencing the outcome. Predictability … captures variability … [and recognizes that] effects may vary so much that properly measuring and statistically characterizing inputs to the model are difficult" (DiGennaro et al. 2012). A causal relationship may be unpredictable because of natural variability in the system or because its effects depend on the interaction of other factors with independent sources for their own variability. Just as the terms for link character provide information analogous to the sign of a correlation coefficient, the terms for link predictability provide information analogous to the size of the range of error for a correlation coefficient. Table 1-5 presents the scoring framework for link predictability.

- **Link understanding** refers to the degree of agreement represented in the scientific literature and among experts in understanding how each driver is linked to each outcome. Table 1-6 presents the scoring framework for understanding. Link predictability and understanding are independent attributes. A link may be considered highly predictable but poorly understood or poorly predictable but well understood.

Conceptual Ecological Model Documentation

The documentation for each CEM provides information in three forms: (1) a narrative report, (2) causal diagrams showing the model components and their causal linkages for each life stage, and (3) a spreadsheet that is used to record the detailed information (e.g., linkage attribute ratings) for each causal linkage. The spreadsheet and diagrams, built using Microsoft Excel™ and Microsoft Visio™, respectively, are linked so that the diagrams provide a fully synchronized summary of the information in the spreadsheet.

The narrative report for each species presents the definitions and rationales for the life stages/events and their outcomes identified for the species' life history; the critical biological activities and processes identified for each life stage; the habitat elements identified as supporting or impeding each critical biological activity or process for each life stage; the controlling factors identified as affecting the abundance, spatial and temporal distributions, and other qualities of the habitat elements for each life stage; and the causal linkages among these model components.

The narrative report includes causal diagrams (*aka* "influence diagrams") for each life stage. These diagrams show the individual components or nodes of the model for that stage (life-stage outcomes, critical biological activities and processes, habitat elements, and controlling factors) and their causal relationships. The causal relationships (causal links) are represented by arrows indicating which nodes are linked and the directions of the causal relationships. The attributes of each causal link are represented by varying line thickness, line color, and other visual properties as shown on figure 1-1. The diagram conventions mostly follow those in the ERP methodology (DiGennaro et al. 2012).

The spreadsheet for each CEM contains a separate worksheet for each life stage. Each row in the worksheet for a life stage represents a single causal link. Table 1-7 lists the fields (columns) recorded for each causal link.

Link Attribute Ratings, Spreadsheet Fields, and Diagram Conventions

Table 1-1.—Criteria for rating the relative intensity of a causal relationship – one of three variables in the rating of link magnitude (after DiGennaro et al. 2012, Table 2)

Link intensity – the relative strength of the effect of the causal node on the affected node *at the places and times where the effect occurs*.	
High	Even a relatively small change in the causal node will result in a relatively large change in the affected node *at the places and times where the effect occurs*.
Medium	A relatively large change in the causal node will result in a relatively large change in the affected node; a relatively moderate change in the causal node will result in no more than a relatively moderate change in the affected node; and a relatively small change in the causal node will result in no more than a relatively small change in the affected node *at the places and times where the effect occurs*.
Low	Even a relatively large change in the causal node will result in only a relatively small change in the affected node *at the places and times where the effect occurs*.
Unknown	Insufficient information exists to rate link intensity.

Table 1-2.—Criteria for rating the relative spatial scale of a cause-effect relationship – one of three variables in the rating of link magnitude (after DiGennaro et al. 2012, Table 1)

Link spatial scale – the relative spatial extent of the effect of the causal node on the affected node. The rating takes into account the spatial scale of the cause and its effect.	
Large	Even a relatively small change in the causal node will result in a change in the affected node across a large fraction of the spatial scope of the model.
Medium	A relatively large change in the causal node will result in a change in the affected node across a large fraction of the spatial scope of the model; a relatively moderate change in the causal node will result in a change in the affected node across no more than a moderate fraction of the spatial scope of the model; and a relatively small change in the causal node will result in a change in the affected node across no more than a small fraction of the spatial scope of the model.
Small	Even a relatively large change in the causal node will result in a change in the affected node across only a small fraction of the spatial scope of the model.
Unknown	Insufficient information exists to rate link spatial scale.

Table 1-3.—Criteria for rating the relative temporal scale of a cause-effect relationship – one of three variables in the rating of link magnitude (after DiGennaro et al. 2012, Table 1)

Link temporal scale – the relative temporal extent of the effect of the causal node on the affected node. The rating takes into account the temporal scale of the cause and its effect.	
Large	Even a relatively small change in the causal node will result in a change in the affected node that persists or recurs over a relatively large span of time – decades or longer – even without specific intervention to sustain the effect.
Medium	A relatively large change in the causal node will result in a change in the affected node that persists or recurs over a relatively large span of time – decades or longer – even without specific intervention to sustain the effect; a relatively moderate change in the causal node will result in a change in the affected node that persists or recurs over only a relatively moderate span of time – one or two decades – without specific intervention to sustain the effect; a relatively small change in the causal node will result in a change in the affected node that persists or recurs over only a relatively short span of time – less than a decade – without specific intervention to sustain the effect.
Small	Even a relatively large change in the causal node will result in a change in the affected node that persists or recurs over only a relatively short span of time – less than a decade – without specific intervention to sustain the effect.
Unknown	Insufficient information exists to rate link temporal scale.

Table 1-4.—Criteria for rating the overall relative link magnitude of a cause-effect relationship based on link intensity, spatial scale, and temporal scale

Link magnitude – the overall relative magnitude of the effect of the causal node on the affected node based on the numerical average for link intensity, spatial scale, and temporal scale. (Calculated by assigning a numerical value of 3 to "High" or "Large," 2 to "Medium," 1 to "Low" or "Small," and not counting missing or "Unknown" ratings.)	
High	Numerical average ≥ 2.67
Medium	Numerical average ≥ 1.67 but < 2.67
Low	Numerical average < 1.67
Unknown	No subattribute is rated High/Large, Medium, or Low/Small, but at least one subattribute is rated Unknown.

Table 1-5.—Criteria for rating the relative predictability of a cause-effect relationship (after DiGennaro et al. 2012, Table 3)

Link predictability – the statistical likelihood that a given causal agent will produce the effect of interest.	
High	Magnitude of effect is largely unaffected by random variation or by variability in other ecosystem dynamics or external factors.
Medium	Magnitude of effect is moderately affected by random variation or by variability in other ecosystem processes or external factors.
Low	Magnitude of effect is strongly affected by random variation or by variability in other ecosystem processes or external factors.
Unknown	Insufficient information exists to rate link predictability.

Table 1-6.—Criteria for rating the relative understanding of a cause-effect relationship (after DiGennaro et al. 2012, Table 3)

Understanding – the degree of agreement in the literature and among experts on the magnitude and predictability of the cause-effect relationship of interest.	
High	Understanding of the relationship is subject to little or no disagreement or uncertainty in peer-reviewed studies from within the ecosystem of concern or in scientific reasoning among experts familiar with the ecosystem. Understanding may also rest on well-accepted scientific principles and/or studies in highly analogous systems.
Medium	Understanding of the relationship is subject to moderate disagreement or uncertainty in peer-reviewed studies from within the ecosystem of concern and in scientific reasoning among experts familiar with the ecosystem.
Low	Understanding of the relationship is subject to wide disagreement, uncertainty, or lack of evidence in peer-reviewed studies from within the ecosystem of concern and in scientific reasoning among experts familiar with the ecosystem.
Unknown	(*The "Low" rank includes this condition*).

Table 1-7.—Organization of the worksheet for each life stage

Col.	Label	Content
A	Species	Identifies the species being modeled by four-letter code.
B	Link#	Contains a unique identification number for each causal link.
C	Life Stage	Identifies the life stage affected by the link.
D	Causal Node Type	Identifies whether the causal node for the link is a controlling factor, habitat element, critical biological activity or process, or life-stage outcome.
E	Causal Node	Identifies the causal node in the link.
F	Effect Node Type	Identifies whether the effect node for the link is a controlling factor, habitat element, critical biological activity or process, or life-stage outcome.
G	Effect Node	Identifies the effect node in the link.
H	Link Reason	States the rationale for including the link in the conceptual ecological model, including citations as appropriate.
I	Link Character Type	Identifies the character of the link based on standard definitions.
J	Link Character Direction	Identifies whether the link is uni- or bi-directional.
K	Link Character Reason	States the rationale for the entries for Link Character Type and Link Character Direction, including citations as appropriate.
L	Link Intensity	Shows the rating of link intensity based on the definitions in table 1-1.
M	Link Spatial Scale	Shows the rating of link spatial scale based on the definitions in table 1-2.
N	Link Temporal Scale	Shows the rating of link temporal scale based on the definitions in table 1-3.
O	Link Average Magnitude	Shows the numerical average rating of link intensity, spatial scale, and temporal scale based on the definitions in table 1-4.
P	Link Magnitude Rank	Shows the overall rating of link magnitude based on the Link Average Magnitude, grouped following the criteria in table 1-4.
Q	Link Magnitude Reason	States the rationale for the ratings for link intensity, spatial scale, and temporal scale, with citations as appropriate.
R	Link Predictability Rank	Shows the rating of link predictability based on the definitions in table 1-5.
S	Link Predictability Reason	States the rationale for the rating of link predictability, with citations as appropriate.
T	Link Understanding Rank	Shows the rating of link understanding based on the definitions in table 1-6.
U	Link Understanding Reason	States the rationale for the rating of link predictability, including comments on alternative interpretations and publications/experts associated with different interpretations when feasible, with citations as appropriate.
V	Management Questions	Briefly notes questions that appear to arise from the preceding entries for the link, focused on critical gaps or uncertainties in knowledge concerning *management actions and options*, with reasoning, including the estimate of relative importance when possible.
W	Research Questions	Brief notes that appear to arise from the preceding entries for the link, focused on critical gaps or uncertainties in *basic scientific knowledge*, with reasoning, including the estimate of relative importance when possible.
X	Other Comments	Provides additional notes on investigator concerns, uncertainties, and questions.
Y	Update Status	Provides information on the history of editing the information on this link for updates carried out after completion of an initial version.

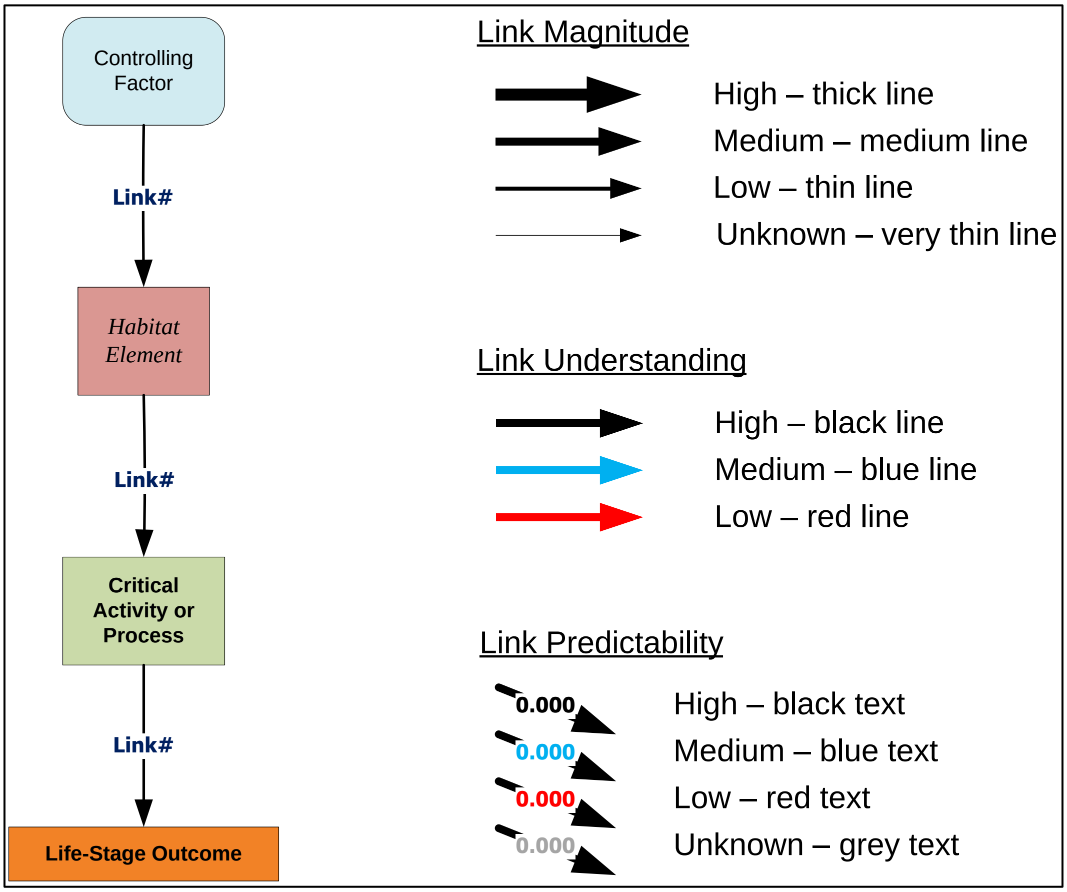

Figure 1-1.—Conventions for displaying cause and effect nodes, linkages, link magnitude, link understanding, and link predictability.

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ATTACHMENT 2

Flannelmouth Sucker Habitat Data

The tables in this attachment are duplicates of the habitat data tables presented in chapter 4. They are duplicated here as reference tables assembled together for convenience.

Table 2-1.—Reported FLSU mesohabitat associations by life stage

Life stage ➔ ↓ Mesohabitat	Spawning	Fry and early juveniles	Older juveniles and subadults	Adults
Backwater		X	X	X
Bar, gravel	X			
Eddy – midchannel				X
Eddy – shoreline		X	X	
Eddy – unclassified			X	X
Glide			X	X
Near-shore slackwater		X	X	X
Pool – confluence		X	X	
Pool – midchannel			X	X
Pool – shoreline		X	X	
Rapid – margins	X			
Rapid – unclassified				X
Riffle	X		X	x
Run – midchannel	X			
Run – unclassified			X	X
Shoreline – unclassified	X	X	X	
Side channel			X	
Slackwater – unclassified		X	X	X
Springs along channel				X

Table 2-2.—Reported FLSU substrate associations by life stage

Substrate type → / ↓ Life stage	Cobble	Gravel	Sand	Silt	Hard	References
Spawning	**X**	**X**	x			McAda 1977 (cited in Holden 1999; Reclamation 2005); Muth and Nesler 1993; Weiss 1993; Carlson et al. 1979; Weiss et al. 1998; Holden 1999; Douglas and Douglas 2000; Ryden 2000; Bezzerides and Bestgen 2002; Snyder and Muth 2004; Reclamation 2005, 2008; Budy and Salant 2011; Best and Lantow 2012
Fry and early juveniles			**X**	**X**		Thieme 1997; Childs et al. 1998; Gido and Propst 1999
Older juveniles and subadults	x	**X**	**X**	**X**	**X**	McAda 1977 (cited in Holden 1999; Reclamation 2005); Gido and Propst 1999; Holden 1999; Bezzerides and Bestgen 2002; Reclamation 2005, 2008; Bestgen et al. 2011; Budy and Salant 2011
Adults	**X**	**X**	**X**	x	**X**	Cross 1975 (cited in Reclamation 2005); Joseph et al. 1977; McAda 1977 (cited in Holden 1999; Reclamation 2005); Carlson et al. 1979; Gido and Propst 1999; Holden 1999; Bezzerides and Bestgen 2002; Reclamation 2005, 2008; Bottcher 2009; Budy et al. 2009; Bestgen et al. 2011; Best and Lantow 2012

Key: "X" = common, and "x" = occasional.

Table 2-3.—Reported FLSU average depth (m) associations by life stage

Life stage	Depth range	Depth	Location	Reference
Spawning adults	0.15–0.25	0.20	Paria River	Weiss 1993; Weiss et al. 1998
	0.22–0.38	0.30	Bright Angel Creek	Weiss et al. 1998
		0.66	White River	Lanigan and Berry 1981
		0.91	Not stated	Unattributed data in Holden 1999
		< 0.91	San Juan River between Lake Powell and Navajo Reservoir	Ryden 2000
		≈ 1.0	Yampa-Green River confluence; lower Gunnison River, upper Colorado River below Gunnison River	McAda and Wydoski 1985
	90% $\geq$ 1.0 and $\leq$ 4.0	3.0	LCR between Davis Dam and Lake Havasu	Best and Lantow 2012
	0.5–1.5		White River	Carlson et al. 1979
	< 1.14		Lower Yampa River	Muth and Nesler 1993
	< 1.2		UCRB in general	Snyder and Muth 2004
Fry and early juveniles	0.19 ± 0.13	0.19	San Juan River	Gido and Propst 1999
	< 0.5		LCR between Davis Dam and Lake Havasu	Best and Lantow 2012
Older juveniles and subadults	0.25 ± 0.17	0.25	San Juan River	Gido and Propst 1999
	0.18–0.49	0.34	Escalante River	UDWR 2009
	0.40 ± 0.18	0.40	San Juan River	Gido and Propst 1999
	0.1–1.25	0.51	San Juan River	Archer et al. 1996
	> 0.3		Paria River	Thieme 1997; Thieme et al. 2001
	0.61–1.00	0.80	San Rafael River	Bottcher 2009
Adults	0.40–0.41	0.41	Riffles in upper Colorado River near Grand Junction, Colorado	Beyers et al. 2001
	0.59 ± 0.49	0.59	Virgin River	Cross 1975 (cited in Reclamation 2005)
	0.48–1.65	1.15	Eddies in upper Colorado River near Grand Junction, Colorado	Beyers et al. 2001
	0.6–2.15	1.16	Runs in upper Colorado River near Grand Junction, Colorado	Beyers et al. 2001
	0.15–2.4	1.27	White and Yampa Rivers	Carlson et al. 1979
	0.5–2.5	1.50	Yampa, Colorado, Gunnison, and Dolores Rivers in Colorado	Stewart and Anderson 2007 (see also Stewart et al. 2005)
	88% $\geq$ 1.0 and $\leq$ 4.0	2.4	LCR between Davis Dam and Lake Havasu	Best and Lantow 2012
	0.9–6.1	3.50	Upper Colorado River and multiple tributaries	McAda 1977; Sigler and Sigler 1996 (cited in UDWR 2006)
	> 2.0		LCR between Davis Dam and Lake Havasu	Mueller and Wydoski 2004

Note: The data presented in this table reflect those available in the literature at the time this model was developed. These data have not been validated.

Table 2-4.—Reported FLSU velocity (m/s) associations by life stage

Life stage	Velocity range	Average velocity	Location	Reference
Spawning adults	97% < 1.0	0.6	LCR between Davis Dam and Lake Havasu	Best and Lantow 2012
Spawning adults		≈ 1.0	Yampa and upper Colorado Rivers	McAda and Wydoski 1985
Spawning adults	0.15–1.0		Paria River	Weiss 1993; Weiss et al. 1998
Spawning adults	0.23–0.89		Bright Angel Creek	Weiss et al. 1998
Fry and early juveniles		0.086 ± 0.109	San Juan River	Gido and Propst 1999
Fry and early juveniles		< 0.2	Nearshore Grand Canyon	Childs et al. 1998
Older juveniles and subadults		0.041 ± 0.186	San Juan River	Gido and Propst 1999
Older juveniles and subadults		0.12 ± 0.24	San Juan River	Gido and Propst 1999
Older juveniles and subadults	< 0.2 – > 0.81	0.49	San Rafael	Bottcher 2009
Adults	0.02–0.15	0.13	Eddies on Colorado River near Grand Junction	Beyers et al. 2001
Adults	0–1.0	0.44	Virgin River	Cross 1975 (cited in Reclamation 2005)
Adults	0.22–1.10	0.54	Runs on Colorado River near Grand Junction	Beyers et al. 2001
Adults	0.61–0.81	0.71	Riffles on Colorado River near Grand Junction	Beyers et al. 2001
Adults	0.25–1.25	0.75	Yampa, Colorado, Gunnison, and Dolores Rivers in Colorado	Stewart and Anderson 2007
Adults	95% < 1.5	0.8	LCR between Davis Dam and Lake Havasu	Best and Lantow 2012
Adults	0.5–1.0		LCR between Davis Dam and Lake Havasu	Mueller and Wydoski 2004
Adults	< 1.22		White River	Carlson et al. 1979

Note: The data presented in this table reflect those available in the literature at the time this model was developed. These data have not been validated.

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