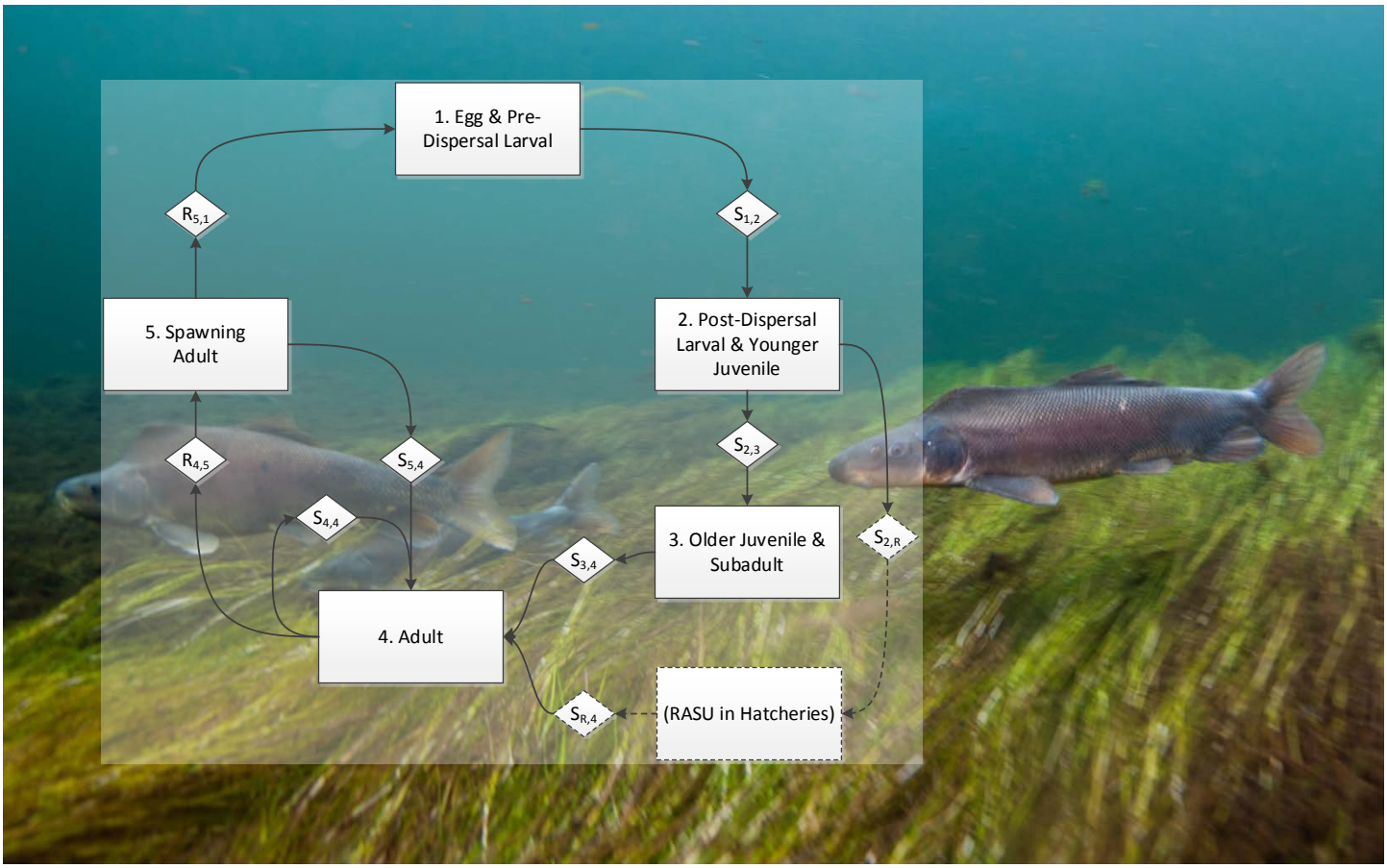
Lower Colorado River Multi-Species Conservation Program

Balancing Resource Use and Conservation

Razorback Sucker (*Xyrauchen texanus*) (RASU) Basic Conceptual Ecological Model for the Lower Colorado River



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Lower Colorado River Multi-Species Conservation Program

Razorback Sucker (*Xyrauchen texanus*) (RASU) Basic Conceptual Ecological Model for the Lower Colorado River

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ACRONYMS AND ABBREVIATIONS

BONY	bonytail (*Gila elegans*)
BP	Before Present
ca.	closeness or approximation in time
CEM	conceptual ecological model
cm	centimeter(s)
CRAB	Colorado River Aquatic Biologists
DNA	deoxyribonucleic acid
DO	dissolved oxygen
DRERIP	Sacramento-San Joaquin Delta Regional Ecosystem Restoration Implementation Plan
FLSU	flannelmouth sucker(s) (*Catostomus latipinnis*)
ft/mi	average channel gradient, in feet per mile
HCP	Habitation Conservation Plan
IPCA	Imperial Ponds Conservation Area
LCR	lower Colorado River
LCRB	Lower Colorado River Basin
LCR MSCP	Lower Colorado River Multi-Species Conservation Program
m	meter(s)
m/s	meters per second
mm	millimeter(s)
NAS	Nonindigenous Aquatic Species
NISIC	National Invasive Species Information Center
NRC	National Research Council
PADCNR	Pennsylvania Department of Conservation and Natural Resources
pH	potential of hydrogen, a measure of how acidic or alkaline a water sample is
PIT	passive integrated transponder
POM	particulate organic matter
RASU	razorback sucker(s) (*Xyrauchen texanus*)
Reclamation	Bureau of Reclamation
TL	total length

UCRB	Upper Colorado River Basin
USDA	U.S. Department of Agriculture
USFWS	U.S. Fish and Wildlife Service
USGS	U.S. Geological Survey

Symbols

≈	approximately
°C	degrees Celsius (*aka* Centigrade)
°F	degrees Fahrenheit
>	greater than
≥	greater than or equal to
<	less than
µS/cm	microsiemens per centimeter
%	percent
™	trademark

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Attachment

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

2 Razorback Sucker (*Xyrauchen texanus*) (RASU) Habitat Data

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.

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[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 Regional Ecosystem Restoration Implementation Plan (DRERIP): https://www.dfg.ca.gov/ERP/conceptual_models.asp. The DRERIP 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 [*Coccyzus americanus occidentalis*]) 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 an updated conceptual ecological model (CEM) for the razorback sucker (*Xyrauchen texanus*) (RASU). It supersedes the previous RASU conceptual ecological model (Braun and McClure 2013) and incorporates an updated CEM methodology that was applied to the flannelmouth sucker (*Catostomus latipinnis*) and bonytail (*Gila elegans*) (BONY) (Braun 2015a, 2015b) as well as to several other species of concern to the Lower Colorado River Multi-Species Conservation Program (LCR MSCP) after completion of the original RASU conceptual ecological model. The purpose of this updated RASU conceptual ecological model is to help the LCR MSCP identify areas of scientific uncertainty concerning RASU ecology, the effects of specific stressors, the effects of specific management actions aimed at species habitat restoration, and the methods used to measure RASU habitat and population conditions. (Note: Attachment 1 provides an introduction to the CEM process. Readers unfamiliar with this process should read attachment 1 before continuing with this document.)

As with the earlier version (Braun and McClure 2013), the present RASU conceptual ecological model does not address RASU development within hatcheries or other artificial rearing environments. The LCR MSCP and its partners routinely harvest RASU larvae from Lake Mohave during their dispersal from spawning sites and deliver these larvae to hatcheries such as the U.S. Fish and Wildlife Service (USFWS) Willow Beach National Fish Hatchery (LCR MSCP 2015, 2016a, 2016b; Kesner et al. 2016). Once they reach a desired size range, these reared RASU are repatriated into lower Colorado River (LCR) waters to augment the small population of RASU that mature in the wild. The present RASU conceptual ecological model only concerns RASU survival and reproduction in the LCR aquatic (river and backwater) system itself, not in the hatcheries or other artificial rearing environments.

The research questions and gaps in scientific knowledge identified through the modeling effort serve as examples of topics the larger scientific community could explore to improve the overall understanding of the ecology and conservation of RASU. These research questions and knowledge gaps 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 RASU 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 RASU conceptual ecological model has five core components:

- **Life stages** – These consist of the major growth stages and critical events through which an individual RASU 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 (survival), or the number of viable eggs produced (fertility). Life-stage outcomes typically are "rate" variables that depend on the rates of the critical biological activities and processes for each life stage.

- **Critical biological activities and processes** – These consist of the activities in which the species engages and the biological and ecological 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 also 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, water demand, and social institutions.

The present 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 RASU conceptual ecological model addresses the RASU population along the Colorado River and its lakes as well as in off-channel ponds and wetlands on the flood plain of the LCR. The basic sources of information for the RASU conceptual ecological model include Minckley (1991), Minckley et al. (1991), USFWS (1998, 2002a), Ryden (1999), LCR MSCP (2004, 2008, 2016a), Minckley and Marsh (2009), Mueller (2006), Valdez et al. (2012a, 2012b, 2012c),

Marsh et al. (2015), and Kesner et al. (2016). These studies summarize and cite large bodies of earlier studies across the entire Colorado River Basin, reflecting the historic distribution of the species. The model also integrates information from numerous other publications, presentations at Colorado River Aquatic Biologists (CRAB) meetings (https://www.lcrmscp.gov/crab/crab.html), current research projects funded by the LCR MSCP, and the expert knowledge of LCR MSCP fish biologists and others.

This document is not intended simply 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 present model updates the previous version (Braun and McClure 2013) with new information on the species, a simplified life-stage model, and an improved conceptual ecological methodology. It adds life-stage outcomes as a model component and updates the terminology for critical biological activities and processes, habitat elements, and controlling factors to match the terminology used in the FLSU and BONY conceptual ecological models (Braun 2015a, 2015b).

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

1. Egg and pre-dispersal larval life stage
    - Egg and pre-dispersal larval survival
2. Post-dispersal larval and younger juvenile life stage
    - Post-dispersal larval and younger juvenile survival
3. Older juvenile and subadult life stage
    - Older juvenile and subadult survival
4. Adult life stage
    - Adult annual survival
    - Adult annual spawning participation rate
5. Spawning adult life stage
    - Spawning adult survival
    - Spawning adult fertility

The model distinguishes 14 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 8 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 14 critical biological activities and processes identified across all life stages are: chemical stress, competition, disease, drifting, egg settling and adhesion, foraging, hybridization, mechanical stress, predation, resting/hiding, ripening, staging and spawning, swimming, and thermal stress. The 16 habitat elements identified across all life stages are aquatic macrophytes; aquatic vertebrates; birds and mammals; genetic diversity; infectious agents; invertebrates and particulate organic matter; macrohabitat structure; mesohabitat structure; monitoring, capture, handling; pre-release conditioning; substrate texture/dynamics; turbidity; water chemistry; water depth; water flow; turbulence; and water temperature. The 8 controlling factors identified across all habitat elements are channel and off-channel engineering, motorboat activity, non-RASU fisheries, nuisance species introduction and management, RASU monitoring and conservation programs, tributary inflows, wastewater and other contaminant inflows, and water storage-delivery system design and operations.

KEY RESULTS

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:

- Five controlling factors have consistently high-magnitude direct potential effects on multiple habitat elements across all RASU life stages. These are, in alphabetical order, channel and off-channel engineering; non-RASU fisheries; nuisance species introduction and management; RASU monitoring and conservation programs; and water storage-delivery system design and operations.

- Eight habitat elements have high-magnitude direct potential effects on one or more critical biological activities and processes across one or more RASU life stages. These are, in alphabetical order: aquatic vertebrates; genetic diversity; invertebrates and particulate organic matter, mesohabitat structure, pre-release conditioning, substrate texture/dynamics, turbidity, and water temperature

- Seven habitat elements consistently have high-magnitude direct potential effects on other habitat elements and thereby have strong indirect effects on one or more critical biological activities or processes across all RASU life stages. These seven are as follows, listed based on the number of affected

habitat elements and then alphabetically: mesohabitat structure, turbidity, water temperature. water depth, aquatic vertebrates, macrohabitat structure, and water flow/turbulence. In two instances, the direct effects of one of these high-impact habitat elements on another are bi-directional (i.e., the "causal" and "affected" habitat elements strongly, reciprocally affect each other). Mesohabitat structure both directly affects and is directly affected by substrate texture/dynamics, with high magnitude. Similarly, turbidity both directly affects and is directly affected by the abundance and composition of the aquatic vertebrate assemblage. Five habitat elements – aquatic vertebrates, mesohabitat structure, substrate texture/dynamics, turbidity, and water temperature – thus have consistently high-magnitude direct *and indirect* potential effects on one or more critical biological activities or processes across all RASU life stages.

- Six critical biological activities or processes have high-magnitude direct potential effects on one or more life-stage outcomes across the five RASU life stages. Predation directly affects survival in all five life stages, with high magnitude. The present CEM proposes that foraging success potentially directly affects survival among older juveniles and subadults, and among adults, and also directly affects adult annual spawning participation, all with high magnitude. The present CEM proposes that thermal stress has the potential to directly affect survival among eggs and pre-dispersal larvae, and among post-dispersal larvae and younger juveniles, both with high magnitude. Egg settling and adhesion is hypothesized to have the potential to directly affect survival among eggs and pre-dispersal larvae, with high magnitude. The present CEM proposes that staging and spawning has the potential to directly affect spawning adult fertility and that swimming activities, strength, and stamina have the potential to directly affect survival among spawning adults, all with high magnitude.

- Eight critical biological activities or processes have high-magnitude direct potential effects on other critical biological activities or processes and thereby have strong indirect effects on one or more life-stage outcomes across the five RASU life stages. Swimming activities, strength, and stamina are hypothesized to have the potential to directly affect drifting, predation, resting/hiding, and staging and spawning, with high magnitude. Foraging success is hypothesized to have the potential to directly affect ripening and swimming strength and stamina, all with high magnitude. Competition is hypothesized to have a high-magnitude direct effect on resting/hiding activity (i.e., on the ability of RASU to find suitable cover habitat) in all four motile life stages. Drifting dynamics, egg settling and adhesion, and resting/hiding activities are all hypothesized to have high-magnitude direct effects on predation in various life stages, and both predation and ripening are hypothesized to have to have high-magnitude direct effects on staging and spawning. The relationship between foraging

and swimming is hypothesized to be bi-directional, as is the relationship between predation and staging and spawning. Four critical biological activities or processes – foraging, predation, staging and spawning, and swimming – thus have consistently high-magnitude direct *and indirect* potential effects on life-stage outcomes across the five RASU life stages.

The assessment of causal relationships also identified those with high magnitude but low understanding. Proposed high-magnitude but poorly understood direct potential effects of habitat elements include the effects of aquatic vertebrate assemblage composition and abundance on competition, predation, and swimming activities; bird and mammal assemblage composition and abundance on predation; genetic diversity on RASU vulnerability to disease and thermal stress; aquatic invertebrate assemblage composition and abundance on competition and predation; mesohabitat structure on aquatic invertebrate assemblage composition and abundance, and resting/hiding, staging and spawning, and swimming behavior; pre-release conditioning on RASU vulnerability to chemical stress, predation, and thermal stress; pre-release conditioning on RASU foraging and swimming behaviors; substrate texture/ dynamics on egg settling and adhesion, and on staging and spawning dynamics; turbidity on aquatic vertebrate assemblage composition and abundance and on predation; and water temperature on aquatic vertebrate activity levels and on ripening and staging and spawning.

Proposed high-magnitude but poorly understood direct potential effects of critical activities or processes include the effects of competition on resting/hiding behaviors in all four motile life stages; foraging behaviors and success on survival among older juveniles, subadults, and adults, on ripening, and on the adult annual spawning participation rate; predation on survival in all five life stages, as well as on mechanical stress; predation on staging and spawning, and vice versa; resting/hiding behaviors, specifically the use of cover, on predation; ripening on staging and spawning; and swimming behaviors, strength, and/or stamina on drifting, monitoring and capture, predation, resting/hiding among post-dispersal larvae and younger juveniles, and staging and spawning.

Finally, the present CEM proposes several causal relationships based on basic ecological and biological concepts for which the literature on RASU does not provide sufficient information to assess the possible magnitude of any effect.

Reviews of the status of the species across the Colorado River Basin in general consistently propose that, as with the other native fishes 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 present CEM did not turn up clear evidence that water pollution currently affects the overall distribution or health of the species. Similarly, RASU appear to be able to spawn in river sections – including impoundments – and isolated ponds with highly altered

temperature and flow regimes, although the present assessment did not evaluate the possible limits of this range of tolerance. On the other hand, the literature strongly suggests that predation by non-native species threatens the persistence of RASU wherever they occur, except apparently in settings where mesohabitat conditions with turbidity and/or good cover afford motile RASU with some measure of protection. A broad spectrum of birds, aquatic vertebrates, and possibly aquatic invertebrates (e.g., odonate larvae and crayfish) are known or thought to prey on RASU. The present CEM also suggests that RASU numbers and distribution may be sensitive to other constraints, including the abundance and quality of food materials as well as the availability of hydrologically and geomorphically suitable spawning, drifting, nursery, and other resting/hiding habitat, including habitat with aquatic macrophyte cover. Finally, the present CEM highlights continuing uncertainties over the effects of pre-release conditioning among RASU reared for repatriation – including both conditioning to ambient conditions at rearing facilities and adaptive conditioning to prepare the reared RASU for the conditions they face upon release.

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 RASU. 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 razorback sucker (*Xyrauchen texanus*) (RASU). 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 RASU ecology, the effects of specific stressors, the effects of specific management actions aimed at species habitat restoration, and the indicators used to measure RASU habitat and population conditions. The CEM methodology follows that developed for the Sacramento-San Joaquin River Delta Regional Ecosystem Restoration Implementation Plan (DRERIP) (DiGennaro et al. 2012), with modifications. (Note: Attachment 1 provides an introduction to the CEM process. Readers unfamiliar with this process should read attachment 1 before continuing with this document.)

The model addresses the RASU population along the main stem Colorado River and its lakes as well as in off-channel ponds and wetlands on the flood plain of the lower Colorado River (LCR), including wildlife refuges and other protected areas managed as RASU habitat under the auspices of the LCR MSCP Final Habitat Conservation Plan (HCP) (LCR MSCP 2004). These protected areas include waters into which hatchery-reared RASU adults are repatriated as part of the augmentation program (LCR MSCP 2006). The model addresses the landscape as a whole rather than any single reach, waterbody, or managed area.

As with the earlier version (Braun and McClure 2013), the present RASU conceptual ecological model does not address RASU development within hatcheries or other artificial rearing environments. The LCR MSCP and its partners routinely harvest RASU larvae in the wild during their dispersal from spawning sites and deliver these larvae to hatcheries such as the U.S. Fish and Wildlife Service (USFWS) Willow Beach National Fish Hatchery (LCR MSCP 2015, 2016a, 2016b; Kesner et al. 2016). Once they reach a desired size range, these reared RASU are repatriated into LCR waters to augment the small population of RASU that mature in the wild. The present RASU conceptual ecological model only concerns RASU survival and reproduction in the LCR aquatic (river and backwater) system itself, not in the hatcheries or other artificial rearing environments.

The present model updates the previous version (Braun and McClure 2013) with new information on the species, a simplified life-stage model, and an improved conceptual ecological methodology. It adds life-stage outcomes as a model component and updates the terminology for several other model components to match the terminology used in CEMs prepared for the flannelmouth sucker (*Catostomus latipinnis*) (FLSU) and bonytail (*Gila elegans*) (BONY) (Braun 2015a, 2015b) subsequent to the development of the previous RASU conceptual ecological model.

RASU are native only to the Colorado River Basin. Their historic range extended from the Colorado River delta in present-day Baja California and Sonora, Mexico, upstream along the main stem Colorado River and its major alluvial tributaries – including the Green, Yampa, Gunnison, and San Juan Rivers in the upper basin and the Gila River and its larger tributaries (Verde, Salt, San Pedro Rivers) in the lower basin (McCarthy and Minckley 1987; USFWS 2002a; Mueller 2006; Valdez et al. 2012a; Marsh et al. 2015). They occurred most abundantly year round in the lower basin upstream to the present-day location of Lake Mohave, with numbers apparently declining with distance further upstream (USFWS 2002a). Archaeological and historical records also document their episodic occurrence in prehistoric Lake Cahuilla and its historic remnant, the Salton Sea, in the Salton Basin, a northwestern extension of the Colorado River delta into California that occasionally receives overflow from the delta during rare extreme flood events (Gobalet and Wake 2000; USFWS 2002a; Gobalet et al. 2005; Mueller 2006). Within this range, they occurred most abundantly in low-velocity settings, such as off-channel and braided-channel waters, including wetlands, but could also at least seasonally move through high-velocity canyons and into smaller, higher-gradient tributaries (Mueller 2006; LCR MSCP 2016a).

No estimates exist for the total pre-regulation population size. However, even after more than a century of presumed decline due to heavy fishing and river alterations, the estimated population in 1988 in Lake Mohave alone stood at roughly 60,000, with individuals reaching 40+ years of age (Minckley et al. 1991).

Today, outside of rearing facilities and protected, isolated ponds, RASU in the Lower Colorado River Basin occupy only scattered locations in the Colorado River delta in Mexico (Zamora-Arroyo et al. 2005); Lakes Havasu, Mohave, and Mead; and adjacent riverine reaches and off-channel marshes (USFWS 2002a; Mueller 2006; Marsh et al. 2015; Ehlo et al. 2016; Mohn et al. 2016; Kegerries et al. 2016; Reclamation 2017). They appear to be recruiting successfully in the deltaic habitat of the Colorado River inflow to Lake Mead and possibly upstream in the western Grand Canyon (Reclamation 2017).

The RASU conceptual ecological model incorporates information from the detailed overviews of RASU biology, ecology, and conservation by Minckley (1991), Minckley et al. (1991), USFWS (1998, 2002a), Ryden (1999), LCR MSCP (2004, 2008, 2016a), Minckley and Marsh (2009), Mueller (2006), Valdez et al. (2012a, 2012b, 2012c), Marsh et al. (2015), and Kesner et al. 2016. These sources summarize and interpret large bodies of earlier studies. The RASU conceptual ecological model also integrates information from numerous other publications, presentations at meetings, including Colorado River Aquatic Biologists (CRAB) meetings (https://www.lcrmscp.gov/crab/crab.html), current research funded by the LCR MSCP, and the expert knowledge of LCR MSCP fish biologists and others.

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

RAZORBACK SUCKER REPRODUCTIVE ECOLOGY

The RASU has at least 2½–5 million years of evolutionary history in the Colorado River Basin, extending back at least into the Pliocene Epoch (USFWS 1998; Spencer et al. 2008). It thus has a long evolutionary history of interaction with, and adaptation to, the natural environmental conditions and other native species of the Colorado River. Several publications (Minckley et al. 1991; USFWS 1998; Mueller 2006) summarize ideas about the evolutionary ecology of the species.

Similar to many fish species adapted to large alluvial rivers in desert basins, RASU have a reproductive strategy characterized by iteroparity, participation of only a portion of the adult population in spawning in any single year, high fecundity among the participating females, a complete lack of parental investment in offspring, low larval survival, large adult body size, and a long adult lifespan (Minckley and Marsh 2009; Mueller 2006; Zeug and Winemiller 2007). The resulting pattern of reproduction fits the definition of 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).

RASU female fecundity in the LCR varies approximately with body length (Gustafson 1975) and averages approximately 2,000 ova per centimeter (Minckley et al. 1991; Dowling et al. 1996), with body totals in the range of approximately 75,000–125,000 ova per female but ranging as high as 200,000 (Mueller 2006). The maximum potential lifespan may exceed 50 years (McCarthy and Minckley 1987), suggesting that females could produce many millions of ova in a lifetime. However, in fact, only a portion of the adults participate in spawning activity in any given year (see chapters 2, 3, and 6), and not all participants may contribute genetically to the resulting cohort. Saltzgiver, Dowling, and others estimate that, on average, only 8% of adults contribute genetically in any single year, and only 30–40% contribute in a generation (Saltzgiver et al. 2014, 2015; Dowling et al. 2016a, 2017). Genetic data on RASU spawning in isolated ponds also indicate that some participating females

may contribute substantially to the resulting larval cohort in a given year while others may contribute relatively little (Saltzgiver et al. 2014, 2015; Dowling et al. 2016a, 2017).

The "8%" figure presented in the preceding paragraph provides a minimum estimate for the rate of participation in spawning activity among females in a single year, since the rate of participation cannot be less than the rate of genetic contribution. This estimate for the rate of female participation, together with the estimated size of the RASU population in Lake Mohave in 1988 and the aforementioned data on fecundity, suggest that the females in Lake Mohave at that time would have produced roughly 180–480 million eggs annually for fertilization. However, the genetic data used to derive the "8%" figure pertain to the larval cohorts resulting from the seasonal spawning cycle, not to egg production. Multiple factors may intervene between egg release at the start of spawning and swim-up of larvae some 10–14 days later (see chapter 2).

Adult RASU spawn multiple times over their lifetimes, as evidenced by their repeated returns to individual spawning sites (see chapters 2, 3 and 6). A hypothetical female that spawns only 5 times over a 40-year lifespan thus, conservatively, might produce roughly 500,000 eggs, only 2 of which need grow into sexually mature offspring for the parents to replace themselves in the population. RASU thus naturally have an extremely low average female lifetime reproductive success rate of perhaps only 4 in 1 million.

The timing of RASU spawning in the LCR roughly correlates seasonally with, but may precede or follow, the timing of the natural spring flood pulse of the river (see chapters 2, 3, and 6). Prior to river regulation, this flood pulse delivered not only a surge of water but colder water temperatures and a surge in main stem turbidity. RASU deposit their eggs into the substrate, where they must remain to develop and hatch. Spawning sites must provide substrates that remain inundated and 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. This flow must then be sufficient – but not too high – at the time of larval swim-up (see chapter 2) to disperse the newly emerged larvae into shallow-water, low-velocity nursery environments without flushing them into hostile environments (Modde et al. 2001).

For those larvae that do reach suitable nursery habitat, this habitat must persist long enough to support larval maturation at least into juvenile body form and size (> 25-millimeter [mm] body length). Maturation to the juvenile stage may take approximately 30–100 days (Gustafson 1975; Clarkson and Childs 2000; Bestgen 2008). Suitable nursery environments include low-velocity shallows, connected backwaters, and lakes and wetlands formed by flood-pulse inundation of the flood plain. These environments must remain connected to the river, or become

reconnected before drying out, to allow the growing RASU to move into the larger ecosystem as they mature. Further, the seasonal drying of flood plain ponds following the spring flood pulse may render them inhospitable to larval RASU due to two other consequences of evaporation – rising water temperatures and increasing salinity – even before they completely dry out. The mechanisms by which RASU larvae disperse into their growth habitats following emergence therefore involve several additional risks to larval survival.

The timing and magnitude of the Colorado River annual flood pulse, which shaped RASU evolution, vary greatly from year to year and over longer timespans (Ely et al. 1993; O'Connor et al. 1994; Woodhouse et al. 2010; Reclamation 2011a). For example, Piechota et al. (2004) identify approximately 11 droughts affecting Upper Colorado River Basin (UCRB) discharge between 1923 and 2004. Analyses by Woodhouse and others (Woodhouse et al. 2010) indicate numerous short- and long-term droughts occurred over the preceding 1,200 years, determined by large-scale dynamics of global circulation and basin topography. A drought in 2000–04, 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) (Woodhouse et al. 2010) but ranked as only the seventh worst drought in the last 500 years (Piechota et al. 2004) based on other types of data. Historic and prehistoric periods of low flow in the basin are products of lower precipitation, but not necessarily higher temperatures, and involve significant deficits in snowpack/snowmelt and smaller flood pulses (Cayan et al. 2010; Woodhouse et al. 2010).

The timing of the annual flood pulse along the LCR varies with the timing of the onset of snowmelt in different parts of the Rocky Mountains and the timing of spring rainstorms, 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) found evidence for such a bottleneck for FLSU in the Colorado River, apparently a consequence of an extreme drought across the intermountain western North America ca. 7,500 years BP. Douglas et al. (2003) did not assess evidence for a similar bottleneck for RASU, but the ranges of the two species significantly overlap. As a result, the same drought would have affected RASU as well (see also Douglas and Douglas 2007; Hopken et al. 2012).

Air temperature also affects RASU embryo, larval, and juvenile development by affecting water temperatures and evaporation rates. For example, the speed and success rate for RASU embryo maturation falls off at water temperatures above and below the optimal range of 15–25 degrees Celsius (°C) (Marsh 1985; 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 RASU spawning, larval dispersal, and maturation in nursery habitat was always a period of temperature variability along the LCR independent of the variability in riverflows. RASU thus evolved in an ecosystem prone to extreme variations in water availability and temperature. This variation affected the spatial pattern, extent, timing, and duration of flooding, pre-regulation; seasonal water temperature variation; and the duration of flood recession and the rate of drying of disconnected waters across the flood plain following flood recession. The rate of drying also depends on the intensity and timing of onset of the naturally hot, dry spring and summer weather – another set of variables affected by long-term variation in weather.

Not surprisingly, therefore, the evidence suggests that most of the hydrology-related mortality experienced by RASU under natural conditions would have occurred during the first few days and weeks following spawning. However, RASU under natural conditions also would have faced other causes of mortality during this same season. Numerous native species consume RASU eggs, including adult RASU (Mueller 2006; see chapter 6). The concentration of eggs at spawning sites makes them particularly vulnerable to predation, and their availability during late winter or early spring would provide a food resource during a season of otherwise low productivity (Mueller 2006). Numerous native species also prey on RASU larvae and smaller juveniles as they mature after dispersal, including the carnivorous, aquatic larvae of several native insects (Horn et al. 1994). RASU egg and larval survival even in a natural setting thus would have been subject to numerous factors that resulted in extremely high rates of mortality in most years.

The RASU reproductive strategy therefore may have evolved as an adaptation to the extremely low probabilities of survival faced by individual embryos (Mueller 2006). The vast majority of eggs and larvae would die in most years, but enough would survive in enough years to perpetuate the species. Post-larval survival may not have been easy either, but it would have been far less tenuous. For example, juvenile and older RASU would naturally have faced competition for food from other RASU and other native species, including their younger life stages, and predation from native species such as the Colorado pikeminnow (*Ptychocheilus lucius*) (see chapters 2, 4, and 6). However, RASU naturally grow rapidly over their first 6 years and develop a characteristic bony nuchal hump. These changes would have reduced the diversity of both competition and predation they had to face as they matured (see chapter 6). RASU become sexually mature in 2–6 years (Minckley et al. 1991), depending on environmental conditions, 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 resource of interest.

CONCEPTUAL ECOLOGICAL MODEL STRUCTURE

The CEM methodology used here expands on that developed for the DRERIP (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 (e.g., Wildhaber et al. 2007, 2011). 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 (survival), or the number of viable offspring produced (fertility). 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 RASU 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 an individual RASU 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 (survival), or the number of viable eggs produced (fertility). Life-stage outcomes typically are "rate" variables that depend on the rates of the critical biological activities and processes for each life stage.

- **Critical biological activities and processes** – These consist of the activities in which the species engages and the biological and ecological 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 also 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, water demand, and social institutions.

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 – RASU 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 RASU in the LCR on which to build the CEM. The life-stage model presented here is an updated version of that presented in the previous RASU conceptual ecological model (Braun and McClure 2013).

The literature on RASU in the Colorado River (both upper and lower basins) does not follow any single classification of RASU life stages. Detailed summaries of RASU life history, with extensive bibliographies, appear in Minckley et al. (1991), USFWS (2002a), Snyder and Muth (2004), LCR MSCP (2008, 2016a), Minckley and Marsh 2009, and Albrecht et al. (2010a). Zelasko et al. (2009) and Valdez et al. (2011, 2012a) present conceptual life history models for the UCRB. The conceptual life history model in Valdez et al. (2011) includes an explicit designation of life stages and lists of biotic and abiotic controlling factors.

The following paragraphs first discuss the available information on RASU life stages in the LCR, under the broad headings of “Embryos and Larvae,” “Juveniles and Subadults,” “Adults,” and “Spawning.” The chapter then proposes a five-stage life history model for the CEM.

EMBRYOS AND LARVAE

RASU embryo development to hatching typically requires approximately 6–7 days, and the hatched larvae swim-up after another 4–7 days, with the pace of development varying with temperature (see chapters 3, 4, and 6). Snyder and Muth (2004) identify four phases of larval development based on morphological changes, termed protolarva, flexion mesolarva, postflexion metalarva, and metalarva. The authors suggest that these phases have different ecological requirements but do not characterize these differences. In contrast, Valdez et al. (2011) identify three phases of larval behavioral develpment:

1. Larvae during the time they remain embedded in the substrate until they swim-up and disperse. Valdez et al. (2011, 2012a; Snyder and Muth 2004) state that newly hatched larvae stay in their natal substrate until they have assimilated their yolks, at which time they become able to swim-up. However, Snyder and Muth (2004) state that the timing of yolk assimilation does not coincide exactly with the timing of any specific changes in larval skeletal morphology or pigmentation. The critical transition involves development of the skeletal and muscular ability to swim-up and begin foraging.

2. Dispersing larvae in the main channel and channel margins. Dispersal involves a combination of passively drifting and actively swimming between higher- and lower-velocity waters, as well as other behaviors, as the larvae attempt to relocate into nursery habitat.

3. Post-dispersal larvae that have successfully relocated into nursery habitat, where they mature into juveniles.

JUVENILES AND SUBADULTS

The transition from larva to juvenile, which takes place after the larvae reach approximately 25 mm total length (TL), involves changes in both behavior and morphology, which occur mostly during the first year of life. These changes include (1) absorption of the larval fin folds and development of the full RASU complement of median and paired fin rays (Snyder and Muth 2004) and (2) a shift in the location of the mouth to a more inferior position, which allows greater access to benthic food resources and brings a shift in foraging and related behaviors (Minckley et al. 1991; Snyder and Muth 2004; Mueller 2006; LCR MSCP 2008, 2016a; Minckley and Marsh 2009; Albrecht et al. 2010a; Bestgen et al. 2011, 2012).

The literature on RASU does not use the terms “juvenile” and “subadult” consistently. Sources may refer to these stages together (e.g., “juvenile/subadult”) or identify juveniles simply as individuals that have attained adult morphology but are still reproductively immature (Minckley et al. 1991; Gibb et al. 2006; LCR MSCP 2008, 2016a). This lack of firm definitions for juvenile versus subadult appears to result from a lack of distinct biological milestones between the initial development of juvenile morphology on the one hand (see above) and sexual maturation on the other. The lack of firm definitions for juvenile versus subadult also may simply reflect the lower level of knowledge often highlighted for these developmental classes compared to earlier and later developmental classes (LCR MSCP 2008, 2016a).

As noted earlier, the LCR MSCP and its partners routinely harvest RASU larvae in the wild during their dispersal from spawning sites and deliver these larvae to hatcheries such as the USFWS Willow Beach National Fish Hatchery (LCR MSCP 2015, 2016a, 2016b; Kesner et al. 2016). Once they reach a desired size range, these reared RASU are repatriated into LCR waters to augment the small population of RASU that mature in the wild (LCR MSCP 2004, 2006).

The repatriated RASU experience massive mortality. Recognition of this pattern of extreme mortality during the first several years of the augmentation program led to studies of what factors contributed to it (Minckley et al. 1991; USFWS 1998, 2002a; Marsh et al. 2005; LCR MSCP 2008, 2016a, 2016b; Schooley and Marsh 2007; Patterson et al. 2012; Kesner et al. 2016). These studies helped to identify the size of released fish as a critical variable affecting post-release survival. In response, the LCR MSCP set a threshold of 300 mm TL for release. Stocking shifted in 2006 to this larger size, which corresponds (on average) to an age of 2 years but with a wide range of variation (USFWS 1998; LCR MSCP 2008; Schooley and Marsh 2007). However, Kesner et al. (2012, 2016) subsequently found that survival of repatriated RASU in Lake Mohave improved significantly more for fish with TLs of > 450 mm and recommended shifting the minimum size for released fish accordingly. Efforts are underway to increase the number of individuals released with TLs of > 450 mm.

The initial selection of 300 mm TL as the desired minimum size for repatriated RASU does not correspond to any specific biological milestone. Bestgen (1990), LCR MSCP (2008, 2016a), and Valdez et al. (2011) indicate that RASU are not sexually mature at 300 mm TL. Rather, on average, they become ready and able to spawn roughly at age 4, corresponding roughly to an average length ≥ 350–400 mm TL.

Development of the present CEM therefore considered the possibility that the RASU life-stage model should distinguish juveniles, 25–300 mm TL, from subadults, ≥ 300 mm TL. Such a size-based distinction would recognize that smaller RASU presumably differ from larger RASU in their swimming abilities, including their abilities, for example, to avoid predators and other hazards, and also differ in their prey preferences, cover habitat preferences, and vulnerabilities to different-sized predators.

Development of the present CEM also considered the possibility that RASU juveniles, too, may fall into different classes that warrant separate treatment in the RASU life-stage model. Specifically, Age-0 juveniles – juveniles in the year of their birth – may have different feeding behaviors and face different predators than Age-1 juveniles due to their smaller size (Minckley et al. 1991; LCR MSCP 2008, 2016a). For example, UCRB studies (Bestgen et al. 2011; Valdez et al. 2011) indicate that Age-0 post-dispersal larval and juvenile *wild-born* RASU often concentrate in flood plain wetlands with limited access to the main channel. They are vulnerable in these settings to summer heat and drying, winter freezing,

and flushing by annual floods. In contrast, Age-1 wild-born juveniles have been caught in a wide variety of settings in, along, and/or more strongly connected to the main channel both in the UCRB and along the LCR (Minckley et al. 1991; LCR MSCP 2008, 2016a; Bestgen et al. 2011, 2012). (The same contrast may not always apply to repatriated RASU, at least not in the UCRB: Hedrick et al. (2012) found that many Age-1, Age-2, and older RASU repatriated into the Stirrup Floodplain site, Green River, simply remained there, rather than exiting to the main stem through the available, monitored outlets).

This shift in spatial distribution between Age-0 and Age-1 juveniles observed in the UCRB suggests that, as they mature into their second year, RASU wild-born juveniles range more widely among settings and develop stronger swimming abilities that presumably allow them to move more effectively out of harm's way from the range of fluvial disturbances that can occur in main channel environments. Further, RASU develop their characteristic bony nuchal hump during or after their second year of life, beginning when they are approximately 200 mm TL (Portz and Tyus 2004), potentially affecting their vulnerability to predation by Colorado pikeminnow, their dominant native predator (see chapter 4).

The particular forms of environmental vulnerability observed in the UCRB among RASU Age-0 juveniles do not apply to the LCR, with its significantly greater regulation of water levels, channelization, and higher winter temperatures. However, the basic biology of the species presumably is the same in the two subbasins. Thus, the UCRB findings suggest that younger, smaller, wild-born juveniles have habitat preferences and vulnerabilities similar to those of resettled (post-dispersal) larvae. This similarity may be related simply to body size: smaller (mostly younger) juveniles presumably have different food preferences from larger (mostly older) juveniles and face predation from a different spectrum of predators that focus on smaller-sized prey. In turn, the UCRB and LCR findings both suggest that older juveniles have habitat preferences and vulnerabilities similar to those of older RASU as they approach sexual maturity.

Nevertheless, neither age nor changes in size or morphology correlate with any *distinctive* milestones in biology along the continuum from early juvenile (post-larval) to late subadult (pre-adult). Indeed, age and size do not always correlate with each other. RASU growth rates vary greatly among juveniles in the LCR, and winter conditions may not significantly limit juvenile growth and maturation in the LCR compared to the colder UCRB (Minckley et al. 1991; LCR MSCP 2008; Bestgen et al. 2011, 2012). Furthermore, while the development of the nuchal hump may have reduced predation on RASU > 200 mm TL by the Colorado pikeminnow in the historic, unregulated river, it is no longer even a minor predator of RASU in the LCR (see chapters 4 and 6). The larger non-native predators in the LCR today do not need to swallow their prey whole, as do

Colorado pikeminnow, and they have different gape sizes and attack behaviors. As a result, development of the nuchal hump in growing RASU may no longer mark a change in vulnerability to predation.

The published evidence summarized in the preceding paragraphs thus suggests dividing juveniles into two classes: (1) younger, smaller juveniles living in nursery habitat prior to their dispersal from this distinctive habitat, which occurs roughly around the middle of their first year and (2) older, larger juveniles following their dispersal from their nursery habitat. Younger juveniles comprise the later end of a continuum with larvae after they have settled into nursery habitat. Older juveniles and subadults, in turn, constitute a continuum that ends with sexual maturation.

ADULTS

Adulthood among RASU begins with their sexual maturation. Bestgen (1990), LCR MSCP (2008, 2016a), and Valdez et al. (2011) indicate that RASU are not sexually mature at 300 mm TL. In turn, Valdez et al. (2012c) state, "sexual maturation [among hatchery broodstock] of the RASU was more a function of size than age. Hatchery-reared males matured as early as 2 years of age and 355 mm in length while females first produced viable eggs at 3 years of age and about 400 mm in length." Adults can live up to 40–50+ years (McCarthy and Minckley 1987; LCR MSCP 2008, 2016a).

The adult population of RASU in the LCR consists of two types of individuals: (1) repatriated individuals that have survived following release and (2) "wild" adults that have matured in situ from birth. The earlier RASU conceptual ecological model (Braun and McClure 2013) and its life-stage model distinguished repatriated from wild RASU beginning with the subadult life stage. This distinction no longer appears useful.

Repatriated RASU originate as wild-born, dispersing larvae captured by netting at night along the shores of Lake Mohave and reared in hatcheries or other artificial rearing environments for the augmentation program (Delrose 2011; see above). The augmentation program from 1991 up to 1999 repatriated reared individuals as small as 250 mm TL. Beginning in 1999, the augmentation program repatriated reared RASU only when they attained a minimum size of 300 mm TL, increasing by 2004 to a minimum of 350 mm TL and an average of 380 mm TL (Kesner et al. 2016). The augmentation program therefore presumably repatriated mostly subadults prior to ca. 2004.

Survival data up to 2004 for the LCR and from a parallel stocking program in the UCRB (Brandenburg and Farrington 2007; Schooley and Marsh 2007; Schooley et al. 2008; LCR MSCP 2008, 2016; Zelasko et al. 2011a; Bestgen et al. 2012;

Kesner et al. 2012) indicate that repatriated RASU suffered very high rates of mortality within the first year (or less) following their release (Kesner et al. 2016). However, the same data also indicated that survival increased with body size. This crucial finding led to a change in stocking practices in the LCR after 2006, to try to raise the minimum stocking size to 500 mm TL (Kesner et al. 2016). This change required temporarily reducing the number of RASU released in order to allow more RASU in the rearing program to attain larger sizes before being released, with only 601 released in 2007 and 108 in 2008 (LCR MSCP 2015). However, a subsequent large drop in the estimated LCR population to ≈ 1,000 RASU led to a resumption of significant stocking, including of RASU TL < 500 mm. The MSCP modified its stocking strategy in 2010 to repatriating as many fish as possible over 300 mm, subsequently modified further to include ≈ 1000 fish > 400 mm TL each year (LCR MSCP 2015). The inclusion of fish as small as 300 mm TL means that some of the stocked individuals may be subadults rather than adults. The LCR MSCP is now working toward a year-class average release size of > 400 mm TL (Rudd 2017), which should ensure that all stocked individuals are adults.

At the same time, monitoring efforts for many years have resulted in the detection of few or no wild-born subadult RASU along the LCR outside of Lake Mead (Kesner et al. 2007, 2008a, 2010, 2012, 2014, 2016; Wydoski and Mueller 2006; Patterson et al. 2012, 2013; Marsh et al. 2015; LCR MSCP 2016a). However, the augmentation program has only minimal release goals for Lake Mead (LCR MSCP 2006; Albrecht et al. 2010a, 2010b), and the present CEM is intended mainly to support the management program below Lake Mead. The relative contributions of wild versus repatriated RASU to the adult population in each reach of the river valley is a matter of great interest (Minckley et al. 1991; Schooley and Marsh 2007; Schooley et al. 2008; LCR MSCP 2008, 2016a, 2016b; Zelasko et al. 2009, 2011a; Albrecht et al. 2010a; Bestgen et al. 2012; Kesner et al. 2007, 2008a, 2010, 2012, 2016).

Wild and repatriated RASU do appear to differ from each other in some respects, even if the present CEM treats all adults as members of a single life stage. For example, repatriated RASU may be inexperienced (unconditioned), with respect to predation and the behaviors they need to learn in order to better avoid predators, or unconditioned to the range of environmental conditions they encounter upon release (Mueller and Foster 1999; Ward and Hilwig 2004; Carveth et al. 2006; Mueller et al. 2007; Avery et al. 2011; Valdez et al. 2012c; Ward and Figiel 2013; LCR MSCP 2015, 2016b; O'Neill and Stewart 2015; O'Neill et al. 2016; Cappelli 2016; Mann et al. 2017). They may aggregate for some period of time following release, a behavior from their rearing environments that, in the open water, may expose them to concentrated predation (Mueller 2006; Schooley et al. 2008). The process of transporting and releasing hatchery-raised fish may itself cause them stress that affects their ability to assimilate (Schooley et al. 2008; Sykes 2013). The present CEM addresses such variation between wild and repatriated RASU adults through its assessment of the causal relationships that affect annual adult survival.

This assessment unfortunately is simplified by the very small presence and lack of natural recruitment of wild RASU in the LCR ecosystem outside of Lake Mead (see chapters 3–6).

SPAWNING

Spawning involves a biologically distinct suite of behaviors within the RASU life cycle. RASU adults aggregate to spawn, traveling sometimes long distances to do so, and apparently have specific preferences for the conditions that must be present where they spawn, although the details and causes of these preferences remain unresolved (Modde and Irving 1998; Tyus 1987; Minckley et al. 1991; USFWS 1998; Mueller et al. 2000; LCR MSCP 2008; Albrecht et al. 2010a, 2010b; Valdez et al. 2012a, 2012b, 2012c). Some spawning aggregation sites are well known, with long histories of use, with evidence of fidelity of RASU individuals to particular spawning sites, but not necessarily their natal sites, and of some females visiting multiple sites in a single season (Tyus and Karp 1990; Minckley et al. 1991; Modde and Irving 1998; USFWS 1998; Mueller et al. 2000; Mueller 2006; LCR MSCP 2008, 2016a; Albrecht et al. 2010a; Wydoski et al. 2010; Wydoski and Lantow 2012). Only a portion of the adults spawn in any given year and the spawning aggregations contain more males than females (Minckley et al. 1991; LCR MSCP 2008, 2016a; Dowling et al. 2017; see chapters 2, 3, and 6). Saltzgiver, Dowling, and others estimate that, on average, only 8% of adults contribute genetically in any single year, and only 30–40% contribute in a generation (Saltzgiver et al. 2014, 2015; Dowling et al. 2016a, 2017).

Spawning RASU apparently may remain in the area of their spawning site for weeks, resting before and after spawning events, the latter of which involves a distinct suite of behaviors (Minckley et al. 1991; Mueller 2006; LCR MSCP 2008, 2016a), as discussed in detail below, in chapter 3. Some of the spawning behaviors have the effect of cleaning fine sediment off the substrate above spots chosen for egg release, creating slight depressions into which the fertilized eggs can settle, and driving fertilized eggs into the substrate (Bozek et al. 1984; Snyder and Muth 2004; Mueller 2006). Evidence of exhaustion and emaciation among post-spawning adults (Mueller 2006) suggests that spawning adults do not give high priority to feeding during the spawning cycle.

Spawning males and females release their gametes into the water above the substrate. Fertilization takes place in the water column. The eggs harden and settle onto or are driven into the substrate (see above) to which they subsequently adhere to over the course of 3–4 hours (Minckley and Gustafson 1982; Bozek et al. 1990; Minckley et al. 1991; LCR MSCP 2008). The eggs are subject to intense predation, including by adult RASU, but apparently becoming less vulnerable to predation once they adhere to and/or become embedded in the substrate (as summarized by Bozek et al. 1984; Minckley et al. 1991; USFWS

1998, 2002a; Mueller 2006; LCR MSCP 2008). Sources sometimes refer to the fertilized eggs as lying "in" rather than simply "on" the substrate (Bozek et al. 1984).

LIFE-STAGE MODEL SUMMARY

The published evidence summarized in the preceding paragraphs thus identifies five distinct RASU life stages: (1) eggs and larvae prior to swim-up and dispersal, in and on the substrates at spawning sites, (2) larvae from the time they disperse through their development into younger juveniles, (3) older juveniles and subadults, (4) adults, and (5) spawning adults. Spawning adults, of course, are simply a subset of all adults in any given year. However, spawning involves a distinct set of behaviors with distinct geographic distributions and timing, affected by a distinct set of environmental constraints. As a result, spawning meets the definition of a life stage as a biologically distinct portion of the life cycle 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.

Table 1 and figure 1 present the five RASU life stages, using simplified labels, numbered sequentially beginning with the egg and pre-dispersal larval stage. Table 1 and figure 1 also show the life-stage outcomes for each of the five RASU life stages in the LCR ecosystem. The most crucial outcome for every life stage is survival. For the egg and pre-dispersal larval, post-dispersal larval and younger juvenile, and older juvenile and subadult life stages, their rates of survival ($S_{1,2}$, $S_{2,3}$, and $S_{3,4}$ on figure 1, respectively) are also their rates of recruitment to the next life stage. For the adult life stage, the rate of survival is designated as the adult *annual* survival rate ($S_{4,4}$ on figure 1), to capture information on persistence. Spawning adults are subject to multiple stresses and threats during their participation in the spawning cycle, potentially resulting in mortality. The adult annual spawning participation rate and the spawning adult survival rate ($R_{4,5}$ and $S_{5,4}$ on figure 1, respectively) together affect the overall adult annual survival rate. Finally, spawning adult fertility ($R_{5,1}$ on figure 1) represents the production of viable fertilized eggs, completing the life cycle.

Figure 1 also includes components to represent the diversion of wild dispersing larvae to supply the rearing program at hatcheries or other artificial rearing facilities. The wild dispersing larvae that supply the rearing program are subject to mortality during capture, transport, and initial acclimation to the rearing environment. Survival during this transition is indicated on figure 1 as $S_{2,R}$, the rate of survival of wild larvae harvested and transported to hatcheries for rearing. In turn, RASU during rearing are subject to mortality prior to repatriation. $S_{R,4}$ on figure 1 denotes the rate of survival of reared RASU in hatcheries or other artificial rearing facilities prior to repatriation. The present CEM addresses

Table 1.—RASU life stages in the LCR ecosystem

Life stage	Life-stage outcome(s)
1. Egg and pre-dispersal larval	• Egg and pre-dispersal larval survival
2. Post-dispersal larval and younger juvenile	• Post-dispersal larval and younger juvenile survival
3. Older juvenile and subadult	• Older juvenile and subadult survival
4. Adult	• Adult annual survival • Adult annual spawning participation rate
5. Spawning adult	• Spawning adult survival • Spawning adult fertility

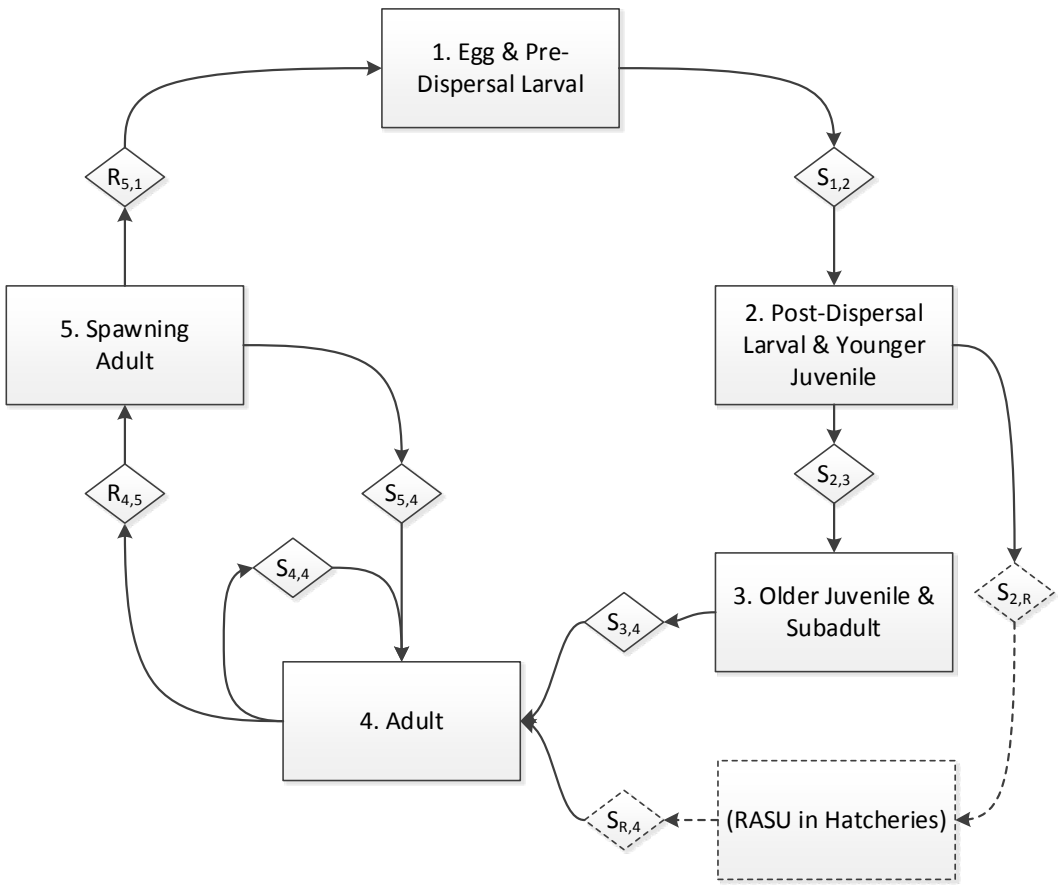


Figure 1.—Proposed RASU life history model.
Squares indicate the life stages; diamonds indicate life-stage outcomes. Objects with dashed outlines are not addressed in the present CEM.
$S_{1,2}$ = the rate of survival of (recruitment from) the egg and pre-dispersal larval life stage, $S_{2,3}$ = the rate of survival of (recruitment from) the post-dispersal larval and younger juvenile life stage, $S_{3,4}$ = the rate of survival of (recruitment from) the older juvenile and subadult life stage, $S_{4,4}$ = the annual rate of survival of adults so that they remain part of the adult population, $R_{4,5}$ = the percentage of adults that participate in spawning per year, $S_{5,4}$ = the rate of survival of spawning adults to return to the adult population following spawning, $R_{5,1}$ = the fertility rate (production of viable fertilized eggs) among adults that participate in spawning per year, $S_{2,R}$ = the rate of survival of wild larvae harvested and transported to hatcheries for rearing, and $S_{R,4}$ = the rate of survival of reared RASU in hatcheries or other artificial rearing facilities prior to repatriation.

dispersing larvae only within the open LCR ecosystem and repatriated RASU only from the time of their release onward. The present CEM thus does not address either of the survival rates related to the rearing program.

The formal definitions of the five RASU life stages are as follows:

1. **Egg and pre-dispersal larval life stage:** This life stage begins when spawning adults release their gametes and depart, leaving the fertilized eggs to survive on their own, continues through egg incubation and hatching, and ends with larval swim-up and dispersal at approximately 12–14 mm TL (Snyder and Muth 2004). Incubation to hatching requires 6–7 days at 18–20 °C or 11 days at 15 °C (Snyder and Muth 2004) . Maturation to swim-up requires an additional 12–13 days at 18–20 °C or 17–21 days at 15 °C (Snyder and Muth 2004). As noted above, this life stage has a single life-stage outcome, designated $S_{1,2}$, the rate of survival of (recruitment from) the life stage.

2. **Post-dispersal larval and younger juvenile life stage:** This life stage begins with larval swim-up and dispersal to nursery habitat, includes the transformation from metalarval to juvenile body morphology and additional changes during younger juvenile development, and ends with dispersal of juveniles beyond their nursery habitat. As noted above, this life stage has a single life-stage outcome, designated $S_{2,3}$, the rate of survival of (recruitment from) the life stage. Under the LCR MSCP augmentation program, dispersing larvae are captured and transported to rearing facilities for growth and later repatriation as adults. The present CEM does not address the internal workings of the rearing program.

3. **Older juvenile and subadult life stage:** This life stage begins after RASU juveniles disperse from their nursery habitat, roughly around the middle of their first year. They grow to roughly 350 mm TL by the time they reach sexual maturity, which can be as early as 2 years for males and 3 years for females in rearing facilities, but it is more typically 4–6 years in the wild (LCR MSCP 2008, 2016a; Valdez et al. 2012c). As noted above, this life stage has a single life-stage outcome, designated $S_{3,4}$, the rate of survival of (recruitment from) the life stage.

4. **Adult life stage:** This life stage covers all age classes of sexually mature RASU, which may achieve lifespans approaching or even exceeding 50 years (see above). RASU adults measure roughly 350 to more than 700 mm TL and historically grew even larger. As noted above, this life stage has two life-stage outcomes: $S_{4,4}$, the annual rate of survival of adults so that they remain part of the adult population, and $R_{4,5}$, the percentage of adults that participate in spawning per year.

5. **Spawning adult life stage:** This life stage covers adult RASU during the times in which they participate in spawning. This life stage begins when would-be spawners leave their home areas to move toward spawning sites and ends when these individuals return to their home areas. This life stage thus encompasses the time RASU spend at spawning sites and the time they spend traveling to and from these sites. As noted above, this life stage has two life-stage outcomes: $S_{5,4}$, the rate of survival of spawning adults to return to the adult population following spawning, and $R_{5,1}$, the fertility rate (production of viable fertilized eggs) among adults that participate in spawning per year.

Chapter 3 – Critical Biological Activities and Processes

Critical biological activities and processes consist of activities in which a species engages and the 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 present CEM identifies 14 critical biological activities and processes that affect 1 or more RASU life stages. Some of these activities or processes differ in their details among life stages. For example, RASU of different life stages differ in their swimming behaviors, 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 14 critical biological activities and processes and their occurrences across the 5 RASU life stages. Each critical activity or process listed in table 2 directly or indirectly affects one or both outcomes for each indicated life stage.

The basic sources of the information used to identify the critical activities and processes are Minckley et al. (1991), USFWS (1998, 2002a), Ryden (1999), LCR MSCP (2004, 2008, 2016a), Mueller (2006), Minckley and Marsh (2009), Zelasko et al. (2009), Albrecht et al. (2010a), Valdez et al. (2012a, 2012b, 2012c), and Marsh et al. (2015). The identification also integrates information from both older and more recent works, meeting presentations by LCR MSCP and partner biologists, and the expert knowledge of LCR MSCP fish biologists. The following paragraphs discuss the 14 critical activities and processes in alphabetical order. The core reference works noted above are implicit citations for all 14 definitions.

CHEMICAL STRESS

All freshwater fishes are vulnerable to stress and mortality due to an insufficient supply of dissolved oxygen (DO), insufficient removal of wastes, exposure to unsuitable levels of salinity, and exposure to harmful dissolved contaminants. Chemical stress, whether acute or chronic, may impair a range of bodily functions, making the affected individuals less fit and therefore vulnerable to mortality from other causes.

Numerous authors have expressed concerns that RASU in the LCR ecosystem may experience or need to be protected from chemical stress, particularly stress resulting from exposure to and/or bioaccumulation of chemical contaminants that are known to occur in the LCR ecosystem (USFWS 1994; Wydoski and Wick

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

Life stage ➔ / **Critical biological activity or process 🡻**	Egg and pre-dispersal larval	Post-dispersal larval and younger juvenile	Older juvenile and subadult	Adult	Spawning adults
Chemical stress	X	X	X	X	X
Competition		X	X	X	X
Disease	X	X	X	X	X
Drifting		X			
Egg settling and adhesion	X				
Foraging		X	X	X	X
Hybridization	X	X	X	X	X
Mechanical stress	X	X	X	X	X
Predation	X	X	X	X	X
Resting/hiding		X	X	X	X
Ripening					X
Staging and spawning					X
Swimming		X	X	X	X
Thermal stress	X	X	X	X	X

1998; Hamilton 1999; Reclamation 2005; Mueller 2007). Cooke et al. (2005) report this threat as a concern for suckers (Catostomidae) across North America in general. Water quality testing in the LCR ecosystem has documented RASU exposure to elevated levels of contaminants in some locations, and analysis of RASU tissue has documented bioaccumulation of some metals and organo-chlorine compounds (Tuttle and Orsak 2002). Metal and organochlorine contaminants are widespread in the LCR ecosystem, with studies documenting their bioaccumulation in both benthivorous and piscivorous fishes from Lake Mead to Imperial Dam (Hinck et al. 2007, 2009; Patiño et al. 2012) – although none of these analyses included RASU.

Laboratory exposure of RASU to contaminants that are known to occur in the LCR ecosystem, in turn, has demonstrated RASU physiological sensitivity to both metals and organochlorine compounds (Buhl et al. 1996; Buhl 1997; Hamilton, 2004, 2005a, 2005b; Sappington et al. 2001; Tuttle and Orsak 2002;

Dwyer et al. 2005). Selenium has received particular attention as a contaminant of concern throughout the Colorado River Basin that potentially affects RASU (Hamilton et al. 2005a; Stolberg 2009, 2012).

Laboratory exposure of RASU eggs and larvae to low concentrations of DO (Stolberg 2009) has demonstrated total to nearly total mortality at the lowest concentrations 1–2 milligrams per liter, but total to nearly total survival at 4–8 milligrams per liter. Stolberg (2012) also exposed RASU larvae to a range of elevated salinities and documented a wide range of tolerance and the ability to acclimate. The larvae exhibited long-term survival in highly saline water at 20,000–23,000 microsiemens per centimeter (µS/cm) but experienced up to 50% mortality in water at 27,000 µS/cm. Both severely depressed levels of DO and severely elevated levels of salinity can occur in the LCR ecosystem (e.g., in flood plain wetlands that become seasonally isolated from the larger flow system due to drying).

The literature thus documents RASU physiological sensitivity to, exposure to, and even mortality from a variety of contaminants that can occur in the LCR ecosystem as well as from very extremely low levels of DO and extremely high levels of salinity. RASU appear to be sensitive in all life stages, including through bioaccumulation, and RASU eggs and larvae exhibit particularly high sensitivities to direct exposure. RASU, as they mature, become increasingly able to avoid or remove themselves from settings in which they may sense chemically unsuitable conditions but only if escape routes are available and/or these conditions are sufficiently localized to permit such avoidance or escape. As noted above, however, some metal and organochlorine contaminants are ubiquitous in LCR surface waters of or fed by the Colorado River.

COMPETITION

RASU in every motile life stage must compete with other species for food and habitat, as must all animal species. For example, RASU may prefer or require the same food materials, same types of cover, or same spawning sites as other aquatic species. RASU also may compete with each other for such resources. Chapters 4 and 6 discuss the range of competitors that RASU in each life stage potentially face. For example, RASU larvae following dispersal 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. Adaptations to avoid or minimize competition may include a preference for resources other than those preferred by other species in the system (resource partitioning) or an ability (flexibility) to switch among alternative resources as needed. However, such adaptations may not be sufficient to afford every

individual RASU full access to all necessary resources. Chapter 6 also discusses the evidence for avoidance and defensive behaviors with which RASU may confront competition in each life stage.

DISEASE

RASU in every life stage are vulnerable to infection, including by fungi and parasites (Flagg 1982; Minckley 1983; Bozek et al. 1984; Marsh 1987; Clarkson et al. 1997; Robinson et al. 1998; Mueller 2006; Marsh 1987; Ward et al. 2007; Ward and Finch 2009). External manifestations of infection in open environments such as Lake Mohave often include cloudiness or complete blindness in one or both eyes (Bozek et al. 1984; Mueller 2006). Non-lethal infections may make the affected individuals vulnerable to mortality from other causes or to secondary infections by other organisms (O'Neill et al. 2011). Numerous exotic viruses, bacteria, fungi, and parasites, including Ich (*Ichthyophthirius multifiliis*), *Lerneae* spp., and *Myxobolus* spp., are present and capable of infecting RASU in the LCR ecosystem (Bozek et al. 1984; Valdez 1990; Clarkson et al. 1997; Robinson et al. 1998; Choudhury 2004 et al.; USFWS 2002a; Mueller 2006; Ward et al. 2007; Ward and Finch 2009; Garnett 2016; Olson 2017). Nevertheless, while infections at hatcheries are a major concern, no studies evince great concern that illness is an important threat to RASU in the wild at any life stage. Multiple factors (e.g., stress from other causes or genetics) determine whether infections lead to debilitating disease. Infections also may make affected individuals vulnerable to further harm or mortality from other causes.

DRIFTING

After moving up from the substrate at their natal sites into the water column, RASU larvae travel over short (< 10 meters [m]) to larger distances (1–10 kilometers or more) primarily passively by the force of water currents (i.e., by drifting). The drifting larvae exert some effort to control their drifting by swimming between high- and low-velocity currents and slack-water environments (Modde and Irving 1998; Tyus et al. 2000; Modde and Haines 2005). They mostly drift at night and spend most of the daylight hours between their drifting periods resting/hiding in slack-water and low-velocity settings, including in interstitial spaces in the substrate (Bozek et al. 1984). The preferences for drifting at night and taking cover in interstitial spaces during the day may have evolved in response to predation pressure (Johnson et al. 1993; Horn et al. 1994; Johnson and Hines 1999).

The currents in which RASU larvae drift do not carry them exclusively downstream. Lateral and reverse currents, such as those that occur in eddies, can carry the drifting larvae between high- and low-velocity settings along their drift paths. The availability and distribution of such lateral and reverse currents depend on channel morphology (including channel geomorphic complexity) and hydraulics (Ryden 1999; Worthington et al. 2014). 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" – a term developed for application to the drifting larvae of the endangered Pallid sturgeon (*Scaphirhynchus albus*) along the Missouri River (Jacobson et al. 2016). Kinzli and Myrick (2010) present a similar concept for the beneficial role of Rio Grande channel shoreline features in intercepting the drifting eggs of the Rio Grande silvery minnow (*Hybognathus amarus*) (see also Worthington et al. 2014). RASU drifting larvae depend on the interplay of downstream and lateral drift, the availability of interception habitat, and their ability to swim between high- and low-velocity currents to move from their natal sites to nursery habitat. The latter consists of very low-velocity shoreline habitats, backwaters, embayments, tributary mouths, and flood plain marshes (see chapters 4 and 6).

EGG SETTLING AND ADHESION

Spawning RASU males and females (see chapter 2) release their gametes into the open water above the substrate at the spawning sites, often directly onto the substrate (Minckley and Gustafson 1982; Bozek et al. 1984; Langhorst and Marsh 1986; Snyder and Muth 2004; Mueller 2006). The spawning activity itself helps prepare the selected sites to receive and protect the eggs by agitating the surface of the substrate, thereby removing fine sediment and/or excavating nest-like depressions (Bozek et al. 1984; Snyder and Muth 2004; Mueller 2006). Mueller (2006) refers to the agitation of the substrate as "finning." Over the course of 3–4 hours after fertilization, the eggs must descend through the water column to settle into the substrate, hardening as they descend, and adhere to the substrate. RASU finning and other agitated behaviors during the spawning act may not only remove fine sediment and excavate depressions in the substrate but may also set the eggs directly on the surface of the substrate or drive them into the substrate, eliminating the "descent" step altogether (Mueller 2006). The present CEM recognizes this suite of events – from the time the spawners release their gametes until egg adhesion to the substrate is complete – as a critical activity or process because the gametes and eggs are vulnerable to a distinct set of potential disruptions as these events unfold (see chapters 4 and 6).

FORAGING

RASU begin foraging once they have assimilated their yolk and become able to swim, and continue through all remaining life stages. They feed on phytoplankton; microinvertebrates such as cladocerans, rotifers, and copepods; and smaller macroinvertebrates such as insect larvae in the water column, along the benthos, and on the surfaces of submerged vegetation; they also feed on vegetative detritus along the benthos (see also Langhorst and Marsh 1986; Marsh 1987). They may consume living vegetation, and they have been observed feeding aggressively on their own and BONY eggs (Mueller 2006). RASU adults also have been observed to form "tight, elongated schools (> 100 individuals) that swim in tight formations, appearing to slurp zooplankton from near the surface" (Mueller 2006). Food item sizes and other dietary preferences vary among the life stages (e.g., depending on larval versus mature mouth position, mouth size, and presumably agility). Zooplankton can make a significant contribution to their diet (Mueller 2006). Their diet may also vary between lentic and lotic environments, and hatchery-reared RASU may develop distinct feeding habits prior to repatriation. The literature (see the list of basic sources of the information at the beginning of this chapter) overwhelmingly describes RASU larvae, juveniles, and subadults – particularly RASU repatriated as subadults – as feeding primarily at night; however, they are not exclusively nocturnal. Mueller (2006) reports that adults feed both at night and during the day, including feeding in daylight directly at the water surface.

The literature does not report any instances of RASU using cover for stealth in attacking prey or lying in wait for prey; rather, other than massed formations feeding near the water surface (see above), RASU appear to feed as opportunities arise as they move through the water and along the substrate. However, they can be selective in what they consume among the potential food materials they encounter (LCR MSCP 2016a).

HYBRIDIZATION

The RASU augmentation program, from its inception, has included monitoring of the genetic diversity of RASU reared for repatriation to help ensure that management actions do not compromise this diversity (Marsh et al. 2015; Kesner et al. 2016; Dowling et al. 2017). Additionally, RASU can hybridize with other catostomids, particularly with FLSU but also potentially with other native and non-native suckers. As summarized recently (LCR MSCP 2016a):

> *As reviewed by Bestgen (1990), hybridization between razorback suckers and other native Colorado River catostomid species has historically been documented to occur. Most often, razorback suckers have been shown to hybridize with flannelmouth suckers, but they may also hybridize with Sonora suckers (Catostomus insignis) and other native catostomids (Hubbs et al. 1943; Hubbs and Miller 1953; Holden 1973; Holden and Stalnaker 1975; McAda and Wydoski 1980; Minckley 1983; Bozek et al. 1984; Tyus and Karp 1990; Douglas and Marsh 1998). Buth et al. (1987) uses allozymic data to directly quantify presumed introgression in the range of 0–5% toward flannelmouth suckers and 0–3% toward razorback suckers. Furthermore, in a natural river setting, Ryden (2000[b]) noted adult flannelmouth suckers were captured consistently over the same cobble-bottomed riffles as mature, adult razorback suckers, suggesting concern for possible hybridization in San Juan River populations due to an overlap in physical habitat usage during the adult life stage of both species. Hybridization of razorback with flannelmouth suckers is also suspected in Lake Mead at the Colorado River inflow (Albrecht et al. 2010c, Kegerries and Albrecht 2011, 2013).*

More recent studies and summaries of RASU-FLSU hybridization include Dowling et al. (2014a, 2014b, 2015, 2016b), Marsh et al. (2015), Kegerries et al. (2016, 2017), Mohn et al. (2016), USFWS (2016), Wolters et al. (2016, 2017), BIO-WEST, Inc., and American Southwest Ichthyological Researchers (2017), and Reclamation (2017).

Conceptual *ecological* models such as the present RASU conceptual ecological model – as contrasted with conceptual models of gene flow – mostly take into account genetic variation only as it bears on species ecology. Hybridization of RASU with other catostomids poses two kinds of threats to RASU ecological circumstances within the LCR. First, the effective fertility of non-hybrid RASU suffers when RASU gametes fertilize or are fertilized by another species. Second, hybrid larvae, juveniles, subadults, and adults potentially may compete with non-hybrid RASU for food or physical habitat. For example, Anderson and Stewart (2007) found that, unlike native catostomids, the non-native white sucker (*Catostomus commersonii*) and its hybrids can persist in western Colorado regardless of alterations to the flow regime, giving them an advantage over the native suckers.

FLSU occur in only two zones within the larger LCR ecosystem, where they potentially could hybridize with RASU: (1) the Colorado River between Davis Dam and Lake Havasu (Mueller and Wydoski 2004; Best and Lantow 2012) and (2) the Colorado River in the western Grand Canyon and its confluence with Lake Mead. Both RASU and FLSU spawn – at least occasionally – in the latter zone, where field surveys regularly capture their hybrids (Dowling et al. 2014a, 2014b, 2015, 2016b; Marsh et al. 2015; Kegerries et al. 2016, 2017; Mohn et al. 2016; USFWS 2016; Wolters et al. 2016; BIO-WEST, Inc., and American Southwest Ichthyological Researchers 2017; Reclamation 2017).

MECHANICAL STRESS

RASU in every life stage are vulnerable to stress and outright physical destruction due to mechanical impacts, abrasions, burial, or exposure. Causes may include encounters with propeller blades, propeller wash, or a jet-ski intake; entrainment by excessive flow velocities and turbulence; scouring of habitat or 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; wounding and buffeting from unsuccessful predator attacks; damage during capture and handling; or damage during transport/release from rearing facilities. Mechanical stress may also be self-inflicted, such as during spawning, when individuals (especially females) may become severely abraded across their genital areas through energetic contact with the substrate (Bozek et al. 1984; Mueller 2006). Non-lethal mechanical stress may leave affected individuals vulnerable to infections and mortality from other causes, and vice versa (see also Brandenburg et al. 2002; Mueller et al. 2003a; Mueller 2006; Hunt 2008; Hunt et al. 2012; Mueller et al. 2008; LCR MSCP 2008; Bestgen et al. 2012). As RASU mature, they become increasingly able to avoid or escape settings in which they may sense mechanically hazardous conditions – if these conditions are sufficiently localized to permit such avoidance or escape. However, in the case of spawning adults, such avoidance or removal could interrupt spawning. For example, waves from storms may disrupt spawning activity even when not a hazard to the health of the participants (Minckley et al. 1991).

PREDATION

RASU may 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 species to detect and avoid, escape, defend against, or demographically compensate for losses from predation.

Predation on RASU, and RASU adaptations to predation, are topics of strong interest throughout the species' range. Predation by non-native fishes is thought to be one of the largest factors in the decline of RASU in recent decades (see reviews in all the basic sources of information listed at the start of this chapter). In fact, RASU face predation from both aquatic and avian species, and the aquatic predators may include not only fishes but also amphibians and aquatic insect larvae. Chapter 4 provides additional information on the species known or suspected to prey on RASU in different life stages. As discussed further in chapter 6, RASU in each life stage experience predation from a distinct spectrum of species, and sometimes different life stages among these species with

potentially different foraging behaviors (see also Bozek et al. 1984; Langhorst and Marsh 1986; Ruppert et al. 1993; Horn et al. 1994; Bonar et al. 2002; Christopherson et al. 2004; Dowling et al. 2005; Mueller et al. 2003a, 2003b, 2005, 2006; Campbell et al. 2007; Bestgen 2008; Carpenter and Mueller 2008; Schooley et al. 2008; Albrecht et al. 2010a, 2010b; Karam and Marsh 2010; Bestgen et al. 2011, 2012; Ley et al. 2013; Ward and Figiel 2013; Best et al. 2017; Ehlo et al. 2017; Mueller 2017). As noted above, RASU at spawning sites may also prey on their own species' eggs.

The spectrum of native predators in the historic, unregulated LCR may have been smaller than the present-day spectrum of non-natives but nevertheless effective in driving the evolution of both behavioral and morphological adaptations in RASU to predation. As discussed in chapter 1, the massive production and fertilization of gametes by RASU may be at least in part an adaptation to predation on RASU eggs and newly emerged, immobile larvae. Franssen et al. (2007) note that the larvae of species that spawn in spring provide an early pulse of prey for a wide spectrum of smaller age classes of predators that depend on small prey. Larval growth rates may affect the intensity of such predation: FLSU larvae, which reportedly grow larger faster than do RASU larvae (McAda and Wydoski 1985; Robinson and Childs 2001; Snyder and Muth 2004; Walters et al. 2006, 2012; LCR MSCP 2008; Sweet et al. 2009), apparently can "run the gauntlet" of spring predators better than RASU larvae.

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 RASU behavioral and morphological adaptations to predation. The Colorado pikeminnow was the only large predatory fish native to the LCR (Minckley 1973; Mueller and Marsh 2002; USFWS 2002b; Portz and Tyus 2004; Franssen et al. 2007; Ward 2017). This species lacks teeth in its jaws and instead uses pharyngeal teeth to grasp and hold its prey. Colorado pikeminnow adults often exceed 500 mm TL and have been recorded to approach 1,800 mm TL (USFWS 2002b), and they become exclusively piscivorous after reaching ≈ 200 mm TL. Their selection of prey is strongly gape limited (Vanicek and Kramer 1969; Portz and Tyus 2004).

Franssen et al. (2007) and D. Ryden (2013, personal communication) estimate that Colorado pikeminnow prefer deep-bodied prey no more than 33–37% of their own body length. Based on size preferences, a 500-mm TL Colorado pikeminnow thus would prey preferentially on fishes less than 165–185 mm TL, and a 1,000-mm TL Colorado pikeminnow would prey on fishes less than 330–370 mm TL. Consequently, RASU up to roughly age 6–8 (i.e., up to early adulthood) would have been subject to pikeminnow predation (e.g., see RASU age-size curves for Grand Canyon presented by Walters et al. 2006, 2012). Further, Colorado pikeminnow consume primarily small-bodied, soft-rayed, cylindrical prey lacking a dorsal keel (Vanicek and Kramer 1969; USFWS 2002b; D. Ryden 2013, personal communication). RASU lack any substantial dorsal

keel, particularly when young. Over evolutionary time, Colorado pikeminnow predation therefore could have shaped the evolution of RASU body form and strategies for coping with predation, which in turn affect RASU vulnerability to the predators in the system today (see chapters 1 and 2).

Human predation on RASU also apparently has a long history along the LCR, as indicated by prehistoric remains in the Gila River Basin, along the LCR, and along the strand lines of former freshwater Lake Cahuilla (McCarthy and Minckley 1987; Gobalet and Wake 2000; Gobalet et al. 2005). The lake, an extension or relocation of the LCR into the Salton Basin (California and Baja California, Mexico), formed and receded several times following the Pleistocene, most recently approximately 500 years ago. Large quantities of RASU bones at prehistoric campsites in the Salton Basin and the remains of hundreds of coeval V- and U-shaped rock weirs at successively descending lake strand lines indicate that the indigenous peoples of the region at least sometimes consumed RASU in large quantities. The weirs are thought to have functioned as traps for schools of fish driven away from lake littoral shallows toward deeper water. RASU were harvested from the Salton Sea in large numbers following its flooding in the early 20th century as well (USFWS 2002a). However, compared to the multi-million-year span of time during which RASU co-existed with Colorado pikeminnow in the Colorado River Basin, the span of time during which humans and RASU coexisted in the basin prior to the drastic effects of river regulation (< 10,000 years) likely was not long enough to entail any significant selective pressure on RASU behavior.

Motile RASU larvae exhibit strong predator avoidance behaviors in response to individual attacks, comparable to those of species that evolved in predator-rich ecosystems (Johnson et al. 1993; Wesp and Gibb 2003). RASU larvae also use cover for protection and show a preference for night drifting, which may help them avoid predators (Johnson et al. 1993; Horn et al. 1994; Johnson and Hines 1999; Wesp and Gibb 2003; Gibb et al. 2006; Valdez et al. 2012a). Larger RASU use cover for protection and may also bury themselves in fine substrates (Mueller 2006; Valdez et al. 2012a), although, as noted above (see “Foraging,” this chapter), adults can be active day and night. Mobility and agility for avoiding or escaping predators presumably increases with age among juveniles, subadults, and adults, and body size alone may provide some protection, at least among adults. Individuals > 450 mm TL experience much lower rates of mortality than do smaller individuals (Kesner et al. 2012, 2016), a relationship assumed to result from the greater vulnerability of smaller RASU to predation. RASU also release and respond to each other’s releases of chemical alarm (aka “fright”) cues triggered by detections of or wounds from predators (Ward and Figiel 2013; O’Neill et al. 2016). Finally, the characteristic deep-bodied, humpbacked RASU body form – which RASU begin to develop during or after their second year of life, when they are approximately 200 mm TL (Portz and Tyus 2004; see chapters 1 and 2 above) – may also have evolved as an outcome of predatory pressure (Hambright 1994; Portz and Tyus 2004; Nowlin et al. 2006; see chapter 4).

However, RASU adaptations to predatory pressure may not provide sufficient defense against the non-native predators that now dominate the ecosystem. These non-native predators find RASU easy targets: some non-native fishes in fact differentially consume RASU and other native fishes compared to their consumption of other non-natives (Pilger et al. 2008; Yard et al. 2011). Further, the non-native striped bass (*Morone saxatilis*) can prey on fishes much larger than itself (Karam and Marsh 2010), making body size less advantageous for defense (Kesner et al. 2016).

Furthermore, compared to wild RASU, repatriated RASU may experience higher rates of predation due to their lack of experience with predators and due to patterns of surfacing behavior developed at rearing facilities (Schooley et al. 2008). Recognition of this possible difference has led to the hypothesis that pre-conditioning of reared RASU might help them better avoid predators upon release (Mueller et al. 2007; Schooley et al. 2008). The topic is the subject of ongoing research by (and funded through Reclamation) and a topic of broad interest in general (Olson et al. 2012; Ward and Figiel 2013; O'Neill and Stewart 2015; O'Neill et al. 2016; Mann et al. 2017). A lack of strong swimming ability among repatriated RASU may also affect their ability to avoid predators (Mueller et al. 2003a; Ward and Hilwig 2004; Mueller et al. 2007; Kegerries and Albrecht 2009; Avery et al. 2011; Senger and Sjöberg 2011). Finally, RASU adults may be distinctly more vulnerable to avian predation during spawning because of the shallowness of staging areas and spawning sites (compare Minckley et al. 1991; Mueller 2006; Campbell et al. 2007; Schooley et al. 2008). Mueller (2006) also reports an observation of a coyote (*Canis latrans*) capturing RASU directly from the shallows of a spawning site.

RESTING/HIDING

RASU need to rest to conserve energy during every mobile life stage but also need to rest in ways that do not leave themselves vulnerable to predation. They select resting/hiding locations with mesohabitat characteristics (see chapter 4) and turbidity levels that afford them protection from predators and from thermal, chemical, or mechanical stress, and these preferences differ among life stages and by season (see chapters 4 and 6; see also Mueller et al. 2000; Lee et al. 2006; Mueller 2006; Hedrick et al. 2009; Bestgen et al. 2011, 2012). As noted above, RASU larvae and juveniles also mostly rest during daylight hours – a behavioral pattern that diminishes as they move into adulthood.

The ability of RASU to find suitable resting/hiding sites presumably increases as their range of mobility increases with size and age. Even drifting RASU larvae, with their limited swimming abilities, actively seek substrates with suitable interstitial spaces in which they can rest during daylight hours. Older RASU juveniles, subadults, and adults move increasingly widely within the LCR, within

and sometimes among connected riverine and lacustrine macrohabitats (Mueller et al. 2000; Wydoski et al. 2010; Kesner et al. 2012; Wydoski and Lantow 2012). They also may increasingly exhibit seasonal variation in their selection of macro- and mesohabitats as resting/hiding sites within these ranges as recorded for adults (Minckley et al. 1991; LCR MSCP 2008, 2016a), and their pattern of selection may vary with water temperature and time of day (night versus day) (Gurtin et al. 2003; Mueller et al. 2006; Valdez et al. 2012). Post-dispersal larvae, younger juveniles, older juveniles, subadults, and adults use a variety of mesohabitat features as cover, including submerged woody debris; interstitial spaces in gravel, cobble, and boulder substrates; and aquatic macrophytes and shoreline vegetation submerged by increasing water surface elevations (see chapter 4).

RIPENING

Ripening is associated only with spawning and consists of the development of secondary sexual traits and mature gametes in both sexes (Minckley et al. 1991). The number of eggs per female RASU in the LCR, estimated from egg mass, increases with body size (Gustafson 1975; Minckley et al. 1991). As noted in chapter 1, RASU female fecundity in the LCR averages approximately 2,000 ova per centimeter body length (Minckley et al. 1991; Dowling et al. 1996), with totals of approximately 75,000–125,000 ova per female. Ripening presumably requires a suitable level of fitness since it diverts energy from other physiological processes and takes place in some fraction of the adult population each year, possibly in part in response to cues in the water, although the exact character of such cues is not well understood (see also Modde and Irving 1998; Mueller 2006; Schooley et al. 2008; Albrecht et al. 2010a, 2010b; Bestgen et al. 2011, 2012; Patterson et al. 2012). Individuals may exhibit external reproductive traits for many months without becoming ripe (Minckley et al. 1991).

STAGING AND SPAWNING

The recognition of staging and spawning as a distinct critical biological activity or process in the present CEM rests on the standard references cited earlier and additional information presented by Modde and Irving (1998), Schooley et al. (2008), Albrecht et al. (2010a, 2010b), Bestgen et al. (2011, 2012), and others. The cumulative evidence indicates that some proportion of the adult population attempts to spawn every year, with males outnumbering females in the spawning aggregations. The literature also indicates that, following ripening (see above), the spawning process involves two major steps, each with several elements: (1) staging, the assembling of RASU at/around spawning sites and (2) a series of interactions between males and females at the spawning site, including site

preparation and the spawning act itself. Staging and spawning success depends on the successful combination of a single – although large – set of habitat conditions and critical biological activities.

Staging in open riverine habitat takes place over several weeks, with males arriving at spawning sites sometimes weeks before the females. Individuals in open riverine environments swim to and from their spawning sites over large distances that encompass entire lakes and, where present, flowing river and tributary reaches upstream within the limits imposed by dams (Mueller et al. 2000; Albrecht et al. 2010a; Kesner et al. 2012; Wydoski and Lantow 2012). Reports sometimes refer to spawning "migrations" (e.g., Mueller 2006).

RASU staging presumably responds to environmental triggers. Most discussions of the cues for staging focus on changes in flow conditions and water temperature. The interaction of these cues is perhaps better understood in the UCRB, where more natural flows and associated changes in water temperature still occur. However, changes in temperature alone, and perhaps also changes in water levels and indicators of season, may continue to provide cues in the LCR ecosystem (Minckley et al. 1991; Modde and Irving 1998; USFWS 1998, 2002a; Mueller 2006; LCR MSCP 2008; Schooley et al. 2008; Albrecht et al. 2010a, 2010b; Bestgen et al. 2011, 2012; Patterson et al. 2012). Spawning of RASU in isolated ponds in refuges along the LCR, with non-riverine hydrologic regimes, suggests that RASU can spawn without any cues from the flow regime at all (Mueller 2006; Dowling et al. 2011; LCR MSCP biologists 2013, personal communications concerning the Imperial Pond Conservation Area (IPCA); Saltzgiver et al. 2015; Dowling et al. 2016a, 2017). Releases of pheromones are thought to be involved in triggering spawning, but data are lacking (Mueller et al. 2008; Albrecht et al. 2010a).

Successful staging requires suitable sites for spawning, where suitability is determined by a suite of habitat conditions. However, the literature reflects much uncertainty concerning why spawning RASU may prefer any one individual site over another (Minckley et al. 1991; Modde and Irving 1998; USFWS 1998, 2002a; Mueller 2006; LCR MSCP 2008; Schooley et al. 2008; Albrecht et al. 2010a; Bestgen et al. 2011, 2012; Patterson et al. 2012; Valdez et al. 2012). For example, field observations indicate that RASU spawn on the artificial boat ramp at the IPCA (LCR MSCP biologists 2013, personal communications). The understanding of substrate selection for spawning is complicated by a lack of quantitative data on substrates at spawning sites and a lack of comparative data on substrates at sites that spawning adults ignore (see "Substrate Texture/Dynamics," chapter 4).

RASU exhibit some fidelity to individual or limited sets of spawning sites (Tyus and Karp 1990; Modde and Irving 1998; USFWS 1998; Mueller et al. 2000; Wydoski et al. 2010; Wydoski and Lantow 2012). Males use a single site per season, while females may visit several spawning sites in succession (Mueller

et al. 2000). The data do not indicate whether, when returning to a previously visited spawning site, males select their natal site or simply repeatedly select sites at which they have successfully spawned in previous years. Once they arrive at spawning sites, RASU males may be territorial when ripe females are not present (Bozek et al. 1984), using "eye flashes" to signal their presence and territorial claim to other males (Mueller 2006; Flamarique et al. 2006).

The act of spawning itself involves a discrete set of behaviors that take place within a limited range of water depths and flow conditions. As described by Minckley et al. (1991) (page 321) "… females remain in deeper water until ripe, then appear singly on the spawning grounds. Major aggregations then break apart to swim along shorelines in groups of three to thirty or more, most often representing a number of males following a female. About twice as many males as females are caught near the spawning grounds… When she is ready to spawn, a female, flanked by two or more males, separates from a group and moves to the bottom. The males press closely against the female's posterior abdomen and caudal peduncle, and all contact and agitate the substrate for three to five seconds in apparent spawning convulsions, after which they typically return to a larger group… The entire sequence lasts from a few seconds to three minutes, usually the former. Females recognizable because of an injury or some other distinctive feature have been observed to spawn repeatedly in a given hour and day, and on successive days within a week… A female presumably releases a small fraction of her eggs with each spawning act. Fish spawn sporadically throughout the day and night, with no evident diel pattern."

Mueller (2006) and the LCR MSCP (2008, 2016a) provide additional descriptions of spawning activity. Bozek et al. (1984), Minckley et al. (1991), Snyder and Muth (2004), and Mueller (2006) note that spawning activity can agitate the surface of the benthic substrate. As noted above (see "Egg Settling and Adhesion," this chapter), this activity removes fine sediment, creates nest-like depressions, and can drive eggs into the substrate. However, the depressions are not actual nests (Minckley et al. 1991). The arrival of a ripe female on the spawning grounds triggers each individual spawning event. Successful spawning during those brief seconds or minutes depends in part on the suitability of environmental conditions, including wave turbulence (Minckley et al. 1991).

SWIMMING

RASU swim to explore, find and position themselves within habitat, avoid hazards, feed, and stage and spawn. Swimming ability first appears among larvae after they assimilate their yolk, and RASU thereafter develop into stronger, more agile swimmers with greater stamina. Older juveniles, subadults, and adults swim over increasingly large distances within and among river macrohabitats

(e.g., within and between the flowing river segment above Lake Mohave and the lake itself) (see also Bradford and Gurtin 2000; Mueller et al. 2000; Gurtin et al. 2003; Kesner et al. 2012; Valdez et al. 2012; Wydoski and Lantow 2012).

Swimming behavior is generally described as solitary or dispersed, except for aggregation during spawning. Individual RASU adults appear to establish home ranges from which they only rarely travel other than to spawn but within which they do not exhibit obvious territoriality (Tyus and Karp 1990; Wydoski and Mueller 2006; Wydoski and Lantow 2012, 2013; Marsh et al. 2015). However, RASU adults aggregate at spawning sites, where males also exhibit territoriality (see above), and RASU of all ages may sometimes engage in non-reproductive aggregating or "schooling" as well. Non-reproductive aggregating first appears among dispersing larvae and has been reported for all subsequent age classes (USFWS 2001; Snyder and Muth 2004; Mueller 2006; Albrecht et al. 2010a), including at rearing facilities (Gorman and VanHoosen 2000). Such aggregation and coordinated movement could produce uneven distributions of older juveniles and subadults, such as those encountered by LCR MSCP biologists during riverine and backwater sampling (LCR MSCP biologists 2013, personal communications). Some authors (e.g., Marsh et al. 2015) prefer to not apply the term "schooling" to RASU behavior. However, given reports of coordinated movement among aggregated RASU across all age classes along the river over many years, non-reproductive aggregation may be within the RASU natural behavioral repertoire, helping RASU collectively avoid predation or exploit concentrations of food resources. "Schooling" behaviors, in turn, could affect the ability of different spatial sampling methods to establish reliable estimates of RASU population size and distribution.

Swimming abilities among hatchery-reared RASU have received special attention. Repatriated RASU may lack stamina for long-distance movement initially following release and lack strength for avoiding predators (Mueller and Marsh 1998; Mueller and Foster 1999; Mueller et al. 2003a, 2007; Ward and Hilwig 2004; Kegerries and Albrecht 2009; Avery et al. 2011; Senger and Sjöberg 2011). The potential benefits of conditioning swimming abilities among reared RASU prior to release are the subject of ongoing research and experimentation with ways to achieve large-scale conditioning at hatcheries (Avery et al. 2011; Finnegan 2013; Cappelli 2015, 2016; LCR MSCP 2014, 2015, 2016b; Garnett 2016). RASU may also develop surfacing behaviors during rearing, in response to feeding practices, possibly making the reared RASU more vulnerable to avian predators following release (Schooley et al. 2008).

THERMAL STRESS

RASU in every life stage are vulnerable to stress and mortality from exposure to water temperatures outside their ranges of tolerance (Bozek et al. 1990; Minckley

et al. 1991; USFWS 1998; Clarkson and Childs 2000; Mueller et al. 2005; Carveth et al. 2006; Mueller 2006; Bestgen 2008; LCR MSCP 2008, 2016a; Bestgen et al. 2011). Exposure to excessively high or low temperatures may suppress metabolic rates and rates of maturation, including embryological development, and (among mobile life stages) inhibit engagement in many types of activities, thus reducing fitness and increasing vulnerability to other hazards.

As noted earlier (see chapter 1), the natural range of environmental variability of the LCR ecosystem necessarily selected for adaptations in RASU that allow it to persist in the warmer waters that can occur here. Wesp and Gibb (2003), for example, did not see evidence of adverse temperature effects on predator avoidance behaviors among RASU larvae in laboratory experiments. Similarly, Carveth et al. (2006) found that RASU have a moderately high tolerance of high water temperatures and can tolerate even higher temperatures if acclimated to an intermediate temperature first. Further, as RASU mature, they become increasingly able to avoid or escape settings in which they may sense thermally unsuitable conditions – if these conditions are sufficiently localized to permit such avoidance or escape. However, RASU that seek cooler water during the summer months may expose themselves to other forms of stress: The cooler hypolimnetic waters of reservoirs and deeper ponds in summer typically have lower concentrations of DO (Mueller 2006). Repatriated RASU also may be more vulnerable to thermal stress than their wild cousins, at least initially following release, due to a lack of conditioning to the range of temperatures they face upon release (see “Pre-Release Conditioning,” chapter 4).

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. The RASU conceptual ecological model identifies 16 habitat elements that affect one or more critical biological activities or processes across the 5 RASU life stages. Table 3 lists the 16 habitat elements and the critical biological activities and processes that they *directly* affect across all RASU life stages. Table 3 also indicates two relationships that are bi-directional (i.e., involve feedback between a habitat element and critical activity or process). Note that aquatic macrophytes do not directly affect any critical biological activity or process.

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

Key: Colored (X) cells indicate bi-directional relationships, in which the habitat element and critical activity or process reciprocally affect each other.

Critical biological activity or process ➔ / **Habitat element ➓**	Chemical stress	Competition	Disease	Drifting	Egg settling and adhesion	Foraging	Hybridization	Mechanical stress	Predation	Resting/hiding	Ripening	Staging and spawning	Swimming	Thermal stress
Aquatic macrophytes														
Aquatic vertebrates		X					X		X				X	
Birds and mammals		X							X					
Genetic diversity			X											X
Infectious agents			X											
Invertebrates and particulate organic matter		X				X			X					
Macrohabitat structure				X									X	
Mesohabitat structure				X		X				X		X	X	
Monitoring, capture, handling					X			X						
Pre-release conditioning	X		X			X			X				X	X
Substrate texture/dynamics					X			X		X		X		
Turbidity						X			X	X		X	X	
Water chemistry	X									X	X	X	X	
Water depth					X			X			X	X		
Water flow/turbulence				X	X			X		X	X	X	X	
Water temperature	X									X	X	X	X	X

Some of the 16 habitat elements differ in their details among life stages. For example, RASU 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.

Habitat elements also may affect individual critical biological activities or processes indirectly through the effects of habitat elements on each other or through the effects of one critical biological activity or process on another. Aquatic macrophytes affect several individual critical biological activities and processes indirectly through their effects on other habitat elements. The effects of habitat elements on each other do not vary among the five life stages. Table 4 shows the interactions among habitat elements identified in the RASU conceptual ecological model and indicates which are identified as bi-directional (i.e., involve feedback between the two elements).

Table 4.—Cause-effect relationships among habitat elements

Key: Colored (X) cells indicate bi-directional relationships in which the two habitat elements reciprocally affect each other.

Affected habitat element ➔ / **Causal habitat element ↓**	Aquatic macrophytes	Aquatic vertebrates	Birds and mammals	Infectious agents	Invertebrates and particulate organic matter (POM)	Macrohabitat structure	Mesohabitat structure	Monitoring, capture, handling	Substrate texture/dynamics	Turbidity	Water chemistry	Water flow/turbulence	Water temperature
Aquatic macrophytes		X	X		X		X		X		X	X	
Aquatic vertebrates	X		X		X					X			
Birds and mammals		X			X								
Invertebrates and POM		X	X						X	X	X		
Macrohabitat structure							X					X	
Mesohabitat structure	X	X	X						X			X	
Substrate texture/dynamics	X				X		X			X			
Turbidity	X	X	X		X			X					
Water chemistry	X	X			X								
Water depth	X						X				X	X	X
Water flow/turbulence	X					X	X		X	X	X		
Water temperature		X	X	X	X						X		

The basic sources of the information used to identify and characterize the habitat elements for the RASU conceptual ecological model are Minckley et al. (1991), USFWS (1998, 2002a), Ryden (1999), LCR MSCP (2004, 2008, 2016a), Mueller (2006), Minckley and Marsh (2009), Zelasko et al. (2009), Albrecht et al. (2010a), Valdez et al. (2012a, 2012b, 2012c), and Marsh et al. (2015). The identification also integrates information from both older and more recent works, meeting presentations by LCR MSCP and partner biologists, and the expert knowledge of LCR MSCP fish biologists.

Valdez et al. (2012a) reviewed the literature and expert knowledge in detail in order to catalog the abiotic (physical and chemical) characteristics of settings in which RASU occur during different life stages, following the life-stage model presented by Valdez et al. (2011). The review also summarizes possible biological and ecological reasons for these associations, although this is not its primary emphasis. The present CEM reorganizes and tabulates the information from Valdez et al. (2012a) by habitat element, incorporating more recent information where available. As with all tabulations of habitat associations, inferences that particular habitat characteristics are critical to a species or life stage require evidence and hypotheses for why each association matters to species viability (Rosenfeld 2003; Rosenfeld and Hatfield 2006).

The habitat characteristics recognized by Valdez et al. (2012a) necessarily mostly correspond 1:1 with the habitat elements recognized in the present CEM. However, the terms used in the two documents differ in a five instances. Table 5 identifies the five habitat elements in the present CEM for which Valdez et al. (2012a) use different terms and identify the corresponding terms used in the earlier document.

Table 5.—RASU conceptual ecological model habitat elements and equivalents in Valdez et al. (2012a)

Habitat element in RASU conceptual ecological model	Habitat characteristic in Valdez et al. (2012a)
Mesohabitat structure	Mesohabitat
Water temperature	Microhabitat: temperature
Depth	Microhabitat: depth
Flow/turbulence	Microhabitat: velocity
Substrate texture/dynamics	Microhabitat: substrate

The present document identifies habitat elements by a one-to-three-word short name. Each short name refers to a longer, complete name. For example, “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 descriptions of the 16 habitat

elements in the RASU conceptual ecological model identify each habitat element in alphabetical order using its short name, provide the full name, and provide a detailed definition of the subject element.

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, its connected backwaters, and isolated wetlands across the LCR flood plain. Table 6 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), the U.S. Department of Agriculture's (USDA) PLANTS Database (USDA 2016), and the National Invasive Species Information Center (NISIC) (2017).

The species listed in table 6 and the detritus from them may provide cover and food for RASU (Burke and Mueller 1993; Mueller 2006); habitat for periphyton that RASU may consume; habitat, including periphyton foods, for aquatic and terrestrial invertebrates that RASU may consume; and habitat for aquatic invertebrates, aquatic vertebrates, and birds that may prey on or compete with RASU (see "Competition," "Foraging," "Predation," and "Resting/Hiding," chapter 3). On the other hand, extremely dense stands of some macrophytes could exclude RASU and also affect water circulation, with consequences for other habitat elements (Finnegan 2013).

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 have helped sustain their own habitat by stabilizing substrates and slowing the movement of water (Carlson et al. 1979; Fernandez and Madsen 2013).

The aquatic macrophyte assemblage along the LCR and its backwaters has changed as a result of river regulation and introductions of non-native plant species. Shallow backwaters, embayments, and tributary confluences continue to support aquatic macrophytes (Fernandez and Madsen 2013). However, 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 2017). Fortunately, control efforts appear to be effective (Thorson et al. 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.

Table 6.—Aquatic macrophytes of the LCR

Species	Origin[1]
Arundo donax, giant reed	I
Certophyllum demersum, hornswort or coon's tail	N
Chara sp., muskgrass	N
Cladophora glomerata	N
Lemna sp., duckweed	N
Myriophyllum spicatum, Eurasian watermilfoil	I
Myriophyllum brasiliense (aka M. aquaticum), parrot feather 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, leafy or 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
Scirpus californicus, giant bulrush	N
Scirpus americanus, three-corner bulrush	N
Stuckenia pectinata (aka Potamogeton pectinatus), sago pondweed	N
Typha angustifolia, narrowleaf cattail	N
Typha domingensis, southern cattail	N
Typha latifolia, broadleaf cattail	N
Typha x glauca, hybrid cattail	?
Utrichularia sp., bladderwort	N
Zannichellia palustris, horned pondweed	N

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

Hybrid cattail also may affect the LCR macrophyte community. The species, *Typha x glauca*, is a hybrid of the native narrowleaf and broadleaf cattail (*T. angustifolia* and *T. latifolia*, respectively) or possibly sometimes a hybrid of broadleaf with the native southern cattail (i.e., with *T. domingensis*) (USDA 2016). Narrowleaf and hybrid cattails have similar habitat requirements and can grow in deeper water compared to broadleaf cattails (Motivans and Apfelbaum 1987). Both narrowleaf and hybrid cattails aggressively out-compete broadleaf and southern cattails for habitat, not only by occupying deeper waters but by establishing themselves in dense, mono-specific stands. Such stands can quickly dominate entire wetlands, eliminating open water and forming dense rhizome mats and litter, thereby crowding out other plants (Motivans and Apfelbaum 1987). Individual hybrid plants can produce as many as 700,000 fruits per year, and can reproduce asexually from their rhizomes, forming clones that can spread up to 8 m per year (Pennsylvania Department of Conservation and Natural Resources [PADCNR] 2016). Aggressive expansion is more likely in disturbed wetlands, and hybridization exacerbates this potential. Triggering disturbances may include changes in hydrology, wildfire suppression, or nutrient enrichment (Wilcox et al. 1984) – common risk factors across the LCR ecosystem.

The PLANTS Database (USDA 2016) currently does not include any occurrences of hybrid cattails within the LCR ecosystem. However, this apparent absence may only reflect a pattern of misidentification resulting from the lack of systematic attention to the taxonomy of cattails along the LCR and difficulties in distinguishing between narrowleaf and hybrid cattails (PADCNR 2016). All three parent *Typha* species occur along the LCR, and hybridization occurs easily; therefore, it is likely that hybrid cattails are present along the LCR.

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 cattails, common reed, or giant salvinia may suppress aquatic invertebrate abundance by reducing light and DO levels (NISIC 2017), and may provide less cover habitat for larger RASU. Conversely, different aquatic macrophytes have different ranges of tolerance for variation in water chemistry, including the availability of nutrients, leading to concerns that changes in water quality may affect aquatic macrophyte composition and density in some LCR ponds (Finnegan 2013).

Table 6 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 RASU or its habitat along the present-day LCR. Interactions may include predation on or competition with RASU. Most of these vertebrates are fishes, including both native and non-native species, but also includes one amphibian, the bullfrog (*Rana catesbeiana*), and its larvae (tadpoles) (Mueller 2006, 2007; Mueller et al. 2006). Activity levels may vary in response to habitat conditions such as water temperature and turbidity (Robinson and Childs 2001; Thieme et al. 2001; Ward 2001).

Table 7 lists the aquatic vertebrates known to occur in the present-day LCR ecosystem based on information presented by Ohmart et al. (1988); Minckley (1991); Mueller and Marsh (2002); Minckley et al. (2003); Gobalet et al. (2005); Marsh and Pacey (2005); and the U.S. Geological Survey's (USGS) Nonindigenous Aquatic Species (NAS) Database (NAS 2017). The table also identifies whether each species is 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 2017). 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 7 therefore does not include them.

Table 7 also does not include hybrids. As noted above (see "Hybridization," chapter 3) RASU and other 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, 2007; Minckley and Marsh 2009; Douglas and Douglas 2010; Zelasko et al. 2011b; Webber et al. 2013). Hybrids of RASU with other catostomids, particularly with FLSU conceivably may compete with pure RASU for food, habitat, and mates.

The "Prey" column in table 7 indicates whether each species is known to prey on RASU along the LCR, indicated by an "X" mark in this column. Alternatively, a species that is either suspected to prey on RASU or has ecological characteristics that suggest it could prey on RASU is indicated by a "?" mark in this same

Table 7.—Aquatic 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	X	?	?
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 (X) or suspected (?) to prey on RASU.
[3] Species for which juveniles (subscript J) or adults (subscript A) of the species are known (X) or suspected (?) to compete with RASU for food or habitat.

column. The information on species with ecological characteristics that suggest it could prey on RASU is from Froese and Pauly (2014), NatureServe Explorer (NatureServe 2014), and the USGS's Nonindigenous Aquatic Species Program (http://nas.er.usgs.gov/default.aspx). Species that are neither known nor suspected to prey on RASU along the LCR are indicated by a blank in the "Prey" column. Numerous sources document or suggest predation on RASU in various life stages by diverse species (Bozek et al. 1984; Langhorst and Marsh 1986; Ruppert et al. 1993; Horn et al. 1994; Brooks et al. 2000; Bonar et al. 2002; Christopherson et al. 2004; Dowling et al. 2005; Mueller et al. 2003a, 2003b, 2005, 2006; Mueller 2006; Campbell et al. 2007; Bestgen 2008; Carpenter and Mueller 2008; Schooley et al. 2008; Albrecht et al. 2010a, 2010b; Karam and Marsh 2010; Bestgen et al. 2011, 2012; Hedrick et al. 2012; Ley et al. 2013; Ward and Figiel 2013; Best et al. 2017; Ehlo et al. 2017; Mueller 2017).

Many of the publications that do identify species as known or suspected predators of RASU note that RASU at different life stages – including eggs – may be subject to predation by different predatory species or different life stages of the same predatory species. For example, RASU at spawning sites may prey on their own species' eggs, as may common carp (*Cyprinus carpio*), given evidence that common carp prey on BONY eggs (Bozek et al. 1984; Mueller 2006). Mueller (2006) and Mueller et al. (2006) document predation by BONY and bullfrogs, both adult and tadpole, on RASU larvae. Bullfrog adults and tadpoles also may feed on RASU eggs (Mueller 2006).

The last two columns in table 7 indicate whether each species is known or suspected to compete with RASU along the LCR or has ecological characteristics that suggest it could compete with RASU for food items or physical habitat. These two columns indicate whether the juvenile or adult form of each species, respectively, is known or suspected to compete with RASU along the LCR, indicated by an "X" mark in one or both of these two columns. Alternatively, a "?" mark in one of these columns indicates that the juvenile or adult form of that species is either suspected to compete with RASU along the LCR or has ecological characteristics that suggest it could compete with RASU. The information on species with ecological characteristics that suggest it could compete with RASU is from Froese and Pauly (2014), NatureServe Explorer (NatureServe 2014), and the USGS's Nonindigenous Aquatic Species Program (http://nas.er.usgs.gov/default.aspx). Species that are neither known nor suspected to compete with RASU along the LCR are indicated by a blank in one or both of these last two columns.

Numerous studies identify competition as a potential factor affecting RASU survival in one or more life stages (Papoulias and Minckley 1992; Wydoski and Wick 1998; USFWS 1998, 2002a; Mueller 2006; Albrecht et al. 2010a; Bestgen et al. 2012; Farrington et al. 2013). However, few studies specifically evaluate which species actually do compete with RASU in the LCR or in what ways

(Mueller and Burke 2005). Minckley (1982) and Brooks et al. (2000) summarize evidence pointing to dietary overlaps among RASU and several native and non-native species in the Lower and Upper Colorado River Basins, respectively.

The large number of entries in table 7 for possible competition reflects the fact that, while RASU may select foods in a limited size range and, as adults, are primarily benthic feeders, they are otherwise omnivorous (see "Foraging," chapter 3). Their omnivory puts them in potential competition with other 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 RASU for food considered only reported ranges of food items, not feeding habitats, behaviors, or schedules.

The intensity, timing, and geographic distribution of predation on RASU by – and competition with RASU from – other aquatic vertebrates depend on more than simply the presence and abundance of potential predators or competitors. Other habitat elements may also affect predator and competitor activity, including the season and time of day, water temperature, flow or turbulence, turbidity, and the availability of cover habitat for the other aquatic vertebrates. The present CEM recognizes the likely importance of such relationships. However, a full assessment of the biology and ecology of the species listed in table 7 lies outside the scope of the present CEM.

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 RASU or its habitat along the LCR and its connected backwaters. This range includes species known or potentially able to prey on RASU specifically when the fish occur in shallows or approach the water surface or shoreline, making the fish visible and accessible.

Specific information on avian and mammalian predation on RASU was limited at the time of preparation of the original RASU conceptual ecological model (Braun and McClure 2013). Mueller (2006) reports observations of, and reasons for suspecting avian predation on RASU at Cibola High Levee Pond by "kingfishers [*Megaceryle alcyon*], osprey [*Pandion haliaetus*], cormorants [*Phalacrocorax* spp.], pelicans [*Pelecanus* spp.], … night herons [*Nycticorax nycticorax*], and great blue herons [*Ardea herodias*]." Kesner et al. (2008b) similarly specifically suspect double-crested cormorants (*Phalacrocorax auritus*) and American white pelicans (*Pelecanus erythrorhynchos*) as significant predators of BONY at the IPCA. Best (2015) also suggests great egrets (*Ardea alba*) and other migratory

fish eaters such as common mergansers (*Mergus merganser*) and grebes (*Aechmophorus* spp.) as species of interest. In turn, Mueller (2006) reports observations of, and reasons for suspecting mammalian predation on RASU at Cibola High Levee Pond by "… raccoons [*Procyon lotor*], ringtail cats (*Bassariscus astutus*), and other fish-eating animals." Mueller (2006) also suggests that coyotes could prey on RASU when the fish approach the shoreline.

Information on avian predation on RASU has increased significantly since preparation of the original RASU conceptual ecological model (Braun and McClure 2013) through the work of Best et al. (2017) and Mueller (2017) at Laughlin Lagoon. Laughlin Lagoon is an artificial backwater connected to the Big Bend of the Colorado River south of Laughlin, Nevada, directly across the river from Bullhead City, Arizona. The study combined photographic arrays on perching/roosting poles and antenna arrays to detect passive integrated transponder (PIT) tags from tagged RASU and BONY consumed by predatory birds using the poles during winter 2015, spring 2016, and winter 2016. The RASU and BONY were deliberately stocked into the lagoon for purposes of the study. The results indicated significant predation on both fish species by double-crested cormorants, with additional but much lower rates of predation by great blue herons and osprey. Further, the birds consumed BONY and RASU regardless of size, up to the largest fishes stocked into the lagoon for the study (the mean size of stocked RASU was approximately 326 mm TL, and the mean size of depredated RASU was approximately 320 mm TL) (Best et al. 2017).

At least one mammal may affect RASU not through predation but by shaping habitat. Specifically, beavers (*Castor canadensis*) conceivably once may have helped create mesohabitat conditions beneficial to RASU by introducing woody debris (Stevens et al. 1997) and creating marshes and pools along backwater channels (Cooke et al. 2005). Beavers 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 RASU.

As with predation by other aquatic vertebrates, the intensity, timing, and geographic distribution of predation on RASU by birds and mammals depends on more than simply the presence and abundance of the potential predators. Other habitat elements may also affect activity among potential avian and mammalian predators, including the season (Campbell et al. 2007) and time of day, air temperature, wave activity and turbidity, the availability of perching (Mueller 2006; Best et al. 2017) or cover habitat for the predators, and so forth. The present RASU conceptual ecological model recognizes the likely importance of such relationships; however, a full assessment of the biology and ecology of potential avian and mammalian predators lies outside the scope of the present CEM.

GENETIC DIVERSITY

Full name: **The genetic diversity of RASU individuals.** This element refers to the genetic homogeneity versus heterogeneity of the RASU population during each life stage. As noted elsewhere in this CEM, the LCR MSCP operates an intensive program of capturing RASU larvae in Lake Mohave for rearing in off-site facilities for later repatriation. Repatriated RASU, in turn, constitute nearly 100% of the individuals that contribute to each generation of larvae produced in the LCR ecosystem outside of Lake Mead. The LCR MSCP augmentation program therefore is the predominant driver of genetic diversity among RASU in the LCR ecosystem outside of Lake Mead. The greater the heterogeneity, the greater the possibility that individuals of a given life stage will have genetically encoded abilities to survive their encounters with the diverse stressors presented by their environment and/or take advantage of the opportunities presented by their environment (USFWS 2002a; Minckley et al. 2003; Hurt and Hedrick 2004; Dowling et al. 2005, 2008, 2011, 2012, 2014a, 2014b, 2015, 2016a, 2016b, 2017; Mueller 2007; Turner et al. 2007; LCR MSCP 2008, 2016a, 2016b; Delrose 2011; Wilson 2011, 2012; Marsh et al. 2015; Kesner et al. 2016).

INFECTIOUS AGENTS

***Full name*: The types, abundance, distribution, and activity of infectious agents to which RASU are susceptible.** As noted above (see "Disease," chapter 3), RASU 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 RASU in the open environment of the LCR, including anchor worms (*Lernea* spp.), ich, and *Myxobolus* spp. (Valdez 1990; Clarkson et al. 1997; Robinson et al. 1998; Choudhury 2004; USFWS 2002a; Mueller 2006; Ward et al. 2007; Ward and Finch 2009). The risk of infection presumably increases with the diversity and abundance of such agents and the spatial extent of their distribution. The present CEM does not address RASU rearing in controlled environments, which have their own concerns about disease (Ward et al. 2007; Ward and Finch 2009). However, the knowledge obtained from these controlled environments does contribute to the understanding of disease among RASU in the open environment of the LCR and its off-channel environments.

Studies often mention non-native fishes as potential sources of the non-native pathogens and parasites that may affect native fishes in the Colorado River Basin (Miller 1952; Heckmann et al. 1986; Haden 1992; Mueller and Marsh 2002; Mueller 2005; Cucherousset and Olden 2011). However, RASU do not appear to be as susceptible to infection by some introduced parasites – e.g., the Asian fish

tapeworm (*Bothriocephalus acheilognathi*) – as are other native fishes in the basin (Brouder and Hoffnagle 1997; Robinson et al. 1998; Landye et al. 1999). Every infectious agent has a distinct life cycle with distinct requirements and limitations for intermediate carriers or hosts. Every native fish species along the Colorado River has different dietary and other requirements that affect their exposure to infectious agents as well as different biological responses to exposure. Consequently, it is not surprising that RASU are susceptible to different infectious agents that occur in the Colorado River ecosystem in the same way as other native fishes of the ecosystem.

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 RASU 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. RASU feed on aquatic invertebrates and POM, with RASU 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 larval and younger juvenile RASU (Horn et al. 1994; Lenon et al. 2002; Mueller 2006; Mueller et al. 2006; Martinez 2012; Moody and Sabo 2013). Two species of non-native crayfish may occur in RASU habitat: the virile crayfish (*Orconetes virilis*; *aka* northern crayfish) and the red swamp crayfish (*Procambarus clarkii*). Both of these non-native crayfish also may compete with RASU in foraging for POM and smaller aquatic invertebrates (Martinez 2012; Moody and Sabo 2013) (see "Competition," chapter 3).

Three non-native mollusks, Asian clam (*Corbicula fluminea*), quagga mussel (*Dreissena rostriformis bugensis*), and zebra mussel (*Dreissena polymorpha*), also occur in RASU habitat in the LCR ecosystem (Ohmart et al. 1988; Nalepa 2010; NISIC 2017). These species are highly efficient filter feeders and therefore may compete with RASU for aquatic invertebrates and POM, and they also form

dense carpets that could interfere with RASU browsing (NISIC 2017). 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 2017). It tolerates warm waters (up to 28 °C) and high salinity (up to ≈ 26%) (NISIC 2017). 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 RASU foraging.

The non-native golden alga (*Prymnesium parvum*) has been detected in Beal Lake (LCR MSCP 2014) and could expand to other isolated, 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 sediment and organic matter from the UCRB now settle 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, other contaminant inputs and from hypolimnetic discharge from dams, and by the effects of introduced species (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). Bozek et al. (1984) also attribute a loss of aquatic insects below Hoover Dam since the 1950s to the effects of dam operations on downstream water temperatures and wetted habitat needed for aquatic insect reproduction.

The LCR MSCP has experimented with fertilizing off-channel habitats around the margins of Lake Mohave using both dissolved nutrients and POM to determine if such mechanical fertilization stimulates primary and/or secondary productivity and thereby increases the quality and quantity of natural resource base for grow-out-stage RASU (Loomis 2014). The results have been ambiguous, affected by high variability between test sites and within individual test sites over time, and impacts of poor water circulation, DO depletion during hot weather, and algal mat formation.

It should also be noted that POM can become incorporated into benthic substrates and that some aquatic invertebrates feed in the substrate (see "Substrate texture/Dynamics," this chapter). As noted elsewhere in this chapter, bioturbation by invertebrates feeding in the substrate can affect turbidity (see "Turbidity," this chapter). Bioturbation presumably also can affect the substrate structure in the LCR ecosystem, as it does in other ecosystems (Allan and Castillo 2007; Mitsch and Gosselink 2007), but the present review did not locate any literature on this possible linkage specific to the LCR ecosystem. Similarly, the organic matter incorporated into benthic substrates potentially can affect benthic water chemistry, particularly by affecting biological oxygen demand (Allan and Castillo 2007; Mitsch and Gosselink 2007). However, again, the present review did not locate any literature on this possible linkage specific to the LCR ecosystem. Consequently, the present CEM does not include explicit linkages between the present habitat element, invertebrates and POM, or either substrate texture/ dynamics or water chemistry. These linkages could be added to a later iteration of the present CEM if new information indicates they matter in RASU ecology.

MACROHABITAT STRUCTURE

***Full name*: The types, abundance, and spatial and temporal distributions of aquatic macrohabitats.** This element refers to the large-scale (i.e., 1–100-kilometer scale) shape and hydraulic gradient of the river channel, backwaters, other off-channel wetted areas, and the connected flood plain. The present CEM distinguishes macrohabitats from mesohabitats, which are smaller-scale features such as eddies, pools, riffles, and runs (see below, this chapter). However, other authors may apply the term "macrohabitat" to both scales (e.g., Holden 1999; Budy et al. 2009). Examples of macrohabitat types, as defined in the present CEM, include the main channel, islands, side channels, tributary mouths, sloughs, bays, disconnected backwaters, etc. Major artificial features of the LCR, such as channel training structures, diversion and return structures, and dams (LCR MSCP 2004) also constitute macrohabitats for purposes of this model.

Macrohabitats define the overall flow paths and gradients for water and sediment moving through a system and establish the template for the formation of mesohabitats. Macrohabitat structure along the LCR historically was shaped by main stem and tributary riverflows and also by their sediment transport, interacting with surficial geology and flood plain vegetation. The historic macrohabitat structure 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, the macrohabitat structure 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.

Valdez et al. (2012a) provide a detailed review of macrohabitat types and conditions in areas of RASU activity during different life stages. Valdez et al. (2012a – table 3 and figure 4) in particular provide quantitative data on the average hydraulic gradient of the major river reaches in the Colorado River Basin with histories of use by RASU, along with a rating of the intensity of current use by RASU. Table 8 summarizes this information, adds a rating to indicate historic use for reaches without current use, and updates several entries (see footnotes to table 8). See Valdez et al. (2012a) for the detailed list of citations supporting this categorization. Table 8 indicates that RASU use of main stem reaches by all life stages occurs or historically occurred predominantly along reaches with low average gradients (< 5 feet per mile [ft/mi]). Use of higher-gradient reaches varies among life stages. Valdez et al. (2012a) indicate that at least some of this variation relates to the availability of low-gradient habitat such as backwaters, embayments, and flood plain wetlands connected to the main channel, or relates to the presence of both high- and low-gradient sections within an overall reach.

MESOHABITAT STRUCTURE

***Full name*: The types, abundance, and spatial and temporal distributions of aquatic mesohabitats, including cover usable by RASU provided by these mesohabitats.** Mesohabitats are finer-scale (i.e., site scale) portions of macrohabitats that differ from each other in physical characteristics that affect RASU use of these settings. Relevant variables that distinguish mesohabitats include depth; horizontal and vertical form, including hydraulic gradient; flow velocity, direction, and turbulence; substrate characteristics, including size, shape, and stability; aquatic vegetation types and density; range of variation in turbidity; and proximity to other mesohabitats.

Valdez et al. (2012a) refer to the variables that distinguish mesohabitats as "microhabitat" characteristics (see table 5). Each combination of conditions among these variables constitutes a distinct setting that RASU and other aquatic species or life stages may find suitable (or unsuitable) for particular critical biological activities, such as foraging, resting/hiding, or spawning (Parasiewicz et al. 2008), or that affect drift path geometry.

Examples of mesohabitat types in the LCR ecosystem include bars, eddies, nearshore slackwaters, littoral and deltaic shallows, pools, islands, point-bars, riffles, and runs. Some authors alternatively refer to such features as macrohabitat types (e.g., Holden 1999; Budy et al. 2009) (see also "Macrohabitat Structure," this chapter). Mesohabitats may include features such as aquatic macrophytes, large woody debris, overhangs, interstitial spaces, and hollows that can provide cover for RASU of different life stages (Burke and Mueller 1993; Muth and Wick 1997; Mueller and Marsh 1998; USFWS 2002a; Mueller 2003, 2006; Mueller et al. 2007; Valdez et al. 2012a; LCR MSCP 2016a, 2016b). However, as Valdez et al. (2012a) note, the RASU literature rarely includes quantitative data for cover

Table 8.—RASU river gradient associations by life stage, after Valdez et al. (2012a)
Usage (association) ratings: H = high use; M = moderate use; L = little use; "-" = no use; X = historic but not current use; "?" = suspected.

River and reach ⬇	**Life stage ➔** / **Gradient ⬇**	Egg and pre-dispersal larval	Post-dispersal larval and younger juvenile	Older juvenile and subadult	Adult	Spawning adults
Green River						
Flaming Gorge Dam to Split Mountain	5.2–20.1 ft/mi	**-**	**-**	**L**	**L**	**-**
Split Mountain to Sand Wash	1.1–4.8 ft/mi	**H**	**H**	**H**	**H**	**H**
Desolation Canyon (Sand Wash to Green River)	9.8 ft/mi	**L?**	**-**	**L**	**L**	**L?**
Green River to Colorado River confluence	1.1–2.1 ft/mi	**L?**	**H**	**L**	**L**	**L?**
Upper Colorado River						
Rifle to Palisade	7.7 ft/mi	**-**	**-**	**-**	**M**	**-**
Palisade to Moab	5.1 ft/mi	**L?**	**H**	**L**	**H**	**L?**
Moab to Green River confluence	2.3 ft/mi	**-**	**-**	**-**	**L**	**-**
Cataract Canyon	10 ft/mi	**-**	**-**	**-**	**-**	**-**
Lake Powell	Impoundment	**-**	**L**	**L**	**L**	**-**
San Juan River						
Navajo Dam to Animas River	9.2 ft/mi	**-**	**-**	**-**	**-**	**-**
Animas River to Bluff	7.4 ft/mi	**H**	**L**	**M**	**H**	**H**
Bluff to Clay Hills (Lake Powell inflow)	8.3 ft/mi	**-**	**H**	**L**	**L**	**-**
Lower Colorado River						
Grand Canyon (Glen Canyon Dam to Lake Mead inflow)[1]	15.4 ft/mi	**L**	**L**	**L**	**L**	**L**
Lake Mead	Impoundment	**H**	**H**	**H**	**H**	**H**
Lake Mohave	Impoundment	**H**	**H**	**H**	**H**	**H**
Lake Havasu	Impoundment	**H**	**H**	**H**	**H**	**H**
Parker Dam to Gulf of California[2]	1.0-1.5 ft/mi	**X**	**X**	**X**	**X**	**X**
Gila River						
Arizona/New Mexico line to San Carlos Lake[2]	12.4 ft/mi	**X**	**X**	**X**	**X**	**X**
Coolidge Dam to Salt River[2]	8.7 ft/mi	**X**	**X**	**X**	**X**	**X**
Salt River to Colorado River confluence[2]	3.5 ft/mi	**X**	**X**	**X**	**X**	**X**
Salt River	—	**-**	**-**	**L**	**M**	**-**
Verde River	—	**-**	**-**	**L**	**M**	**-**

Note 1: Usage ratings updated with recent information on RASU occurrence in all life stages in western Grand Canyon (Reclamation 2017).

Note 2: Usage ratings updated to indicate historic use (see also chapter 1).

conditions, mostly noting only the types of conditions that RASU seek for cover in different life stages. The present CEM recognizes this pervasive lack of quantitative data on cover conditions in its rating of link understanding of the effects of mesohabitat conditions on other components of each life-stage model.

RASU exhibit strong fidelity to individual or a very few spawning sites (Tyus and Karp 1990; Modde and Irving 1998; USFWS 1998; Mueller et al. 2000; LCR MSCP 2008; Wydoski et al. 2010; Wydoski and Lantow 2012) and to overwintering sites (Mueller et al. 2000). RASU presumably select these locations for some suite of characteristics among the available mesohabitats.

As noted earlier (see "Drifting," chapter 3), channel sections along which lateral and reverse currents draw drifting larvae out of the main downstream flow path into low-velocity settings constitute a distinct type of mesohabitat. This document suggests referring to such settings as "interception habitat," as discussed under "Drifting," chapter 3. 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.

The mesohabitat structure along the LCR historically was shaped by the same factors that shaped macrohabitat structure, but at finer spatial scales, such as by main stem and tributary riverflows and their loads of sediment and snags interacting with flood plain vegetation and geology. The sizes and distribution of large woody debris historically also affected the types, distribution, and stability of mesohabitats along the LCR (Minckley and Rinne 1985; Mueller and Marsh 2002; Utah Department of Natural Resources, Division of Wildlife Resources 2009). 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 structure similar to historic conditions presently occurs only in a few places where the channel is confined by bedrock and at tributary confluences. Otherwise, today, mesohabitat structure depends on main stem water storage-delivery system design and operations, tributary inflows, channel and shoreline engineering, and the effects of macrohabitat structure. Remnants of individual historic mesohabitat sites persist, and some may serve as spawning sites (Tyus and Karp 1990; Minckley et al. 1991; Modde and Irving 1998; USFWS 1998,

2002a; Mueller et al. 2000; Mueller 2006; LCR MSCP 2008; Schooley et al. 2008; Albrecht et al. 2010a; Patterson et al. 2012; Valdez et al. 2012a).

Valdez et al. (2012a) categorize all mesohabitat types associated with RASU activity during different life stages, and also by season for adults, based on a detailed literature review and survey of experts. Table 9 summarizes the findings from Valdez et al. (2012a – specifically their Chapter 3) – see Valdez et al. (2012a) for the detailed list of citations supporting this categorization.

Table 9.—RASU mesohabitat associations by life stage and, for adults, by season, after Valdez et al. (2012a)

Life stage ➔ / **Mesohabitat type 🡻**	Egg and pre-dispersal larval	Post-dispersal larval and younger juvenile	Older juvenile and subadult	Adults in spring	Adults in summer	Adults in fall	Adults in winter	Spawning adults
Cobble/gravel bars	X				X			X
Cobble/gravel shore, bays/coves	X							X
Cobble/gravel shore, tributary inflows	X							X
Deep eddies			X					
Deep pools			X			X		
Flood plain wetlands	X	X	X					X
Gravel pit ponds	X		X	X	X			X
High-velocity runs					X	X		
Inundated vegetation				X				
Low-velocity backwaters		X	X	X	X	X	X	
Low-velocity cove shallows		X						
Low-velocity eddies			X	X	X	X	X	
Low-velocity main stem shallow shores		X	X					
Low-velocity pools			X	X	X	X	X	
Low-velocity runs			X	X	X	X	X	
Low-velocity tributary-mouth shallows		X	X					
Pool edges							X	
Riffles					X			
Side channels				X	X	X	X	
Slackwaters							X	

The findings in table 9 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) present detailed classifications, but other studies use mesohabitat terms less formally. Different investigators may also use alternative terms to refer to essentially the same mesohabitat type, and terms may vary between the LCR and UCRB. For example, as shown in table 9, terms such as "slackwater" and "low-velocity" may refer to similar conditions, and investigators distinguish substrate types among mesohabitats only for spawning sites.

Table 9 also shows that reports of RASU mesohabitat associations sometimes qualify their labels for mesohabitat types with information on depth (e.g., "deep" pools, or tributary mouth "shallows") or "low-velocity" versus "high-velocity." 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). RASU use of different mesohabitats may vary with other conditions such as water temperature and turbidity, as discussed below, this chapter, and in chapter 3.

MONITORING, CAPTURE, HANDLING

Monitoring of RASU along the LCR often involves their capture by a variety of methods, followed by examination, tagging, and, in most cases, return to the waterbody from which they were captured. Detection and capture methods and their associated sampling designs vary in their suitability for different mesohabitats, in their likelihood of encountering RASU of different sizes and life stages, and presumably in their effects on captured individuals. Muth and Ruppert (1996), for example, report reduced egg viability among spawning RASU exposed to electrofishing fields. Hunt (2008), Mueller et al. (2008), and Hunt et al. (2012) discuss other possible impacts of RASU monitoring on RASU stress.

The RASU augmentation program (see also chapter 5) depends on the capture and removal of RASU larvae as they disperse from their natal sites in Lake Mohave and their transport to the USFWS Willow Beach National Fish Hatchery and Nevada Department of Wildlife-Lake Mead Fish Hatchery (LCR MSCP 2015, 2016a, 2016b; Kesner et al. 2016). Conceivably, this process of capture and transport could result in some mortality or at least mechanical stress among the captured larvae. Upon arrival at the hatcheries, the larvae are acclimated to the water temperatures of the hatchery rearing tanks, another opportunity for stress during the transition to the rearing environment. The hatchery does not keep records of mortality during transport or acclimation because it is very low and not noteworthy (G. Cappelli, personal communication to N. Rudd, 2017). Lake Mead hatchery data for January – May 2017 indicate a 0.3% mortality rate during transport and an additional 5.1% mortality rate during temperature acclimation (C. Burg, personal communication to N. Rudd, 2017).

The rearing facilities subsequently may acclimate their RASU to water temperatures and flow velocities similar to what the fish will encounter upon release (see "Pre-Release Conditioning," this chapter). Eventually, RASU that have grown sufficiently at rearing facilities are captured, place in tanks, transported to their designated release sites, and released. The LCR MSCP maintains and regularly reviews protocols to minimize stress to the RASU during transport and release because such stress potentially can affect survival among the freshly released individuals (Hawkins 2008; Schooley et al. 2008; Sykes 2013).

PRE-RELEASE CONDITIONING

***Full name*: The types and extent of pre-release conditioning of physiology and behavior among reared RASU.** This element refers to the pre-release conditioning of reared RASU to the range of environmental conditions they will encounter upon release, including flow velocities and water temperatures, food items, infectious agents, and predator attacks. Growing literature sources indicate or propose that such conditioning can increase survival among repatriated fishes, including RASU (Minckley et al. 1991; Mueller and Foster 1999; Mueller et al. 2000; USFWS 2002a; Mueller et al. 2003a, 2007; Ward and Hilwig 2004; Lee et al. 2006; Mueller 2006; Schooley et al. 2008; LCR MSCP 2006, 2008, 2015; Kegerries and Albrecht 2009; Avery et al. 2011; Valdez et al. 2012b, 2012c; Senger and Sjöberg 2011; Bestgen et al. 2011, 2012; Olson et al. 2012).

RASU are subject to two broad types of conditioning in their rearing environments, which this CEM proposes calling "ambient" and "adaptive" conditioning. The ambient rearing environment itself conditions the growing RASU to specific physical habitat dimensions, ranges of flow velocities, water temperatures, food items, and the spatial availability of foods (see "Foraging" and "Swimming," chapter 3). The rearing environments also necessarily are kept as free of infectious agents as possible. Further, the rearing environments are kept completely free of aquatic predators, although RASU in open-air facilities without protective covering are exposed to avian predators.

In turn, the LCR MSCP and its partners for several years have been exploring methods of adaptive conditioning, through which RASU are exposed to conditions more similar to what they will experience upon release in order to prepare them for life in these wild conditions. The LCR MSCP and its partners have expressed concerns about, and/or have ongoing or planned experiments to assess, whether and how best to pre-condition RASU to the physical scale and novelty of the environment into which they will be released, its range of water temperatures, the strength and stamina for swimming this environment will demand, and the presence and behaviors of aquatic predators. The following paragraphs discuss each of these topics in adaptive conditioning in turn.

Investigators have long reported that, immediately upon release, repatriated RASU tend to scatter over long distances, particularly in the downstream direction (Mueller and Marsh 1998; Foster and Mueller 1999; Mueller and Foster 1999; USFWS 2002a; Mueller et al. 2003a; Mueller and Burke 2005; LCR MSCP 2006; Valdez et al. 2012b, 2012c). This is generally termed a "fright response" to the novelty of the environment into which the RASU are released and possibly also to the stress of transport for release. No studies have sought to determine specifically what properties of the release environment trigger this response, but Valdez et al. (2012c) propos that "foreign chemical cues may cause individuals to become frightened and swim great distances in an attempt to locate a more familiar area."

Investigators have proposed reducing this unwanted response by releasing RASU initially into pens in the river, rather than directly into open waters, to allow them to acclimate to the novel environment for a few days (e.g., Valdez et al. 2012b). Foster and Mueller (1999), Mueller and Foster (1999), and Mueller et al. 2003a experimented with acclimating tagged RASU in holding pens in backwaters prior to release into Lake Powell and the Green River. These experiments compared the acclimated RASU to other tagged RASU released at the same time but without acclimation in holding pens. Both the acclimated and non-acclimated RASU dispersed rapidly upon release into the open environment, but within 2 weeks, the acclimated RASU either slowed, stopped, or reversed course, while the non-acclimated suckers continued to drift downstream. After 4 weeks, the originally acclimated RASU had cumulatively moved far less distance from the release site. After 2 months, the investigators concluded that site acclimation reduced both the range and rate of short-term dispersal. However, the experiments did not assess the effects of acclimation on survival.

The LCR MSCP, recognizing the implications of the earlier experiments, moved in 2006 to require the release of RASU only into backwater habitats and shoreline areas near weed beds to provide areas with cover where the fish can acclimate to ambient conditions (LCR MSCP 2006, 2015). RASU released in the UCRB also are routinely acclimated in pens for up to 24 hours (Furr 2014).

The LCR MSCP in 2015–16 also began formally testing whether initial acclimation of RASU for 3 days in net pens in backwater environments prior to release into the open environment specifically results in greater survival among repatriated RASU. The experiments involved the simultaneous release of batches of penned and control (non-acclimated) tagged RASU, several times per year, at three connected backwaters immediately above Lake Havasu, with subsequent analysis of survival based on tag contact data from system-wide monitoring. However, system-wide monitoring for tagged RASU released into the open LCR environment often does not recontact repatriated RASU for 3–5 years following release. Consequently, it will take several years for these experiments to develop sufficient data for any statistically reliable analysis of results (B. Blasius, J. Lantow, and J. Stolberg 2017, personal communications). The

LCR MSCP experiments with net pens are part of a larger program that involves investigating the effects of several variables on the stocking program, including the time of year at which releases take place, the time of day, and conditioning to water quality conditions, flows, and the presence of aquatic predators (Finnegan 2013).

Altered water temperatures initially (i.e., in the 1990s) were cited as one of the suspected causes of RASU declines in both the Upper and Lower Colorado River Basins following river regulation (Bozek et al. 1990; Minckley et al. 1991; USFWS 1991, 1994; Clarkson and Childs 2000). The hatcheries involved in the augmentation program for the LCR take care to acclimate the newly arrived larvae to hatchery water temperatures and maintain the temperatures throughout the rest of the rearing process in a range that supports greatest growth, within the limits of their abilities to control water temperatures using water heaters and the mixing of water surface and groundwater sources (O'Neill et al. 2011; Burg 2017; Cappelli 2017).[2] Data from Pond 10b at the USFWS's Southwestern Native Aquatic Resources and Recovery Center in Dexter, New Mexico (formerly the Dexter National Fish Hatchery & Technology Center) for March 31, 2016 – March 23, 2017, show that temperature in the pond ranged between 2.3 °C in February and 26.9 °C in July, with 5th and 95th percentiles of 5.7 and 25.7 °C, respectively (Knight 2017). However, the resulting rearing temperatures at the time RASU are collected for release may not match the temperatures at the individual release sites, which vary with the effects of hypolimnetic releases from dams, air temperatures, and mixing.

As Valdez et al. (2012c) note, "[t]raditionally and historically, [RASU] transported to a release site were simply released with perhaps only attempts to adjust the temperature of the water in the holding tank to the approximate temperature of the receiving water. Small RASU that have been released directly into receiving waters have experienced low survival, although all factors affecting survival of stocked fish are not fully understood." Experiments during the 1990s with the acclimation of reared RASU in backwater pens prior to release were motivated in part by concerns that RASU needed time to adjust to the difference in temperature between rearing and open environments (Mueller and Foster 1999). Nesler et al. (2003), the LCR MSCP (2006), and Schooley et al. (2008) subsequently explicitly recommend that, prior to release, all reared RASU

[2] For example, Cappelli (2017, personal communication) states, "The larvae arrive in river water, in January – April, which is typically 50–60 degrees F (°F) [10–15.5 °C]. Then they are slowly acclimated in our 10-gallon aquaria to our 77 °F [25 °C] water. This is done over a matter of many hours. The larvae are reared in 77 °F water [25 °C] for 2 weeks, then they are put into larger cement raceway-type tanks. We try to keep the water in the cement tanks at 77 °F [25 °C] also, but due to the volume of water we must deliver to the tanks, we have recently given up on heating because our heaters cannot keep up. We are gaining 1 °F [0.5 °C] running six heaters 24 hours a day. So short answer, they are in 77 °F [25 °C] water for 2 weeks then reared inside for approximately 5 months on 63 °F [17 °C] well water."

should be acclimated to the water conditions – including temperatures – they would experience upon release in order to reduce stress and its potential effects on survival following release.

As discussed and documented both above (see "Thermal Stress," chapter 3) and below (see "Water Temperature," this chapter), RASU in every life stage experience physiological impairment, developmental delays, stress, and mortality from exposure to water temperatures outside their ranges of preference or tolerance. The most frequently mentioned impacts of exposure to water temperatures outside their ranges of preference in different life stages are slower rates of growth, slower movement, or movement into either cooler or warmer mesohabitats depending on whether they faced waters warmer or cooler than their normal preferences (Bozek et al. 1984, 1990; Ryden 2000c; Bestgen 2008; LCR MSCP 2008, 2016a; Valdez et al. 2012a; Marsh et al. 2015). Altered water temperatures may also exacerbate the effects of other stressors such as altered pH or extremely low concentrations of DO (Burke and Mueller 1993; LCR MSCP 2015, 2016b).

The need for pre-conditioning reared RASU to the water temperatures of the open environment perhaps could be challenged by noting that RASU encountered a wide range of temperatures across their the historic geographic range, from rivers emerging from the western side of the Rocky Mountains to the Colorado River delta. RASU in these environments would have faced temperatures approaching 0 °C in winter and over 30 °C in summer (see chapter 1). Variability in growth rate, variability in movement rate, and movement from less- to more-hospitable waters appear to be part of a wide adaptive repertoire that allowed RASU to occupy such a wide range of environments, even while apparently preferring warmer waters overall. RASU appear to experience significant thermal stress or mortality only from extreme winter and summer temperatures (Valdez et al. 2011). However, the fact that RASU can tolerate environments with a wide range of temperatures and patterns of temperature variation does not itself indicate how well RASU can adjust to rapid changes in temperature or whether rapid changes in temperature may result in stress, disorientation, or other adverse effects. Further, the difference in temperature that reared RASU may experience upon release may be larger and more rapid than any changes the fish might experience under natural conditions.

Nevertheless, the literature does not provide sufficient information to assess the potential effects of thermal pre-conditioning for released RASU with high confidence. The LCR MSCP experiments with net pens (see above) may not be able to help distinguish whether acclimation specifically to the water temperatures of their new, open environment is more or less important than acclimation to the water chemistry, lighting conditions, mesohabitat structure, distribution of foods, and flows of this environment, or for reducing RASU fright, disorientation, or stress upon release. However, such a distinction may not be either necessary or useful for adaptive management of release practices.

Some investigators also have proposed that RASU may develop surfacing behaviors during rearing, in response to feeding practices, and that such behaviors also may make repatriated RASU more vulnerable to avian predators following release (Schooley et al. 2008). However, this idea is not presently under investigation, and the literature does not report proposals for ways in which to adaptively condition RASU to the range of foods and spatial distributions they will encounter after release.

Additionally, as noted above (see "Swimming," chapter 3), the LCR MSCP and its partners for several years have been exploring the possibility that repatriated RASU may lack stamina for long-distance movement initially following release and lack strength for avoiding predators (Mueller and Marsh 1998; Mueller and Foster 1999; Mueller et al. 2003a, 2007; Ward and Hilwig 2004; Kegerries and Albrecht 2009; Avery et al. 2011; Senger and Sjöberg 2011). The potential benefits of conditioning swimming abilities among reared RASU prior to release also are the subject of ongoing research and experimentation, focused on finding ways to achieve large-scale conditioning (Avery et al. 2011; Finnegan 2013; Cappelli 2015, 2016; LCR MSCP 2014, 2015, 2016b; Garnett 2016).

As also noted above (see "Predation," chapter 3), the LCR MSCP and its partners for several years have discussed and explored the possibility that adaptive pre-conditioning might help repatriated RASU better avoid predators (Mueller et al. 2003a, 2007; Schooley et al. 2008; Olson et al. 2012; Ward and Figiel 2013; O'Neill and Stewart 2015; O'Neill et al. 2016; Mann et al. 2017). Experiments indicate that RASU can be conditioned to detect and avoid predators and that RASU have means for communicating to each other when one detects the presence of a predator. Such pre-conditioning remains experimental, and limited to small scales involving only a few RASU at a time, but with interest in developing means for scaling up.

It should also be noted that the release of RASU – whether into holding pens in backwaters or directly into the open environment – involves the capture of RASU at their rearing facilities, transfer to tanks for transport, transport to their designated release sites, and release. The LCR MSCP maintains and regularly reviews protocols to minimize stress to RASU during transport and release because such stress potentially can affect survival among the freshly released individuals (Hawkins 2008; Schooley et al. 2008; Sykes 2013).

SUBSTRATE TEXTURE/DYNAMICS

***Full name*: The abundance, spatial distributions, and stability of substrate types (textures).** This element refers to the size distribution of particles and interstices in the benthic substrate within mesohabitats; substrate dynamics such

as the frequency and magnitude of shifting, scour, and burial; substrate particle embeddedness and stabilization by biofilms; and other potentially ecologically important features of the substrate. These features may affect substrate suitability for RASU spawning and embryo development, suitability as resting/hiding habitat for free-swimming individuals, and the composition and quality of the associated benthic invertebrate assemblage.[3] As noted earlier, for example, the literature on RASU recognizes a strong fidelity to spawning sites with gravel and cobble substrates within a limited range of depths. The abundance and distribution of substrates along the LCR today depend on main stem water storage-delivery management, tributary inflow, and mesohabitat structure, the latter of which in turn depends on numerous other controlling factors and habitat elements as discussed above and in other chapters of this document. Valdez et al. (2012a) categorize substrate types associated with RASU activity during different life stages, and also by season for adults, based on a detailed literature review and survey of experts. Table 10 summarizes the findings from Valdez et al. (2012a – specifically their Chapter 4) – see Valdez et al. (2012a) for the detailed list of citations supporting this categorization.

Unfortunately, the literature on RASU, including the literature used by Valdez et al. (2012a) to develop the information in table 10, does not consistently indicate what particular features make a given substrate attractive or unattractive to RASU for particular activities in different life stages. For example, the literature does not explicitly indicate what particular features of the substrate make any one site attractive for spawning compared to other sites with similar substrates (compare Minckley et al. 1991; Modde and Irving 1998; USFWS 1998, 2002a; Mueller 2006; LCR MSCP 2008; Schooley et al. 2008; Albrecht et al. 2010a, 2010b; Bestgen et al. 2011, 2012; Patterson et al. 2012; Valdez et al. 2012a).

Part of the difficulty in formulating hypotheses concerning RASU interactions with substrates stems from limitations in how the literature reports substrate data. Few of the reports listed in table 10 provided either measurement values or citations to indicate the size criteria (particle size ranges) used to distinguish "cobble," "gravel," "sand," or "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 (Allan and

[3] Theoretically, the presence/absence or intensity of hyporheic discharge also might affect substrate suitability for use by some RASU life stages. For example, hyporheic discharge might shape the spectrum of benthic organisms in different substrate settings (mesohabitats) along the LCR, as it does in other alluvial river settings (Hancock et al. 2005; Boulton et al. 2010), or it may affect substrate suitability as resting/hiding or spawning habitat, as has been observed for salmonids in other river systems (Geist et al. 2008; Kondolf et al. 2008; Tonina and Buffington 2009). However, the literature on RASU habitat requirements (e.g., Valdez et al. 2012a) does not address this topic.

Table 10.—RASU substrate associations by life stage, after Valdez et al. (2012a)
(X = frequent use; x = occasional use)

Life stage ➔ / **🡻 Substrate type**	Egg and pre-dispersal larval	Post-dispersal larval and younger juvenile	Older juvenile and subadult	Adult	Spawning adults
Bedrock			x	x	
Boulder			x	x	
Cobble	X				X
Cobble/gravel	X				X
Cobble/gravel/sand	X		X	X	X
Gravel	X				X
Gravel/sand		X			
Gravel/sand/silt	X		X	X	X
Sand/silt			X	X	
Silt dominant		X	X	X	

Castillo 2007), and numerous other ecologically relevant metrics such as substrate particle embeddedness can be applied to sediment (Fischenich 2006). As stated in LCR MSCP (2008), for example:

> *Bliesner and Lamarra (2005) measured substrate size and depth to embeddedness at a suspected razorback sucker spawning site on the San Juan River and compared the information with another nearby riffle. They found that the suspected spawning site had smaller substrate (average of 3.5 cm), deeper depth to embeddedness, and fewer fine materials than the control riffle. This suggests that razorback sucker may have narrower preferences for spawning habitat when given the opportunity to select a site than has been generally known.*

Table 10 shows significant differences in substrate preferences among the five life stages. With the exception of one anomalous report associating post-dispersal larval and younger juvenile with gravel and sand, all other reports associate this life stage with silt substrates. The single anomaly for post-dispersal larvae and younger juveniles appears in a report by Bozek et al. (1984) on larval habitat around the margins of Lake Mohave, an environment starved of silt by the presence of numerous upstream dams. The association of larvae and younger

adults with fine-grained substrates presumably results from their selection of nursery habitat settings with low velocities (see "Water Flow/ Turbulence," this chapter).

The substrate associations shown for eggs and pre-dispersal larvae in table 10 are identical to those shown for spawning adults because the former life stage necessarily plays out only at spawning sites. Table 10 documents the well-recognized attraction of spawning RASU to sites with predominantly cobble and gravel substrates with admixtures of sand. Older juveniles, subadults, and adults use the full spectrum of substrates available, including bedrock and boulder substrates. However, the majority of the studies reviewed by Valdez et al. (2012a), on which table 10 is based, did not use survey methods that produced statistically representative data on substrate conditions among macro- and mesohabitat types. Without such statistically representative sampling data or direct telemetric data, it is not possible to assess statistical preferences (Hightower et al. 2012).

As noted earlier in this report (see "Razorback Sucker Reproductive Ecology," chapter 1; "Spawning," chapter 2; "Staging and Spawning," chapter 3), RASU spawning sites must provide substrates that remain inundated and 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. However, at the same time, RASU appear to prefer spawning sites with little or no fine sediment at the substrate surface. As noted in chapter 2, for egg settling and adhesion, RASU actions during spawning also serve to clean fines from the substrate surface. The evolutionary benefits of this avoidance or removal of fines have not been evaluated but could include ensuring the availability of interstitial spaces within which the eggs might be better protected from disturbance and predators, and ensuring unimpeded water movement over the eggs to deliver oxygen and remove wastes.

TURBIDITY

***Full name*: The magnitude and spatial and temporal distributions of turbidity.** This element refers to the turbidity at sites potentially used by RASU in each life stage and its pattern of variation over time (i.e., the turbidity regime in different macro- and mesohabitat settings). Historically, turbidity levels along the LCR and across its backwaters – including their variation over time and space – depended on main stem and tributary flows, channel and backwater geometry, and sediment loads. The Colorado River prior to its regulation was highly turbid, especially along its main channel and during flow pulses, with lower turbidity along channel margins and in off-channel settings (Ohmart et al. 1988; Minckley

1991; NRC 1991, 1999). RASU evolved in this environment, and turbidity therefore presumably affects – both directly and indirectly – several aspects of RASU 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). However, turbidity levels, the spatial extent and persistence of turbidity pulses, and their variation in the modern regulated river still depend on flow rates and turbulence, a habitat element affected by main stem water storage-delivery management, tributary inflows, and both macro- and mesohabitat structure. Specifically, elevated discharge from one of the dams or pulses of elevated discharge from tributaries may deliver pulses of suspended sediment to the river or one of its impoundments, resulting in episodes of elevated turbidity along the affected river reach. Other factors affecting turbidity levels, the spatial extent and persistence of turbidity pulses, and their variation in the modern regulated river include channel and shoreline engineering (LCR MSCP 2004), nuisance species introduction and management, and (in a feedback relationship) planktonic and benthic (periphyton) productivity.

Changes in the lake level, for example, can expose formerly submerged fine sediments, particularly in deltaic mesohabitats, where the exposed sediments are subject to "erosion and suspension by river currents and wave action, resulting in increased turbidity levels at the inflow" (Valdez et al. 2012a). Bioturbation of benthic sediments, such as by common carp during feeding and spawning (Rogers et al. 2008; Cucherousset and Olden 2011) or by mayfly larvae (Osterling et al. 2007), also may cause localized increases in turbidity for the duration of the disturbance. Nuisance species may also affect turbidity when algae form blooms or, conversely, when non-native quagga and zebra mussels filter out large amounts of plankton and POM.

Turbidity directly affects several critical RASU behaviors, such as foraging, navigating, resting/hiding, and predator avoidance; the rate of predation on RASU; and consequently RASU survival in all life stages, particularly among larvae (Minckley et al. 1991; USFWS 1998, 2002a; Johnson and Hines 1999; LCR MSCP 2008; Valdez et al. 2012a; Vaage et al. 2015). Vaage et al. (2015) found that elevated turbidity protected Colorado River native fishes, including RASU, from non-native fish predation more than any other environmental factor. The factors examined included turbidity, vegetative cover such as aquatic plants and flooded terrestrial vegetation, and rocky substrates. The study also found significant reductions in predation on Colorado River native fishes, including RASU, at turbidity levels as low as ≈ 5% of the median value (in Formazin Turbidity Units) observed in the Colorado River at Lees Ferry prior to river regulation (Vaage et al. 2015). Turbidity also can affect RASU indirectly by affecting planktonic and benthic (periphyton) productivity (see "Invertebrates and

Particulate Organic Matter," this chapter; "Competition and Predation," chapter 3; and "Mesohabitat Structure," this chapter) through its effects on light penetration and sighting distances.

Turbidity also may affect monitoring, capture, and handling of RASU for 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 fish by monitoring methods that require visual contact, including recovery of individuals stunned by electroshocking and (2) they attenuate transponder signals (recently Bestgen et al. 2007; Rogers et al. 2008; Stone 2010; Van Haverbeke et al. 2013).

WATER CHEMISTRY

***Full name*: The magnitudes and horizontal, vertical, and temporal distributions of water chemistry properties that affect RASU.** This element refers to the water chemistry at sites potentially used by RASU 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, several metals, and artificial organic compounds (Ohmart et al. 1988; Seiler et al. 2003; LCR MSCP 2004; Reclamation 2005, 2010, 2011b, 2011c; Hinck et al. 2007, 2009; Patiño et al. 2012). Contaminants in the LCR arrive from both point and non-point sources (see "Chapter 5 – Controlling Factors"). Water storage-delivery system design and operations (see chapter 5) also affect water chemistry, including salinity and DO concentrations, through their effects on reservoir operations and releases, diversions and flow management for off-channel wetlands and ponds, and well-water supply to ponds (see below). Numerous habitat elements affect water chemistry at any given location, particularly water depth, temperature, circulation, and their variation over time.

As discussed above – see "Chemical Stress," chapter 3 – RASU during different life stages are known or suspected to be vulnerable to stress from changes in water chemistry, either from direct exposure to harmful conditions in the water column or from the consumption of contaminants that have bioaccumulated in invertebrates on which RASU feed (USFWS 1994; Buhl et al. 1996; Buhl 1997; Wydoski and Wick 1998; Hamilton 1999, 2001a, 2001b, 2004, 2005a; Sappington et al. 2001; Tuttle and Orsak 2002; Dwyer et al. 2005; Reclamation 2005; Mueller 2007; Stolberg 2009, 2012). Cooke et al. (2005) report exposure to contaminants as a concern for suckers (Catostomidae) across North America in general.

Alterations to water chemistry along the LCR, specifically nutrient enrichment, also affect planktonic and benthic primary productivity (Ohmart et al. 1988; NRC 1991; Melis et al. 2010), which in turn affect turbidity. However, productivity

along the LCR may be more limited by the availability of phosphorus than that of nitrogen (Turner et al. 2011). As noted above (see "Invertebrates and Particulate Organic Matter," this chapter), the LCR MSCP has experimented with fertilizing off-channel habitats around the margins of Lake Mohave using both dissolved nutrients and POM. These experiments were conducted in order to determine if such mechanical fertilization stimulates primary and/or secondary productivity and thereby increases the quality and quantity of the natural resource base for grow-out-stage RASU (Loomis 2014). The results have been ambiguous, affected by high variability among test sites and within individual test sites over time, and impacts of poor water circulation, DO depletion during hot weather, and algal mat formation. As also noted above concerning invertebrates along the LCR, toxins released by golden alga blooms could also harm RASU in backwaters and other waterbodies with limited water circulation.

Pheromones and other olfactory cues in the water also provide RASU with much-needed information about their environment. As noted above (see "Staging and Spawning," chapter 3), some investigators have proposed that releases of pheromones are involved in triggering RASU spawning, although data are lacking (Mueller et al. 2008; Albrecht et al. 2010a). Investigators have also proposed that RASU release "alarm" or "fright" pheromones when they detect threats such as predators (Mueller 2006; LCR MSCP 2015; O'Neill et al. 2015).

Water chemistry may also affect RASU identification of and fidelity to spawning sites. Muth et al. (2000) propose and provide additional citations that "[n]atal imprinting on distinctive chemical odors may be involved in selection of spawning sites by adult RASU via olfactory recognition" (see also Valdez et al. 2012c).

WATER DEPTH

***Full name*: The spatial and temporal distributions of water depth.** This element refers to the depth of water covering habitat sites potentially used or avoided by RASU in each life stage and the ways in which depths vary over time and space. Depth may directly affect site suitability for RASU spawning, resting/hiding, 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 mesohabitat structure, water temperature or chemistry, flow velocities or turbulence, or the aquatic macrophyte and invertebrate biological communities. In turn, other factors, such as substrate texture/dynamics, turbidity, or mesohabitat structure may affect RASU use of settings with different depths. Depending on timing, changes in depth may be a cue for spawning (Albrecht et al. 2010b). The range of depths suitable for each life stage may also vary depending on whether the fish are in a reservoir or a flowing reach (e.g., as documented for spawning sites)

(USFWS 1998). Water depths along the LCR main stem depend almost entirely on channel and impoundment engineering and operational decisions at the dams above and within the LCR. Water depths in off-channel settings, including marshes and ponds, depend almost entirely on engineering and operational decisions affecting the intakes, water elevation control structures, and pumps used to control water levels in these features (see chapter 5).

Valdez et al. (2012a) refer to water depth as an important "microhabitat" characteristic of mesohabitats, and categorize the range of depths associated with RASU activity during different life stages and also by season for adults, based on a detailed literature review and survey of experts. Table 11 summarizes the findings from Valdez et al. (2012a – specifically their Chapter 4) – see Valdez et al. (2012a) for the detailed list of citations supporting this tabulation. Table 11 specifically tabulates the ranges of minimum and maximum depths reported among the numerous studies summarized by Valdez et al. (2012a) for each life stage and, for adults, by season. The depth associations shown for eggs and pre-dispersal larvae in table 11 are identical to those shown for spawning adults because the former life stage necessarily plays out only at spawning sites. The depth associations for post-dispersal larvae and younger juveniles presumably are for resting/hiding habitat during dispersal and nursery habitat following dispersal.

Table 11.—RASU depth (m) associations by life stage and, for adults, by season, after Valdez et al. (2012a)
(Values in parentheses are extreme outliers.)

Life stage ➔ / **Value ↓**	Egg and pre-dispersal larval; spawning adults	Post-dispersal larval and younger juvenile	Older juvenile and subadult; subadults in spring	Older Juvenile and subadult; adults In summer	Older juvenile and subadult; adults in fall	Older juvenile and subadult; adults In winter	Older juvenile and subadult; adults year round
Minimum depth, m	0.2–0.8 (2.75)	0.1–1.4	0.2–1.5	0.2–1.2 (9.1)	0.2–1.2 (9.1)	0.4–1.9	0.4–0.6
Maximum depth, m	1.0–5.5	0.2–6.1	0.8–6.1	1.9–3.0 (18.3)	1.2–3.0 (18.3)	1.1–6.1	0.4–3.4

Table 11 indicates a small number of extreme outlier values. Valdez et al. (2012a) list several studies in Lake Mead that report the depth of spawning as simply "< 2.75 m." No other study summarized by Valdez et al. (2012a) identifies a minimum depth greater than 0.8 m. However, the value 2.75 m is well within the range of maximum depth values reported in the other studies

reviewed. In turn, Valdez et al. (2012a) list a single study in Lake Mead (Albrecht et al. 2008) reporting large juveniles and adults at depths between 9.1 and 18.3 m during summer and fall. No other study summarized by Valdez et al. (2012a) identifies a minimum depth for this age class in summer and fall greater than 1.2 m, or a maximum depth for this age class in summer and fall greater than 3.0 m.

Table 11 indicates little variation in minimum depth of occurrence across life stages, except perhaps for a greater minimum depth of occurrence for older juveniles, subadults, and adults in winter. Older juveniles, subadults, and adults may occur at greater maximum depths than may post-dispersal larvae and younger juveniles. Spawning appears to occur within a narrower range of shallower depths than is the case with any of the other motile life stages. However, the majority of the studies reviewed by Valdez et al. (2012a), on which table 11 is based, do not report statistically representative data on depth associations that could be used to identify the ranges of depths avoided in comparison to the range used. Without such statistically representative sampling data or direct telemetric data, it is not possible to assess statistical preferences (Hightower et al. 2012). The apparent distribution of depths used by RASU in different life stages or seasons may be a consequence of their seeking out specific mesohabitats with specific ranges of flow velocities rather than seeking out specific depths per se (Minckley et al. 1991; Ryden 1999).

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 RASU in each life stage in the mesohabitats they occupy or through which they pass. Velocity fields may be large (e.g., spanning an entire interreservoir 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 (LCR MSCP 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 structure and substrate. Weather also affects flow/turbulence through the effects of storms on wave formation – a factor outside the scope of this CEM.

Valdez et al. (2012a) refer to flow velocity as an important "microhabitat" characteristic of mesohabitats and categorize the range of velocities associated with RASU activity during different life stages, and also by season for adults, based on a detailed literature review and survey of experts. Table 12 summarizes the findings from Valdez et al. (2012a – specifically their Chapter 4) – see Valdez et al. (2012a) for the detailed list of citations supporting this tabulation. Table 12 specifically tabulates the ranges of minimum and maximum velocities reported among the numerous studies summarized by Valdez et al. (2012a) for each life stage and, for adults, by season. The velocity associations shown for eggs and pre-dispersal larvae in table 12 are identical to those shown for spawning adults because the former life stage necessarily plays out only at spawning sites. The velocity associations for post-dispersal larvae and younger juveniles appear to be for resting/hiding habitat during dispersal and nursery habitat following dispersal.

Table 12 indicates little variation in the low end of the range of minimum velocities for RASU occurrence across life stages but indicates that the high end of the range of minimum velocities is highest (0.9 meter per second [m/s]) for spawning adults (and, consequently, for eggs and pre-dispersal larvae as well) – nearly twice as high as the comparable value for any other life stage or season. Table 12 also indicates that the high end of the range of maximum velocities is also highest (1.4 m/s) for spawning adults (and, consequently, for eggs and pre-dispersal larvae as well) – twice as high as the comparable value for any other life stage or season. Finally, table 12 indicates that the ranges of minimum and maximum velocities are identical for post-dispersal larvae and younger juveniles (0.0–0.06 m/s), much lower than that reported for any other life stage.

Table 12.—RASU velocity (m/s) associations by life stage and, for adults, by season, after Valdez et al. (2012a)

Life stage ➔ / **Value 🡻**	Egg and pre-dispersal larval; Spawning adults	Post-dispersal larval and younger juvenile	Older juvenile and subadult; adults in spring	Older juvenile and subadult; adults in summer	Older juvenile and subadult; adults in fall	Older juvenile and subadult; adults in winter	Older juvenile and subadult; adults year round
Minimum velocity, m/s	0–0.9	0–0.06	0–0.3	0–0.5	0–0.5	0–0.2	0.1
Maximum velocity, m/s	0.4–1.4	0–0.06	0.3–0.7	0.5–0.7	0.5–0.7	0.4–0.5	0.1–0.2

However, the majority of the studies reviewed by Valdez et al. (2012a), on which table 12 is based, do not report statistically representative data on velocity associations that could be used to identify the ranges of depths avoided in

comparison to the range used. Without such statistically representative sampling data, it is not possible to assess statistical preferences (Hightower et al. 2012).

Nevertheless, the literature indicates that RASU do seek out specific mesohabitats with specific ranges of flow velocities for different activities (Minckley 1991; Ryden 1999). As discussed above (see chapters 1–3), RASU may select sites for spawning that experience flows (1) strong enough to remove fine sediment and maintain a matrix of sand, gravel, and cobbles with an appropriate range of interstitial spaces but also (2) not so strong as to otherwise disturb the substrate matrix during the timespan between egg settling and larval swim-up. Similarly, post-dispersal larvae and younger juveniles may select sites as resting/hiding habitat during dispersal and nursery habitat following dispersal that experience only very low flow velocities against which these small life forms need exert very little effort to stay in place or move in search of food and safety.

In addition to field reports of RASU occurrences in relation to flow velocities, a second body of literature addresses laboratory studies of RASU swimming strength in relation to flow velocities (see "Swimming," chapter 3, and "Pre-Release Conditioning," this chapter) (Mueller and Marsh 1998; Mueller and Foster 1999; Mueller et al. 2003a, 2007; Ward and Hilwig 2004; Kegerries and Albrecht 2009; Avery et al. 2011; Senger and Sjöberg 2011). Ward and Hilwig (2004) examined the failure velocity of pond-reared RASU with an average size of approximately 140 mm TL. Failure velocity is the velocity at which an individual fish can no longer maintain its position in a flow chamber and is forced back by the flowing water. Ward and Hilwig (2004) found that the pond-reared RASU had an average failure velocity of 0.66 m/s before being subjected to experimental exercise to increase their stamina and 0.72 m/s after such conditioning. Mueller et al. (2007) measured the related variable – critical swimming performance – for pond-reared RASU, average size approximately 220 mm TL, and found similar values of 0.50 m/s before exercise and 0.53 m/s after exercise. Avery et al. (2011) used a slightly different method from the previous two experiments and observed average failure velocities of 0.63 m/s before conditioning and 0.88 m/s after. Avery et al. (2011) do not state the sizes of the tested RASU, but do state that they tested RASU that were mature enough for repatriation, for which the typical body size at that time was approximately 300 mm TL.

Comparison of the results of these three flow/stamina experiments in table 12 suggests that RASU may spawn at locations at which flow velocities exceed the failure velocities of reared RASU even after conditioning. However, the RASU used in the three experiments would all fall within the size range of subadults (see chapter 2). RASU presumably develop greater swimming strength and stamina as they mature as adults.

Finally, flow velocities potentially can affect the scientific study of RASU, 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. Hoffnagle et al. (1999) report such difficulties for fish surveys in general in the Grand Canyon, and Thieme (1997) and Beyers et al. (2001) reported such difficulties in the monitoring of other sucker species elsewhere in the Colorado River Basin.

Few studies of RASU specifically refer to or include information on flow turbulence other than to indicate whether locations where RASU occur contain eddies. As noted above (see "Mesohabitat Structure" and table 9, this chapter), older juveniles, subadults, and adult RASU all may use eddies. Further, as also noted above (see "Drifting," chapter 3), channel sections along which lateral and reverse currents draw drifting larvae out of the main downstream flow path into low-velocity settings constitute a distinct type of mesohabitat crucial to the successful movement of dispersing larvae into nursery habitat. Otherwise, the literature on RASU does not provide information on how RASU respond to or position themselves in relation to turbulence.

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 RASU 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 temperature along the river and within its lakes depends strongly on operational decisions at the dams above and within the LCR, which affect the temperature of dam releases and also water depths (Clarkson and Childs 2000), which in turn affect thermal gradients in the reservoirs. Similarly, groundwater pumped into refuge ponds can alter water temperatures within these isolated waters.

As discussed above – see "Thermal Stress," chapter 3 – RASU in every life stage are vulnerable to physiological impairment, developmental delays, stress, and mortality from exposure to water temperatures outside their range of tolerance (Bozek et al. 1990; Minckley et al. 1991; USFWS 1998; Clarkson and Childs 2000; Mueller et al. 2005; Mueller 2006; Bestgen 2008; LCR MSCP 2008; Bestgen et al. 2011). For example, the speed and success rate for RASU embryo maturation falls off at water temperatures above and below the optimal range of 15–25 °C (Marsh 1985). Water temperature and its variation also may affect RASU indirectly through their effects on other habitat elements such as water chemistry, infectious agents, the abundance and diversity of plankton and benthic organisms, and predator and competitor activity.

Valdez et al. (2012a) refer to water temperature as an important "microhabitat" characteristic of mesohabitats and categorize the range of temperatures associated with RASU activity during different life stages and, for adults, also by season, based on a detailed literature review and survey of experts. Table 13 summarizes the findings from Valdez et al. (2012a – specifically their Chapter 4) – see Valdez et al. (2012a) for the detailed list of citations supporting this tabulation.

Table 13 specifically tabulates the ranges of minimum and maximum water temperatures reported among the numerous studies summarized by Valdez et al. (2012a), for each life stage and, for adults, by season. The temperature associations shown for eggs and pre-dispersal larvae in table 13 are identical to those shown for spawning adults because the former life stage necessarily plays out only at spawning sites. The temperature associations for post-dispersal larvae and younger juveniles appear to be for resting/hiding habitat during dispersal and nursery habitat following dispersal.

Table 13.—RASU temperature (°C) associations by life stage and, for adults, by season, after Valdez et al. (2012a)
(Values in parentheses are extreme outliers.)

Life stage ➔ / **Value ⬇**	Egg and pre-dispersal larval; spawning adults	Post-dispersal larval and younger juvenile	Older juvenile and subadult; adults in spring	Older juvenile and subadult; adults in summer	Older juvenile and subadult; adults in fall	Older juvenile and subadult; adults in winter
Minimum temperature, °C	6.0–14.4	11–21.7 (34.0)	7.8–10.9	7.8–15.0	0.0–11.5	0.0–1.3
Maximum temperature, °C	14.8–27.0	15.0–29.0 (34)	14.8–27.0	12.5–27.0	10.5–27.0	4.3–10.5

Table 13 indicates one outlier value, corresponding to a record of two young juvenile RASU collected in shallow (0.1–0.2 m) and slack (0.0 m/s) water at 34.0 °C, reported by Gutermuth et al. (1994) for the Lower Green River on July 30, 1991. No other study summarized by Valdez et al. (2012a) records the presence of young juvenile RASU in water warmer than 29.0 °C. However, RASU prefer shallow, low-velocity settings as nursery habitat for post-dispersal larvae and younger juveniles, including settings only slightly connected to the main flow path of the river (see chapters 2 and 3). Such settings would be expected to develop higher temperatures during the months following the arrival

of dispersing larvae in spring. The ranges of minimum and maximum temperature reported for this life stage, shown in table 13, in fact are higher than the ranges reported for any of the other life stages in any season.

Table 13 shows a wide range of minimum and maximum temperatures at spawning sites during spawning events. However, this wide range does not necessarily contradict the idea that temperature plays a role in triggering spawning activity. RASU could ripen and spawn in response to a *relative change* in temperature rather than to the absolute temperature per se (see "Staging and Spawning," chapter 3). This could occur even in isolated ponds, where air temperatures rather than seasonal changes in riverine water temperature would be the main determinant of water temperature.

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 eight immediate controlling factors that lie within the scope of potential human manipulation (table 14).

Table 14.—Controlling factors and the habitat elements they directly affect

Habitat elements ➔ / **Controlling factors ⬇**	Aquatic macrophytes	Aquatic vertebrates	Birds and mammals	Genetic diversity	Infectious agents	Invertebrates and POM	Macrohabitat structure	Mesohabitat structure	Monitoring, capture, handling	Pre-release conditioning	Substrate texture/dynamics	Turbidity	Water chemistry	Water depth	Water flow/turbulence	Water temperature
Channel and off-channel engineering							X	X				X		X		
Motorboat activity											X				X	
Non-RASU fisheries		X			X											
Nuisance species introduction and management	X	X	X		X	X										
RASU monitoring and conservation programs				X					X	X						
Tributary inflows						X	X	X			X	X	X		X	X
Wastewater and other contaminant inflows					X	X						X	X		X	X
Water storage-delivery system design and operations											X	X	X	X	X	X

The eight controlling factors identified in this CEM do not constitute individual variables; rather, each identifies a suite of variables (including human activities) that share specific features that make it useful to treat them together. Table 14 identifies the habitat elements that each controlling factor affects *directly*.

Controlling factors also may affect individual habitat elements indirectly, through the effects of habitat elements on each other (see chapter 4) or through the effects of one controlling factor on another. The present CEM recognizes two controlling factors that directly affect other controlling factors. Briefly (see below, this chapter, for details), non-RASU fisheries affect nuisance species introduction and management, and water storage-delivery system design and operations affect channel and off-channel engineering. The effects of controlling factors on each other and on habitat elements are the same for all five RASU life stages.

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 (LCR MSCP 2004). These activities strongly shape the macro- and mesohabitat structure and moderately shape depth profiles throughout the system. However, there are few areas of active mechanical shaping along channel and off-channel habitats, and only 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 RASU (LCR MSCP 2004). However, the effects will be localized and brief due to the limited flow velocities present in the regulated LCR.

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 river reaches potentially occupied by RASU 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.

NON-RASU FISHERIES

This factor addresses State management of fisheries other than RASU along the LCR, including management of sport fishes and other fish species covered under the HCP. 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 bait and forage species to support the sport fisheries. These bait and forage species may be caught as sport fishes and may also be considered (by the States) to be nuisance species. Arizona lists the official sport fishes for the State (https://www.azgfd.com/fishing/species/) and State records for any caught along the LCR (https://www.azgfd.com/Fishing/records/).

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 RASU, 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 III 1991; Mueller and Marsh 2002; Minckley et al. 2003; Marsh and Pacey 2005; Clarkson et al. 2005). Table 7 lists non-native sport species introduced into the LCR ecosystem and species introduced as bait or forage species for the sport fisheries, and it indicates whether the species are known to prey on or compete with RASU or could be proposed as predators or competitors based on their feeding ecology. Infectious (including parasitic) organisms that are known to infect RASU 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 RASU. Three of these are covered under the HCP (LCR MSCP 2004) – FLSU, humpback chub (*Gila cypha*), 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 of RASU.

Recreational anglers also could have effects on RASU. However, anglers do not specifically target RASU, and the species ignores efforts to take it by line. On the other hand, anglers also are known to transplant desired sport or forage/bait fishes to waterbodies where they appear to be absent and where RASU may be present.

NUISANCE SPECIES INTRODUCTION AND MANAGEMENT

This factor addresses animals and plants introduced into LCR waters and wetlands that affect RASU survival or reproduction but are not officially managed by the States for recreation or as bait or forage species for a sport fishery. The introductions may have occurred intentionally or accidentally. As noted above (see "Aquatic Macrophytes," "Aquatic Vertebrates," and "Invertebrates and Particulate Organic Matter," chapter 4), introduced nuisance species along the LCR include plants, amphibians, crustaceans, mollusks, and fishes. The potential list of species in this group also 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 RASU during one or more life stages; cause other alterations to the aquatic food web that affect RASU; alter water chemistry; or affect physical habitat features such as cover, substrate stability, or turbidity. Interactions of nuisance species with RASU 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 form dense mats along shorelines that block sunlight and reduce DO levels (McFarland et al. 2004; NISIC 2017).

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

- Asian clams, quagga mussels, and zebra mussels 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 aquatic 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) report a possible positive relationship between common reed expansion and non-native American bullfrog productivity.

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

- Nuisance fish species, including threadfin shad (*Dorosoma petenense*), red shiner (*Notropis lutrensis*), western mosquitofish (*Gambusia affinis*), and fathead minnow (*Pimephales promelas*) likely prey on and/or compete with RASU (see table 7).

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 RASU 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).

RASU MONITORING AND CONSERVATION PROGRAMS

The U.S. Department of the Interior classified RASU as an endangered species (per the U.S. Endangered Species Act of 1973) in 1991, identified the LCR ecosystem as part of the critical habitat for the species, approved a recovery plan for the species in 1998, and approved recovery goals in 2002 (USFWS 2002a). An unofficial group of Federal and State agencies, universities, and private interests, known as the Lake Mohave Native Fishes Work Group, began a systematic program of RASU monitoring and conservation along the LCR in the early
1990s. Lead responsibility for these efforts shifted in 2005 to the LCR MSCP, a partnership of Reclamation, the USFWS, Tribes, the three states that border the LCR, and a large community of other interested parties. The monitoring and conservation actions of the LCR MSCP focused on RASU are guided by its Final Habitat Conservation Plan, approved in 2004 (LCR MSCP 2004). These actions include the creation and management of off-channel habitat, population augmentation with controls to maintain genetic diversity, and extensive monitoring and research to support adaptive management of these actions. Valdez (2012a, 2012b, 2012c), Marsh et al. (2015), and Kesner et al. (2016) summarize the history of efforts to conserve RASU across their remaining range, including in the LCR ecosystem. The LCR MSCP annually publishes a

combined final implementation report, fiscal year work plan and budget, and accomplishment report for the previous fiscal year (e.g., LCR MSCP 2016b) that describes in detail the activities of the program.

As noted above (see "Monitoring, Capture, Handling," chapter 4), monitoring of RASU along the LCR often involves their capture by a variety of methods, examination, tagging, and, in most cases, return to the waterbody from which they were captured. Detection and capture methods and their associated sampling designs vary in their suitability for different mesohabitats, in their likelihood of encountering RASU of different sizes and life stages, and presumably in their effects on captured individuals.

As also noted above (see "Monitoring, Capture, Handling," chapter 4), the augmentation program depends on the removal of RASU larvae as they disperse from their natal sites and their transport to one or more rearing facilities – mostly to the USFWS Willow Beach National Fish Hatchery (LCR MSCP 2015, 2016a, 2016b; Kesner et al. 2016). While under the care of the rearing facilities, RASU may be acclimated to water temperatures and flow velocities similar to what they will encounter upon release in order to condition them for release (see "Pre-Release Conditioning," chapter 4). Subsequently, RASU that have grown sufficiently at rearing facilities are captured, place in tanks, transported to their designated release sites, and released. The LCR MSCP maintains and regularly reviews protocols to minimize stress to RASU during transport and release (Hawkins 2008; Schooley et al. 2008; Sykes 2013).

TRIBUTARY INFLOWS

Almost all 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 River into Lake Havasu, and the Gila River into the Colorado River 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.

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 all of these reasons, RASU 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 and small municipal wastewater systems. The largest of these inputs comes from Las Vegas via the Las Vegas Wash, which flows into Lake Mead and is recognized as a major source of several metal and organochlorine contaminants affecting waters not only in Lake Mead but also far downstream (Patiño et al. 2012). The Clark County (Nevada) Water Reclamation District, Laughlin Wastewater Reclamation Facility, discharges into Reach 3 between Davis Dam and Lake Havasu. Bullhead City, Arizona, and both Needles and Blythe, California, also operate municipal wastewater facilities but discharge their effluent into infiltration ponds rather than directly into the river. The Colorado River Sewage System Joint Venture, which serves Parker, Arizona, and the Colorado River Indian Tribes, discharges into an irrigation return canal that flows directly into the Colorado River. The river also receives storm runoff from all developed areas along its course and reservoirs; Lake Havasu also 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 from Reach 3 below Davis Dam downstream (Seiler et al. 2003; LCR MSCP 2004; Reclamation 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).

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

WATER STORAGE-DELIVERY SYSTEM DESIGN AND OPERATIONS

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 (LCR MSCP 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 dams along the river release sediment-free, hypolimnetic water, resulting in tailwater flows with no turbidity and unique chemistry and thermal ranges that affect the water chemistry and temperature for some distance downstream (LCR MSCP 2004).

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 of surface and groundwater pumping to deliver water.

Chapter 6 – Conceptual Ecological Model by Life Stage

This chapter contains five sections, each presenting the CEM for a single RASU 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 also 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."

Constructing the CEM for each life stage involves identifying, assembling, and rating each causal link one at a time. Analyses of the resulting information for each life stage can then help identify 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. Analyses also can help identify which, among these potentially high-impact relationships, are not well understood.

All potential causal links – among controlling factors, habitat elements, critical biological activities and processes, and life-stage outcomes – affecting each life stage are recorded on a spreadsheet. This spreadsheet is then used to assign a unique identification number to each causal link, and to record information on the character and direction, magnitude, predictability, and scientific understanding for that link, along with the underlying rationale and citations for each life stage. The CEM for each life stage, as cataloged on its spreadsheet, is displayed in the form of a diagram. This diagram shows the controlling factors, habitat elements, critical biological activities and processes, and life-stage outcomes for that life

stage. The diagram labels each link with its unique identification number and displays information on the character and direction, magnitude, predictability, and 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 2 illustrates these conventions.

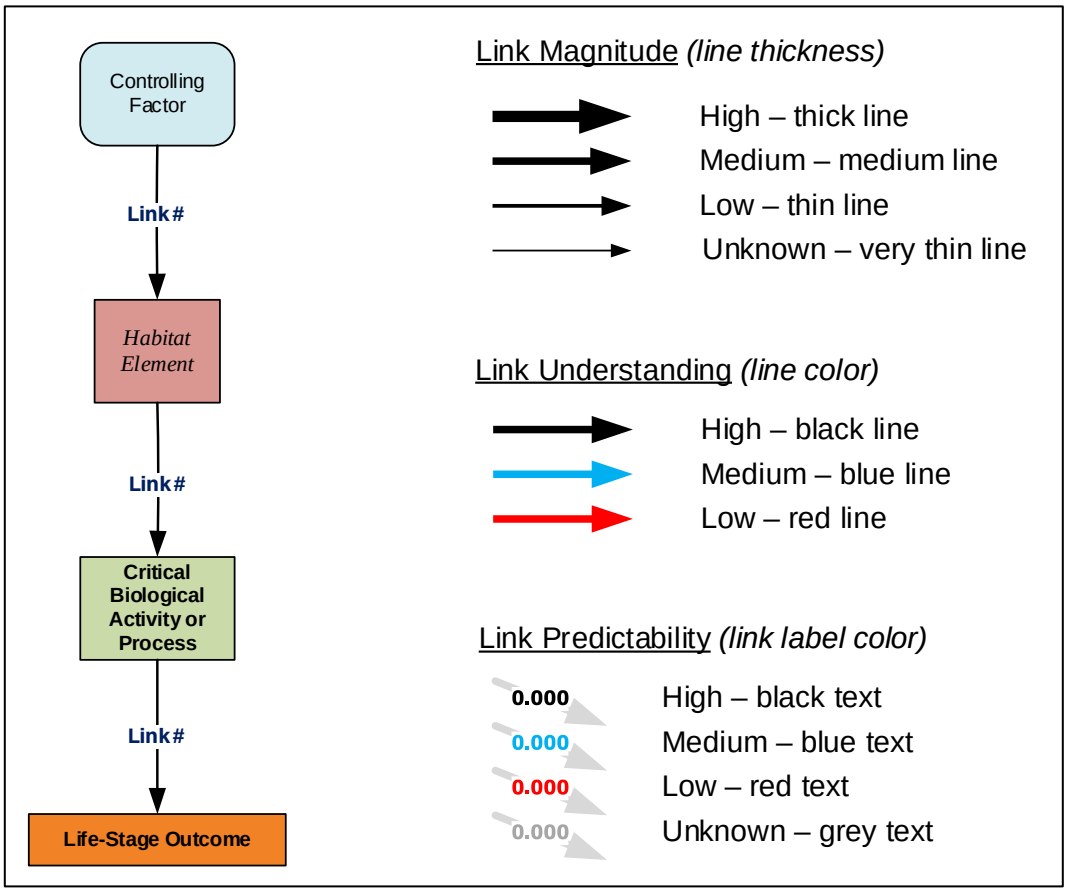


Figure 2.—Diagram conventions for LCR MSCP species CEMs.

The discussions of each life stage in this chapter, and the discussion 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.

RASU LIFE STAGE 1 – EGG AND PRE-DISPERSAL LARVAL LIFE STAGE

As described in chapter 2, this life stage begins when spawning adults release their gametes and depart, leaving the fertilized eggs to survive on their own, continues through egg incubation and hatching, and ends with larval swim-up and dispersal at approximately 12–14 mm TL. Incubation to hatching requires 6–7 days at 18–20 °C or 11 days at 15 °C. Maturation to swim-up requires an additional 12–13 days at 18–20 °C or 17–21 days at 15 °C. This life stage has a single life-stage outcome (see figure 1), egg and pre-dispersal larval survival.

The information reviewed for the present CEM identifies 7 (of 14) critical biological activities or processes affecting the single outcome for this life stage, as shown on figure 3 (see also table 2). However, the present CEM identifies only three of these seven critical biological activities or processes – egg settling and adhesion, predation, and thermal stress – with high-magnitude direct effects on egg and pre-dispersal larval survival. As noted above (see also attachment 1), magnitude refers to the degree to which a given factor controls some condition relative to other factors affecting that same condition. In the present instance, the CEM proposes that predation and thermal stress have greater effects on egg and pre-dispersal larval survival than do any other critical biological activities or processes.

Egg settling and adhesion directly affects egg survival simply because any disruption of the process of egg settling and adhesion potentially will result in damage to the egg or its exposure to sources of mortality. Egg settling and adhesion also affects egg and pre-dispersal larval survival indirectly through high-magnitude direct effects on predation. As discussed in chapter 3, RASU eggs are completely exposed to predation during the time it takes for them to descend the water column after release, settle to the bottom, and adhere to the substrate. The actions of spawning RASU may minimize this timespan by directly embedding eggs into the substrate. Subsequently, the shorter the time it takes for the eggs to adhere to the substrate, the shorter the time they are vulnerable to being easily dislodged by predators foraging along or pushing into the substrate.

The hypothesis that predation can strongly affect the survival rate for this life stage rests on the literature indicating that several invertebrate and vertebrate species may or are known to prey on RASU in this life stage (e.g., Bozek et al. 1984; Horn et al. 1994; Mueller 2006), including odonate larvae, channel catfish (*Ictalurus punctatus*), common carp, juvenile largemouth bass (*Micropterus salmoides*), bullfrogs and their tadpoles, and red swamp crayfish. All these species are ubiquitous in the LCR ecosystem, except in isolated ponds cleared of non-native aquatic fauna. RASU adults may also prey on RASU eggs, as they also may on BONY eggs (Mueller 2006).

The hypothesis that thermal stress can strongly affect survival for this life stage rests on two bodies of information. First, as noted above, water temperature significantly affects egg incubation and larval maturation. Second, RASU in the *next* life stage (post-dispersal larvae and younger juveniles) experience significantly decreasing rates of development at temperatures of 16.5 °C and lower, which this CEM defines as thermal stress. This CEM proposes extrapolating that inference concerning thermal stress back to the present life stage: Numerous authors (see Ehlo et al. 2015) have noted and continue to suggest that the lower water temperatures along the main stem LCR inhibit development and survival of RASU larvae. Off-channel ponds and refuges, with warmer waters, may not pose such challenges to egg or larval survival (Dowling et al. 2016a).

The present CEM identifies another of the seven critical biological activities or processes for this life stage, mechanical stress, as having medium-magnitude direct effects on egg and pre-dispersal larval survival. The present CEM proposes that mechanical stress has a greater effect on egg and pre-dispersal larval survival than do any other critical biological activities or processes *except for egg settling and adhesion, thermal stress, and predation*. This hypothesis rests on indications in the literature that physical disruptions of the substrate at spawning sites can disrupt egg maturation and larval development prior to swim-up. Such disruptions could result from mechanical disturbance by elevated flows or turbulence or by people or foraging aquatic fauna, or by a drop in water elevation leading to exposure and desiccation (Bozek et al. 1984). However, water regulation along the LCR and its backwaters and isolated ponds constrains the extent to which drops in water elevation can expose spawning sites to desiccation.

The present CEM also identifies two critical biological activities or processes that may affect the single outcome for this life stage either directly, or through effects on another critical biological activity or process, for which there is not sufficient information available to estimate the magnitude of the effect. First, unsuccessful predator attacks could damage eggs or pre-dispersal larvae, resulting in mechanical stress that affects survival. Although this is a reasonable hypothesis based on RASU ecology, the topic has not been addressed in the literature. As noted above, several predators likely consume RASU eggs. As a result, the potential exists for predator activity to damage the eggs, but whether this occurs, at what intensity or frequency, and whether it affects egg survival are all unknown. Second, numerous habitat factors could disrupt egg settling and adhesion, thereby again affecting survival. However, the literature does not indicate the extent to which RASU eggs in the LCR may experience disruption during egg settling and adhesion.

The present CEM identifies two habitat elements with a high-magnitude direct effect on predation, the aquatic vertebrate assemblage and turbidity. The literature provides numerous examples of predation on RASU eggs specifically by aquatic vertebrates. Bozek et al. (1984) document predation on BONY eggs

by channel catfish and common carp, although analyses of stomach contents confirmed this only for catfish. By analogy, this CEM hypothesizes predation on RASU eggs by these two species as well. Mueller and colleagues (Mueller et al. 2005; Mueller 2006) document predation on RASU eggs by RASU adults and by bullfrog adults and tadpoles. However, the overall abundance and diversity of aquatic vertebrate predators may not shape the rate of predation on this RASU life stage as much as does the simple presence of just one or two aquatic vertebrate generalist predators with an affinity for RASU eggs. It should also be noted that data on stomach contents will likely underrepresent consumption of RASU eggs and pre-dispersal larvae because the consumed materials disintegrate rapidly in the digestive system (Schooley et al. 2008; Ehlo et al. 2017). The activity of aquatic vertebrates, in turn, is controlled by other habitat elements, including turbidity, as discussed in chapter 7. However, turbidity also directly affects predation with high magnitude because it affects the ability of sight-feeding predators to detect and locate RASU eggs, including detecting and targeting the spawning RASU themselves.

The present CEM also identifies another habitat element with a medium-magnitude effect on predation, the aquatic invertebrate assemblage. Benthic macroinvertebrates in the LCR ecosystem include some, such as odonate larvae (Horn et al. 1994), which can prey on RASU larvae and therefore plausibly might also prey on RASU eggs at least once they settle to the substrate. Such invertebrate predators may be ubiquitous, including (or perhaps especially) in refuges. However, such macroinvertebrate predators may prefer mesohabitats with vegetative cover, and spawning sites are typically open habitat without emergent or submerged vegetation.

The present CEM identifies two habitat elements with high-magnitude effects on thermal stress, water temperature and genetic diversity. Studies indicate that rates of RASU development during this life stage are affected by water temperature, with an optimal temperature range for growth and development bracketed by upper and lower temperature ranges that limit growth and development. For purposes of this CEM, temperatures that inhibit growth and development are considered causes of thermal stress. As noted above, this hypothesis is largely an extrapolation from data on post-dispersal larvae for which the literature indicates an optimal temperature range of 19.5–25.5 °C (Bestgen 2008), with strong inhibition of development at temperatures of 16.5 °C and lower. RASU in this life stage may encounter waters in the colder, inhibiting range along the main stem LCR, the water temperatures of which are strongly influenced by hypolimnetic releases from dams, such as Lake Mohave (Bozek et al. 1990). RASU in this life stage may experience less thermal stress in shallow and/or off-channel settings that are not strongly connected to and influenced by main stem water temperatures.

The present CEM hypothesizes that genetic diversity has a high-magnitude effect on thermal stress during this life stage based simply on biological theory: The

genetic diversity of a population affects its resilience in the face of temperature variation. The greater the genetic diversity, the greater the likelihood that portions of the population will be able to tolerate or even benefit from altered water temperatures. However, the literature does not indicate whether or how genetic diversity actually matters for the health and survival of RASU in this or any other life stage.

The present CEM identifies only one habitat element, water depth, with a high-magnitude effect on thermal stress. As noted above, a drop in water elevation during this life stage could lead to exposure and desiccation of eggs and/or pre-dispersal larvae (Bozek et al. 1984). However, as also noted above, water regulation along the LCR and its backwaters and isolated ponds constrains the extent to which drops in water elevation can expose spawning sites to desiccation.

The present CEM identifies only one habitat element, substrate texture/dynamics, with a high-magnitude effect on egg settling and adhesion. The texture and stability of the substrate crucially affect the outcome of this process, as discussed in chapters 1, 2, 3, and 4.

Finally, the present CEM identifies one habitat element that potentially could directly affect one of the critical biological activities or processes with a high-magnitude impact on survival for which there is not sufficient information available to estimate the magnitude of the effect. The rate of predation on this life stage at any given location could depend on the overall level of activity of egg- and
larva-eating birds at that location and the ability of those avian predators that are present to forage under different conditions of turbidity and cover. However, the literature does not document the frequency or severity of avian predation on RASU eggs and larvae at spawning sites. The relationship is reasonable given the ecology of wading birds but only hypothetical for RASU in the LCR ecosystem.

The information reviewed for the present CEM (figure 3) indicates a low level of understanding of the effects of predation and mechanical stress on egg and pre-dispersal larval survival; the effects of substrate texture/dynamics on egg settling and adhesion; the effects of turbidity and aquatic invertebrates on predation; and the effects of genetic diversity on thermal stress for this life stage. That is, the literature presents insufficient information or shows little agreement concerning the character, magnitude, and/or predictability of the proposed causal relationships. In turn, the information reviewed for the present CEM indicates a medium level of understanding of the effects of thermal stress on egg and pre-dispersal larval survival, the effects of egg settling and adhesion and various properties of the aquatic vertebrate assemblage on predation, and the effects of water temperature on thermal stress. There appears to be a high level of understanding of the ways in which variation in water depth can result in mechanical stress.

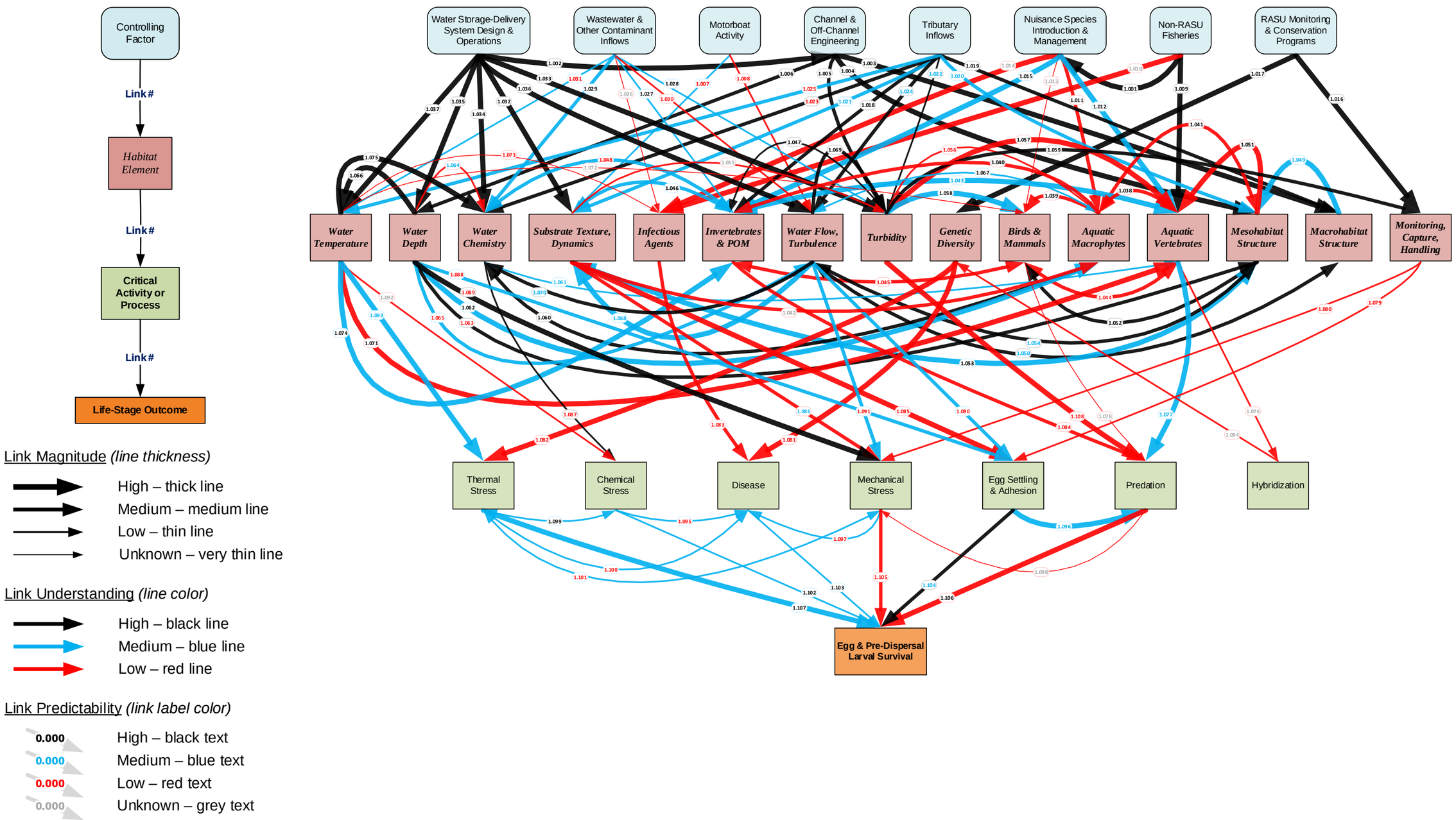


Figure 3.—RASU life stage 1 – eggs and pre-dispersal larval life stage, showing the relevant controlling factors, habitat elements, and critical biological activities and processes.

RASU LIFE STAGE 2 – POST-DISPERSAL LARVAL AND YOUNGER JUVENILE LIFE STAGE

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 additional changes during younger (Age-0) juvenile development, and ends with dispersal of juveniles beyond their nursery habitat after roughly their first year of life. This life stage has a single life-stage outcome, post-dispersal larval and younger juvenile survival (see figure 1). Under the LCR MSCP augmentation program, dispersing larvae are captured and transported to rearing facilities for growth and later repatriation as adults. The present CEM does not address the internal workings of the rearing program.

The information reviewed for the present CEM identifies 11 (of 14) critical biological activities or processes affecting post-dispersal larval and younger juvenile survival as shown on figure 4 (see also table 2). However, the present CEM identifies only two critical biological activities or processes that have direct, high-magnitude effects on post-dispersal larval and younger juvenile survival – predation and thermal stress. As noted above (see also attachment 1), magnitude refers to the degree to which a given factor controls some condition relative to other factors affecting that same condition. In the present instance, the CEM proposes that predation and thermal stress have greater direct effects on post-dispersal larval and younger juvenile survival than do any other critical biological activities or processes. Limited food supply and some physical habitat constraints also may affect survival, but with medium magnitude, as discussed below.

The hypothesis that predation can strongly affect survival for this life stage rests on two bodies of information. First, the literature indicates that several invertebrate and vertebrate species may or are known to prey on RASU in this life stage (e.g., Bozek et al. 1984; Horn et al. 1994; Mueller 2006), including odonate larvae, channel catfish, common carp, juvenile largemouth bass, bullfrogs and their tadpoles, and red swamp crayfish. All these species are ubiquitous except in isolated ponds cleared of non-native aquatic fauna. Second, RASU in this life stage outside of isolated, predator-free (or predator-reduced) settings apparently experience very high rates of mortality throughout their dispersal, which the literature mostly attributes to mortality from predation (e.g., most recently Ehlo et al. 2015, Marsh et al. 2015; Kesner et al. 2016).

The hypothesis that thermal stress can strongly affect survival for this life stage rests on evidence that RASU in this life stage experience significantly decreasing rates of development at temperatures 16.5 °C and lower, which this CEM defines as thermal stress. Numerous authors (see summary in Ehlo et al. 2015) have noted and continue to suggest that the lower water temperatures along the main

stem LCR inhibit development and survival of RASU larvae. Off-channel ponds and refuges, with warmer waters, may not pose such challenges to survival for this life stage (e.g., Dowling et al. 2016a).

The present CEM identifies three other critical biological activities and processes for this life stage – drifting, foraging, and resting/hiding – as having medium-magnitude direct effects on survival. That is, the present CEM proposes that these three critical biological activities or processes have greater effects on post-dispersal larval and younger juvenile survival than do any other critical biological activities or processes *except for thermal stress and predation*.

Several factors determine whether, after dispersing, drifting RASU larvae successfully reach suitable nursery habitat: the location and strength of currents they encounter as they disperse from their natal sites, the array of mesohabitat settings (with associated cover) past which these currents carry them as they drift, and the spatial proximity and accessibility of these mesohabitats. Drifting success for dispersing RASU larvae means being carried by currents that (1) transport them to and along mesohabitat types and conditions suitable for resting/hiding, foraging, avoiding predators, or resettling and (2) are not so strong as to prevent the larvae from controlling their movements in and out of different portions of the velocity field to allow them to move in and out of these other mesohabitats. The literature contains a growing number of hints that some combination(s) of such conditions that favor drift success might increase survival in this life stage in Lake Mead (e.g., Albrecht et al. 2010a, 2010b, 2010c; Kegerries et al. 2011). However, as discussed below, this literature mostly focuses on the ways in which drifting success may affect survival indirectly by minimizing vulnerability to predation. The concept of "interception habitat" introduced above (see chapters 3 and 4) addresses the direct effect of drifting success on survival. When present, such habitat conditions allow drifting larvae to reach nursery habitat without being swept into physically inhospitable environments.

Successful foraging is necessarily a key factor in survival in this life stage: RASU that do not forage successfully necessarily will be weaker and grow less rapidly, leaving them vulnerable to various causes of stress and mortality. As noted above (see chapter 3), some reports suggest that limited food availability or quality could limit survival of RASU in this life stage along the LCR. However, the subject has not been studied in detail. Most of the present life stage plays out after the larvae have reached nursery habitat and typically lasts for most of the first year of life. If RASU are food limited during this life stage, the reasons would have to lie in the nursery habitat itself. As discussed above, RASU feeding morphology changes over the course of this life stage, from a forward-feeding morphology with a small mouth at the start to a downward-feeding morphology with a larger mouth later. Any study of food availability for this life stage would need to consider the different types of foods RASU would seek as they transform and grow.

RASU in this life stage may face a limited range of mesohabitat settings suitable as resting/hiding sites along their dispersal pathways, as suggested above in the discussion of drifting success. This relationship is probably secondary to the potential effects of alterations to drifting (see above) and swimming (see below) success.

The present CEM identifies three critical biological activities or processes for this life stage – drifting, resting/hiding, and swimming – that affect survival indirectly by having direct, high-magnitude effects on predation. Drifting larvae appear to control the timing of when they drift – versus resting/hiding in low-velocity mesohabitats (see below) – so that they drift preferentially at night. The literature suggests that this behavior evolved because it reduces predation. Drifting during higher turbidity could have a similar effect. Conversely, drifting larvae and older individuals in this life stage experience lower rates of predation if they can find suitable resting/hiding sites (see below) along their drift pathways and, later, in their nursery habitat. RASU even in this life stage can swim away from at least some predators. However, the literature suggests that their success in avoiding attacks potentially varies with mesohabitat conditions as well as by being active preferentially at night. Avoidance or escape may be more achievable in habitats with plentiful cover, such as in dense emergent vegetation or substrate interstices, as well as at night and in turbid waters. However, in open water, in daylight and low turbidity, there is probably little that RASU in this life stage can do to swim away from predators.

The present CEM also identifies two critical biological activities or processes that may affect the single outcome for this life stage indirectly through effects on other high-impact critical biological activities or processes for which there is not sufficient information available to estimate the magnitude of the effect:

- RASU in this life stage weakened or potentially otherwise impaired by disease will have reduced swimming strength and stamina. However, the literature does not present any data with which to assess any of the variables affecting the magnitude of this possible effect. Further, both disease and impaired swimming ability could arise as consequences of some other factor such as reduced condition due to poor foraging or low temperature.

- The aquatic flow pathways along which the RASU in this life stage drift during their dispersal could affect their likelihood of encounters with different types and abundances of plankton, benthic food options, and POM. However, the literature does not indicate whether differences in drifting behavior can affect the range of food materials that RASU encounter during drifting.

- The aquatic flow pathways along which RASU in this life stage drift also potentially could affect their frequency of encounters with mesohabitat settings with different suitabilities as resting/hiding locations. However, the literature does not indicate whether differences in drifting behavior can result in RASU in this life stage passively encountering different ranges of sites that differ in their suitability as resting/hiding locations, as has seemingly been documented for the UCRB.

The present CEM identifies four habitat elements with high-magnitude direct effects on predation – the composition, spatial and temporal distributions, abundances, and activity levels of the aquatic vertebrate; birds and mammals; aquatic invertebrate assemblages; and turbidity.

- The literature provides numerous examples of aquatic vertebrate predation on RASU in this life stage. Ehlo et al. (2017) and others summarize the available literature on the subject and provide new data based on analyses of deoxyribonucleic acid (DNA) in the stomach contents of potential predators of RASU in this life stage, particularly green sunfish (*Lepomis cyanellus*), and bluegill (*Lepomis macrochirus*) < 70 mm TL. Ehlo et al. (2017) also note that the analysis of DNA in predator stomach contents provides more comprehensive data on larval predation than can visual inspection of stomach contents because consumed larvae disintegrate rapidly in the digestive system (Schooley et al. 2008; Ehlo et al. 2017). The activity of aquatic vertebrates, in turn, is controlled by other habitat elements, as discussed in chapter 7.

- The present CEM hypothesizes that the rate of predation on this life stage at any given location may depend on the overall level of activity of birds that feed on small macrofauna in the water at that location and on the ability of those avian predators that are present to forage under different conditions of turbidity and cover. The literature does not document the frequency or severity of avian predation on RASU in this life stage. However, the hypothesis is reasonable given the ecology of wading birds and the use of wetlands and other shallow mesohabitats as nursery habitat by this life stage. Birds capable of detecting and feeding on the small RASU in this life stage in shallows are ubiquitous and active year round along the LCR and especially across its off-channel habitats. On the other hand, the hypothesis may be weakened by the possibility that such birds may feed mostly in the daytime, when RASU in this life stage tend to avoid moving about.

- Benthic macroinvertebrates likely to occur in RASU nursery habitat for this life stage could include crayfish and odonate larvae (Horn et al. 1994; Mueller et al. 2006), which can prey on RASU in this life stage.

- RASU in this life stage, as in all life stages, are vulnerable to attack by sight-feeding predators. RASU in this life stage also may find it increasingly difficult to detect predators in turbidities above some threshold of reduced clarity, but potential sight-feeding predators conversely may find it increasingly difficult to detect RASU at higher turbidities as well. The benefits for RASU of turbidity in suppressing predator activity may outweigh the effects of elevated turbidity on the ability of RASU to detect predators, particularly because RASU may have other behaviors that help reduce their vulnerability to detection in turbid water, including moving into cover habitat.

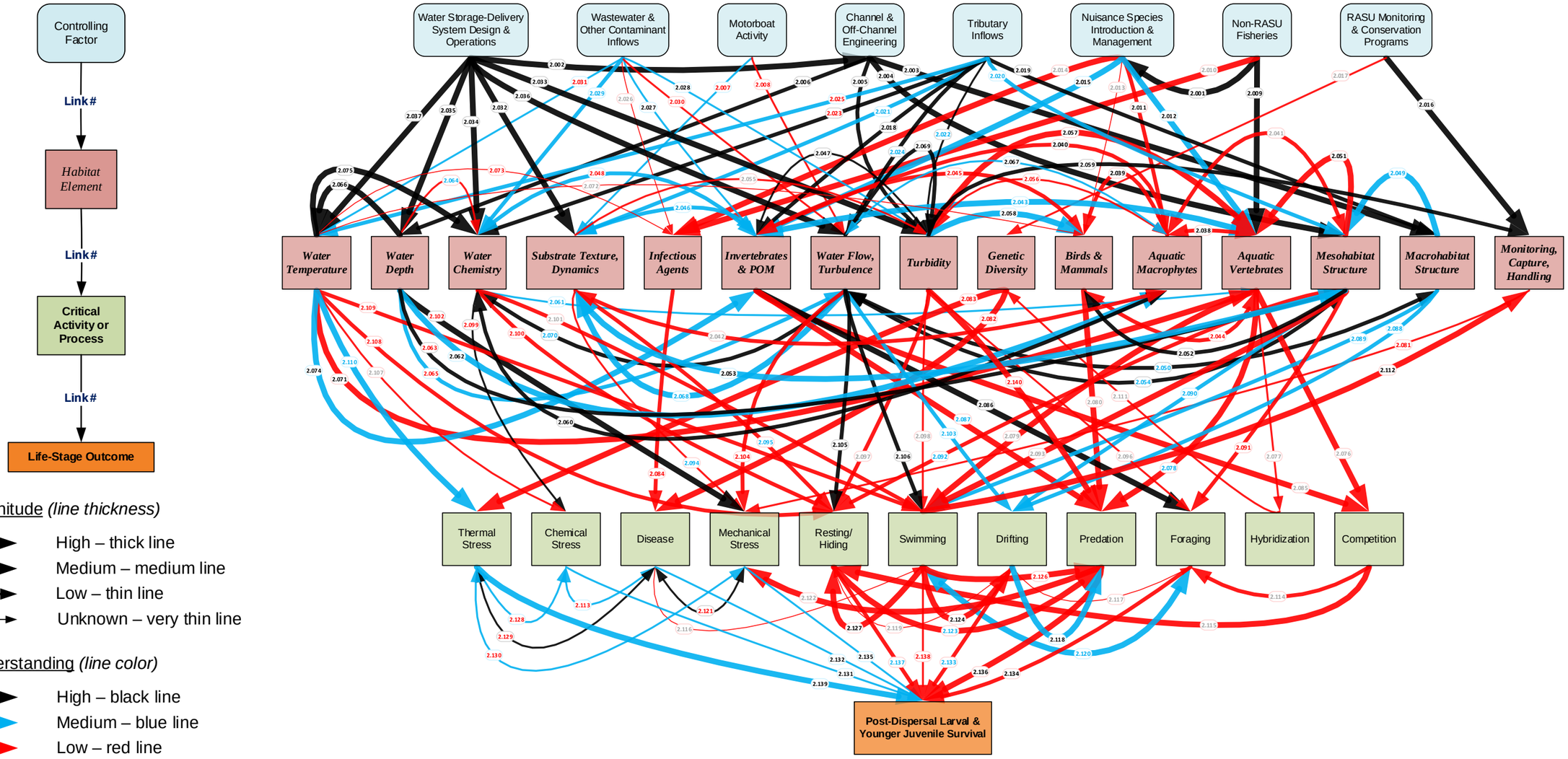
As with the preceding life stage, the present CEM for this life stage identifies two habitat elements with high-magnitude direct effects on thermal stress – water temperature and genetic diversity. The reasoning for hypothesizing these two causal relationships is the same as for the preceding life stage (see "RASU Life Stage 1 – Egg and Pre-Dispersal Larval Life Stage").

The present CEM identifies two habitat elements – aquatic vertebrates and mesohabitat structure – with high-magnitude direct effects on the three critical biological activities or processes for this life stage – drifting, resting/hiding, and swimming – that affect survival indirectly by having direct, high-magnitude effects on predation. The present CEM hypothesizes that, in addition to directly contributing to the rate of predation itself, predatory aquatic vertebrates also affect RASU swimming behaviors by triggering avoidance behaviors. RASU in this life stage can swim away to try to avoid other aquatic vertebrates, but the speed of such avoidance behaviors (i.e., the distances of movement achievable per second) necessarily are small because the RASU are small. Consequently, RASU in this life stage appear to be highly vulnerable to predation unless the mesohabitat structure of the environment provides suitable cover in suitable proximity. Cover conditions identified in the literature as potentially used in this life stage include turbidity, gravel/cobble interstices, and aquatic macrophytes. RASU larvae in Lake Mohave disappear before they reach 12 mm TL, presumably entirely as a result of predation (see summaries in Ehlo et al. 2015, 2017). The availability of suitable cover along drift pathways and in nursery habitat, in turn, is proposed as the reason for RASU larval and juvenile survival in the Colorado River inflow area of Lake Mead (Reclamation 2017).

RASU in this life stage may also exhibit a specific type of swimming behavior that could affect their vulnerability to predation. Snyder and Muth (2004) report aggregating behavior in early juveniles (TL > 25 mm). LCR MSCP field biologists (September 2013, personal communications) report some unevenness in the spatial distribution of RASU in this life stage encountered during nighttime capture activities, raising the possibility of variation in aggregation behavior even at this younger life stage. However, it is not clear how such aggregating might affect vulnerability to predation.

Finally, the present CEM identifies one habitat element that potentially could directly affect one of the other habitat elements with a high-magnitude effect on a critical biological activity or process that, in turn, has a high-magnitude effect on survival for which there is not sufficient information available to estimate the magnitude of the effect. Water temperature presumably affects the activity of all birds and mammals that may feed in or along the shorelines of LCR waters. However, this suite of relationships has not been studied for the LCR ecosystem.

The information reviewed for the present CEM (figure 4) indicates a low level of understanding of most of the high-magnitude causal linkages described in the preceding paragraphs that affect post-dispersal larval and younger juvenile survival. The poorly understood causal relationships include (1) the effects of predation on post-dispersal larval and younger juvenile survival, (2) the effects of genetic diversity on thermal stress, (3) the direct effects of aquatic vertebrates, birds and mammals, aquatic invertebrates, and turbidity on predation, (4) the effects of swimming and resting/hiding behaviors on predation, (5) the effects of aquatic vertebrate abundance and activity on RASU swimming behaviors, and (6) the effects of mesohabitat structure on RASU swimming behaviors in this life stage. That is, the literature presents insufficient information or shows little agreement concerning the character, magnitude, and/or predictability of these proposed causal relationships. The information reviewed for the present CEM indicates a medium level of understanding of the effects of thermal stress on post-dispersal larval and younger juvenile survival, the effects of water temperature on thermal stress, and the effects of drifting behaviors on predation.



Link Magnitude *(line thickness)*

- High – thick line
- Medium – medium line
- Low – thin line
- Unknown – very thin line

Link Understanding *(line color)*

- High – black line
- Medium – blue line
- Low – red line

Link Predictability *(link label color)*

- 0.000 High – black text
- 0.000 Medium – blue text
- 0.000 Low – red text
- 0.000 Unknown – grey text

Figure 4.—RASU life stage 2 – post-dispersal larval and younger juvenile life stage, showing the relevant controlling factors, habitat elements, and critical biological activities and processes.

RASU LIFE STAGE 3 – OLDER JUVENILE AND SUBADULT LIFE STAGE

As described in chapter 2, this life stage begins after older RASU juveniles disperse from their nursery habitat, beginning as early as the middle of their first year. They grow to roughly 350 mm TL by the time they reach sexual maturity, which can be as early as 2 years old for males and 3 years for females in rearing facilities, but is more typically 4–6 years old in the wild (LCR MSCP 2008, 2016a; Valdez et al. 2012c). As noted above, this life stage has a single life-stage outcome, older juvenile and subadult survival (see figure 1). Under the LCR MSCP augmentation program, as noted above, dispersing larvae in Lake Mohave are captured and transported to rearing facilities for growth and later repatriation as adults. A few larvae may survive in the LCR ecosystem below Hoover Dam to mature into juveniles and subadults (Marsh et al. 2015; Ehlo et al. 2016; Kesner et al. 2016; LCR MSCP 2016a), and there is clear evidence of recruitment of older juveniles and subadults in Lake Mead and the western Grand Canyon (Reclamation 2017). Otherwise, the vast majority of RASU older juveniles and subadults are to be found in facilities operating as components of the augmentation program. The present CEM does not address the internal workings of the rearing program.

The information reviewed for the present CEM identifies 10 (of 14) critical biological activities or processes affecting older juvenile and subadult survival, as shown on figure 5 (see also table 2). Of these 10 critical biological activities or processes, however, the present CEM identifies only 2 that have direct, high-magnitude effects on older juvenile and subadult survival – foraging and predation. As noted above (see also attachment 1), magnitude refers to the degree to which a given factor controls some condition relative to other factors affecting that same condition. In the present instance, the CEM proposes that foraging and predation have greater direct effects on older juvenile and subadult survival than do any other critical biological activities or processes. Resting/hiding behaviors also may directly affect survival, but with medium magnitude, as discussed below.

Predation by non-native fishes and birds is the most commonly proposed cause of the observed poor survival among RASU of all life stages, particularly the poor survival of the older juveniles and subadults repatriated in the earlier years of the augmentation program, as discussed above (chapters 3, 4, and 5) (Marsh et al. 2015; Kesner et al. 2016; LCR MSCP 2016a). Conversely, the successful recruitment of RASU juveniles and subadults in portions of Lake Mead in recent years (Albrecht et al. 2010a, 2010b, 2010c; BIO-WEST Inc., and American Southwest Ichthyological Researchers 2017; Reclamation 2017) is suspected to be a consequence of some at least minimally sufficient availability of mesohabitat conditions that provide cover from predation (see below).

Successful foraging is necessarily a key factor in survival in this life stage: RASU that do not forage successfully necessarily will be weaker and grow less rapidly, leaving them vulnerable to various causes of stress and mortality. However, the literature provides little information on foraging in this life stage or on the possibility of limitations in food availability. The literature instead notes that this life stage is encountered too infrequently in the LCR ecosystem to support many inferences concerning its dynamics at all. The present CEM includes this hypothesis of a high-magnitude impact on survival within the LCR ecosystem with the caveat that neither food availability nor foraging success rates have received substantial study. RASU in this life stage have a fully adult feeding morphology, but mouth size presumably increases with body size. Any study of food availability for this life stage would need to consider the different types of foods the RASU would seek as they grow.

The present CEM also identifies two critical biological activities or processes for this life stage – resting/hiding and swimming – that affect survival indirectly by having direct, high-magnitude effects on foraging and predation. The relationship between foraging and swimming behaviors is bi-directional. Foraging provides RASU in this life stage with the energy needed for swimming strength and stamina. Conversely, RASU in this life stage need swimming strength and agility to forage successfully. As RASU in this life stage become stronger and more agile, they can maneuver increasingly well during foraging. Aggregation behavior may also contribute to foraging success, as discussed above (see chapter 3).

Similarly, swimming behaviors affect predation because, as RASU in this life stage become stronger and more agile, they presumably can maneuver increasingly well to avoid and potentially escape predation, at least from aquatic predators. To the extent that strength and agility increase with size, this may help explain why larger, adult RASU (> 300 and especially > 400 mm TL) have higher rates of survival, which many researchers attribute to a lower rate of successful predation on them (e.g., Kesner et al. 2016). At the same time, RASU success in this life stage in avoiding predation potentially also may vary with mesohabitat conditions, as discussed further below, as well as by being active preferentially at night. As RASU in this life stage become stronger and more agile, they can maneuver increasingly well to seek and move to/from resting/ hiding locations that provide protective cover – if suitable resting/hiding locations are available. However, in open water, in daylight and low turbidity, there is probably little that RASU in this life stage can do to swim away from faster or more agile aquatic predators or to detect and avoid avian predators (see below). The aggregation behavior noted above may also potentially help with mutual detection and avoidance of predators. Snyder and Muth (2004) report aggregating behavior in early juveniles (TL > 25 mm).

Additionally, the present CEM identifies a third critical biological activity or process for this life stage – competition – that potentially affects survival

indirectly by having direct, high-magnitude effects on resting/hiding behavior. The abundance and range of species competing with RASU in this life stage for habitat, particularly cover, conceivably could constrain RASU success in finding suitable resting/hiding habitat. Competitors with RASU in this life stage for cover habitat may be abundant and ubiquitous in the LCR and associated off-channel sites. However, there is no literature on the topic. The present CEM proposes this relationship based on basic ecological concepts and identifies competition as only having a medium-magnitude effect on foraging. RASU in this and the adult life stage exhibit great dietary flexibility, which should limit the intensity of impacts of competition on foraging success.

The present CEM also identifies one critical biological activity or process that may affect the single outcome for this life stage indirectly through effects on another high-impact critical biological activity or process for which there is not sufficient information available to estimate the magnitude of the effect. RASU weakened or potentially otherwise impaired by disease conceivably will have reduced swimming strength and stamina. However, no data were found with which to assess any of the variables affecting the magnitude of this potential relationship. Further, both disease and impaired swimming ability could arise as consequences of some other factor, such as reduced condition due to poor foraging or low temperature.

The present CEM identifies four habitat elements with high-magnitude direct effects on foraging and predation – the taxonomic composition, spatial and temporal distributions, abundances, and activity levels of aquatic vertebrates; birds and mammals; aquatic invertebrate assemblages; and turbidity.

- The literature provides numerous examples of aquatic vertebrate predation on RASU in this life stage (e.g., Ehlo et al. 2015; Marsh et al. 2015; LCR MSCP 2016a). Ehlo et al. (2017) provide a recent summary of the literature on the subject, although the data from their study concern predation on the preceding life stage, particularly by green sunfish and bluegill < 70 mm TL.

- The literature does not document the frequency or severity of avian predation on RASU in this life stage. Ongoing studies discussed above (see "Predation," chapter 3, and "Birds and Mammals," chapter 4), which use evidence of PIT tags left behind at avian predation sites, necessarily concern predation of larger, repatriated individuals (see "RASU Life Stage 4 – Adult Life Stage," below). Nevertheless, those studies indicate the ease with which birds can locate and prey on RASU in clear-water settings. The smaller sizes of the present RASU life stage may even make them suitable targets for a wider range of bird sizes. The relationship is reasonable given the ecology of wading birds, but hypothetical, pending further study. Birds capable of detecting and feeding on RASU in this life stage in shallows are ubiquitous and active year round along the LCR and

especially across its off-channel habitats. However, such birds feed mostly in the daytime, when RASU in this life stage tend to avoid shallow waters when deeper waters and cover are available (LCR MSCP 2016a).

- RASU in this life stage feed primarily on benthic organisms and POM but may also consume zooplankton and suspended POM (see "Foraging," chapter 3). The abundance and composition of the planktonic and benthic communities and the abundance and composition of POM therefore necessarily shape the availability of suitable foods for RASU in this life stage. The benthic macroinvertebrate assemblage also includes some species, such as odonate larvae (see Horn et al. 1994) and crayfish, which can prey on smaller RASU juveniles, but as RASU juveniles increase in size, this vulnerability presumably declines to zero.

- RASU in this life stage, as in all life stages, are vulnerable to attack by sight-feeding predators. As in the preceding life stage, RASU in this life stage may find it increasingly difficult to detect predators in turbidities above some threshold of reduced clarity, but potential sight-feeding predators conversely may find it increasingly difficult to detect RASU at higher turbidities as well. The benefits for RASU of turbidity in suppressing predator activity may outweigh the effects of elevated turbidity on the ability of RASU to detect predators particularly because RASU may have other behaviors that help reduce their vulnerability to detection in turbid water, including moving into cover habitat.

The present CEM identifies three habitat elements with high-magnitude direct effects on competition, resting/hiding, and swimming – the taxonomic compositions, spatial and temporal distributions, abundances, and activity levels of the (1) aquatic vertebrate assemblage, (2) aquatic invertebrate assemblage, and (3) mesohabitat structure.

- Theoretically, RASU in this life stage may experience competition from other aquatic vertebrates not only for food items but also for habitat, especially for cover. The literature does not indicate which species (including other RASU) may compete with RASU in this life stage for habitat or food, but any species competing with RASU in this life stage for habitat or food are likely spatially ubiquitous, highly persistent, and active year round.

- RASU in this life stage can detect and swim away from other aquatic vertebrates, and the speed of such an avoidance behavior – the distance of movement achievable per second – presumably increases as their body size increases. The relationship between body size and swimming performance has not been tested for RASU, but tests on the closely related FLSU do show a strong positive relationship (Ward et al. 2002). At the

same time, the aquatic vertebrates they might seek to avoid would likely be ubiquitous, and RASU in this life stage may have only limited ability to detect and escape attacks by swimming, given the range of avian and aquatic predators present.

- Theoretically, some macroinvertebrates may feed on the same aquatic invertebrates and fine POM on which RASU feed during this life stage, thus competing with RASU in this life stage for these foods. Given the diversity of introduced invertebrate species and their broad ranges of diets, it is reasonable to hypothesize that these species may compete with RASU for food. The literature provides no information on this possible relationship, but any macroinvertebrate species competing with RASU in this life stage for food will be spatially ubiquitous, highly persistent, and active year round.

- Swimming ability and strength among RASU in this life stage probably have only a moderate effect on their success in avoiding or escaping predator attack because of the abundance of strong, agile aquatic vertebrate predators in the system (except where these have been removed) and RASU vulnerability to avian predators. The major determining factors appear to relate to mesohabitat conditions that afford cover/protection. RASU in this life stage may identify suitable or unsuitable resting/hiding locations based in part on mesohabitat form, especially the availability of turbidity, gravel/cobble interstices, aquatic macrophytes, and deeper (darker) water (see chapters 3 and 4). The apparent contrast in RASU survival in this life stage, between Lake Mead and Lake Mohave, may be particularly informative: smaller RASU survive in the former, but not the latter, which provides more protective cover (turbidity, aquatic vegetation, etc.) in places such as the Colorado River inflow. Further, the spatial distribution of mesohabitat types and associated cover among these types will affect the distances over which RASU in this life stage may swim (e.g., during seasonal movement, the amount of open-water across which they will be exposed during movement, and the density of cover available among mesohabitats). The latter variables may also affect the likelihood that RASU in this life stage will aggregate ("school") versus disperse as they move over longer distances.

Finally, the present CEM identifies one habitat element that potentially could directly affect one of the other habitat elements with a high-magnitude effect on a critical biological activity or process which, in turn, has a high-magnitude effect on survival, but for which there is not sufficient information available to estimate the magnitude of the effect. Water temperature presumably affects the activity of all birds and mammals that may feed in or along the shorelines of LCR waters. However, as noted for the preceding life stage, this suite of relationships has not been studied for the LCR ecosystem.

The information reviewed for the present CEM (figure 5) indicates a low level of understanding of most of the high-magnitude causal linkages described in the preceding paragraphs that affect older juvenile and subadult survival. The poorly understood causal relationships include (1) the effects of foraging and predation on older juvenile and subadult survival, (2) the effects of swimming and resting/hiding behaviors on predation, (3) the effects of competition on resting/hiding behaviors, (4) the effects of turbidity and aquatic vertebrate, predatory bird, and predatory aquatic invertebrate abundance and activity on predation, (5) the effects of aquatic vertebrate abundance and activity on competition and on RASU swimming behaviors, (6) the effects of aquatic invertebrate abundance and activity on competition, and (7) the effects of mesohabitat structure on RASU resting/hiding and swimming behaviors in this life stage. That is, the literature presents insufficient information or shows little agreement concerning the character, magnitude, and/or predictability of these proposed causal relationships.

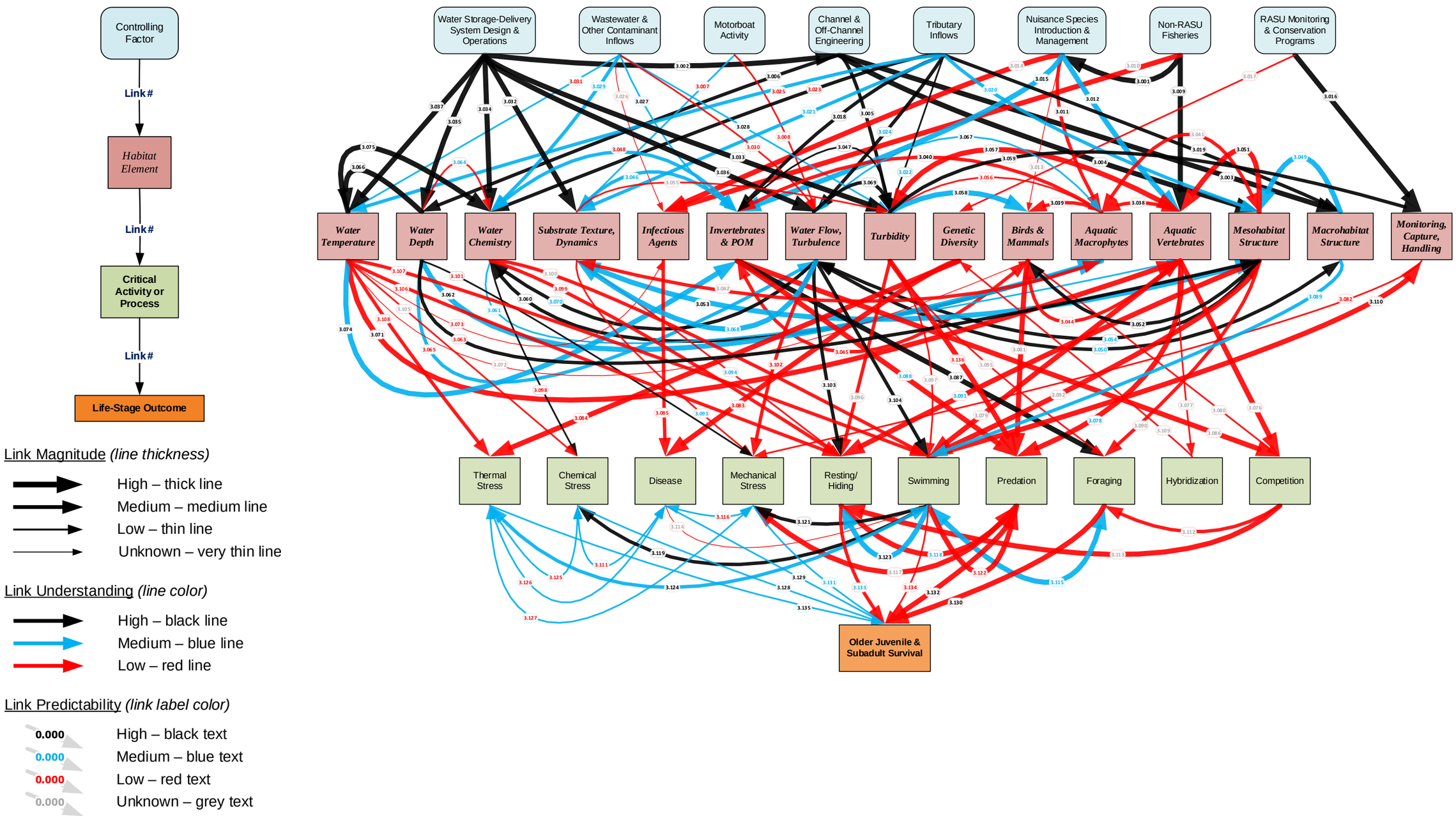


Figure 5.—RASU life stage 3 – older juvenile and subadult life stage, showing the relevant controlling factors, habitat elements, and critical biological activities and processes.

RASU LIFE STAGE 4 – ADULT LIFE STAGE

As described in chapter 2, this life stage covers all age classes of sexually mature RASU, which may achieve lifespans approaching or even exceeding 50 years (see chapters 1 and 2). RASU adults measure roughly 350 mm TL to more than 700 mm TL and historically grew even larger. This life stage has two life-stage outcomes – adult annual survival and the adult annual spawning participation rate. As noted above, under the LCR MSCP augmentation program, dispersing larvae in Lake Mohave are captured and transported to rearing facilities for growth and later repatriation as adults. A few larvae may survive in the LCR ecosystem below Hoover Dam to mature into adults (Marsh et al. 2015; Ehlo et al. 2016; Kesner et al. 2016; LCR MSCP 2016a), and there is clear evidence of recruitment of adults in Lake Mead and the western Grand Canyon (Reclamation 2017). Otherwise, the vast majority of RASU adults present in the LCR ecosystem are individuals repatriated by the augmentation program. The present CEM does not address the internal workings of the rearing program. Repatriated RASU adults suffer high rates of mortality within the first few weeks to months following repatriation (Marsh et al. 2015; Kesner et al. 2016; LCR MSCP 2016a), but sufficient numbers survive to support an estimated population of approximately 2,000 (Pacey and Marsh 2017).

The information reviewed for the present CEM identifies 10 (of 14) critical biological activities or processes affecting the 2 outcomes for this life stage, as shown on figure 6 (see also table 2). However, among these 10 critical biological activities or processes, the present CEM identifies only 2 that have direct, high-magnitude effects on adult annual survival and the adult annual spawning participation rate – foraging and predation. As noted above (see also attachment 1), magnitude refers to the degree to which a given factor controls some condition relative to other factors affecting that same condition. In the present instance, the CEM proposes that foraging and predation have greater direct effects on the two outcomes for this life stage than do any other critical biological activities or processes. Resting/hiding behaviors also may directly affect survival, but with medium magnitude, as discussed below.

Successful foraging is necessarily a key factor in survival in this life stage, as in the preceding two life stages. RASU that do not forage successfully necessarily will be weaker and grow less rapidly, leaving them vulnerable to various causes of stress and mortality. In addition, the higher the foraging success among RASU adults, presumably the higher their likely developing secondary sexual attributes, developing gametes, and participating in spawning, other things being equal. However, the literature provides little information on foraging success rates in this life stage or on the possibility of limitations in food availability. The present CEM includes this hypothesis of a high-magnitude impact on survival within the

LCR ecosystem with the caveat that neither food availability nor foraging success rates have received substantial study. RASU adult mouth size presumably continues to increase with body size throughout this life stage.

Predation by non-native fishes and birds is the most commonly proposed cause of the observed poor survival among RASU of all life stages, particularly the poor survival of the smaller adults repatriated in the earlier years of the augmentation program, as discussed above (chapters 3, 4, and 5) (Marsh et al. 2015; Kesner et al. 2016; LCR MSCP 2016a). Direct evidence of predation on RASU adults comes from studies of striped bass stomach contents, data from isolated ponds such as Cibola High Levee Pond from which predators were removed and then later reintroduced (Mueller 2006), and data on PIT tags recovered from the stomachs of sport fish catches, as cited earlier in this report (chapter 3). Otherwise, direct observations of predation are limited to studies of smaller, especially larval RASU, and studies of overall survival among RASU in isolated, predator-free ponds. Successful recruitment of RASU adults in portions of Lake Mead but not in Lake Mohave in recent years (Albrecht et al. 2010a, 2010b, 2010c; BIO-WEST Inc., and American Southwest Ichthyological Researchers 2017; Reclamation 2017) is suspected to be a consequence of the availability of mesohabitat conditions in Lake Mead that provide cover from predation (see below).

As with the preceding life stage, the present CEM also identifies two critical biological activities or processes for the adult life stage – resting/hiding and swimming – that affect survival indirectly by having direct, high-magnitude effects on foraging and predation. The direct effects of swimming behaviors on foraging also thereby indirectly affect the spawning participation rate. The relationship between foraging and swimming behaviors is bi-directional. Foraging provides RASU in this life stage with the energy needed for swimming strength and stamina as well as the energy needed to develop secondary sexual characteristics and participate in spawning. Conversely, RASU in this life stage need swimming strength and agility to forage successfully. As RASU in this life stage become stronger and more agile, they can maneuver increasingly well during foraging. Aggregation behavior may also contribute to foraging success, as discussed above (see chapter 3).

As RASU in this life stage become stronger and more agile, they can maneuver increasingly well to seek and move to/from resting/hiding locations that provide protective cover – if suitable resting/hiding locations are available. Swimming behaviors also affect predation because, as they become stronger and more agile, RASU in this life stage presumably also can maneuver increasingly well to avoid and potentially escape predation, at least from aquatic predators. To the extent that strength and agility increase with size, this may help explain why larger, adult RASU (> 300 and especially > 400 mm TL) have higher rates of survival. As noted above, many researchers attribute a lower rate of successful predation on them (e.g., Kesner et al. 2016). RASU success in this life stage in avoiding

predation potentially also may vary with mesohabitat conditions, as discussed further below, as well as by being active preferentially at night. However, in open water, in daylight and low turbidity, there is probably little that RASU in this life stage can do to swim away from faster or more agile aquatic predators or to detect and avoid avian predators (see below). The aggregation behavior noted above (see "Swimming" in chapter 3) may also help with mutual detection and avoidance of predators, as also noted for the preceding life stage.

Additionally, the present CEM again identifies a third critical biological activity or process for this life stage – competition – that affects survival indirectly by having direct, high-magnitude effects on resting. The abundance and range of species competing with RASU in this life stage for habitat, particularly cover, conceivably could constrain RASU success in finding suitable resting/hiding habitat in this life stage, as in the preceding life stage. Competitors with RASU in this life stage for cover habitat may be abundant and ubiquitous in the LCR and associated off-channel sites. However, there is no literature on the topic. The present CEM proposes this relationship based on basic ecological concepts. The present CEM again identifies competition as only having a medium-magnitude effect on foraging. RASU in this life stage exhibit great dietary flexibility, which should limit the intensity of impacts of competition on foraging success.

The present CEM also identifies one critical biological activity or process that may affect both outcomes for this life stage indirectly through effects on another high-impact critical biological activity or process for which there is not sufficient information available to estimate the magnitude of the effect. As with the preceding life stage, adult RASU weakened or potentially otherwise impaired by disease conceivably will have reduced swimming strength and stamina. However, no data were found with which to assess any of the variables affecting the magnitude of this potential relationship. Further, both disease and impaired swimming ability could arise as consequences of some other factor, such as reduced condition due to poor foraging or low temperature.

The present CEM identifies four habitat elements with high-magnitude direct effects on foraging and/or predation – the taxonomic compositions, spatial and temporal distributions, abundances, and activity levels of the (1) aquatic vertebrate assemblage, (2) aquatic invertebrate assemblage, (3) pre-release conditioning, and (4) turbidity.

- The literature provides numerous examples of aquatic vertebrate predation on RASU in this life stage (e.g., Ehlo et al. 2015; Marsh 2015; LCR MSCP 2016a), as noted above. As also noted above, the literature also increasingly documents the frequency or severity of avian predation on RASU in this life stage. These studies indicate the ease with which birds can locate and prey on RASU, including adult RASU, in clear-water settings. Birds capable of detecting and feeding on RASU in this life stage in shallows are ubiquitous and active year round along the LCR and

especially across its off-channel habitats. However, such birds feed mostly in the daytime, when RASU in this life stage tend to avoid shallow waters when deeper waters and cover are available (LCR MSCP 2016a). The larger body sizes of adult RASU, compared to older juvenile and subadult RASU, also reduces the diversity of avian species capable of preying on adult RASU compared to younger RASU (see above). As a result, the present CEM assigns a medium magnitude to the direct effects of the bird assemblage on the predation rate for this life stage.

- RASU in this life stage, as in the preceding life stage, feed primarily on benthic organisms and POM but may also consume zooplankton and suspended POM (see "Foraging," chapter 3). The abundance and composition of the planktonic and benthic communities and the abundance and composition of POM therefore necessarily shape the availability of suitable forage for RASU in this life stage.

- As discussed above (see "Pre-Release Conditioning," chapter 4), RASU during their time in the rearing environment may acquire little experience with the range of food types and behaviors that they will encounter after release. They may also be subjected to focused pre-release conditioning to help them learn how to recognize and feed on some of the food types and feeding locations they will encounter upon release. The present CEM uses the term "adaptive" conditioning to refer to the latter. Both types of conditioning affect the ability of repatriated RASU to feed successfully and adequately upon release. The present CEM estimates that such conditioning has a high-magnitude potential to affect RASU foraging after their release. However, this has not been studied enough to know how much difference such conditioning could have in practice.

- Similarly, as also discussed above (see "Pre-Release Conditioning," chapter 4), reared RASU typically do not acquire any experience with predators during their time in the rearing environment. On the other hand, again, they may also be subjected to focused pre-release conditioning to help them learn how to recognize and respond to the presence and behaviors of some of the predators they will encounter upon release – another type of adaptive conditioning. Both types of conditioning affect the ability of repatriated RASU to cope with predators upon release. If properly designed and conducted at a scale to benefit the majority of reared RASU, programs of adaptive conditioning of reared RASU to predator behaviors could reduce vulnerability to predation among the released fish. Recent studies suggest that it may be possible to achieve success at the larger scale by training smaller cohorts of RASU, which other RASU can then follow or mimic via social learning (O'Neill and Stewart 2015; O'Neill et al. 2016).

- RASU in this life stage, as in all life stages, are vulnerable to attack by sight-feeding predators. As in the preceding two life stages, RASU in this life stage may find it increasingly difficult to detect predators in turbidities above some threshold of reduced clarity, but potential sight-feeding predators conversely may find it increasingly difficult to detect RASU at higher turbidities as well. The benefits for RASU of turbidity in suppressing predator activity may outweigh the effects of elevated turbidity on the ability of RASU to detect predators particularly because RASU may have other behaviors that help reduce their vulnerability to detection in turbid water, including moving into cover habitat.

The present CEM identifies four habitat elements with high-magnitude direct effects on competition, resting/hiding, and swimming – the taxonomic compositions, spatial and temporal distributions, abundances, and activity levels of the (1) aquatic vertebrate assemblage, (2) aquatic invertebrate assemblage, (3) mesohabitat structure, and (4) pre-release conditioning.

- Theoretically, as in the preceding life stage, RASU in this life stage may experience competition from other aquatic vertebrates not only for food items but also for habitat, especially for cover. The literature does not indicate which species (including other RASU) may compete with RASU in this life stage for habitat or food, but any species competing with RASU in this life stage for habitat or food are likely spatially ubiquitous, highly persistent, and active year round.

- Theoretically, some macroinvertebrates also may feed on the same aquatic invertebrates and fine POM on which RASU feed during this life stage, thus competing with RASU in this life stage for these foods. Given the diversity of introduced invertebrate species and their broad ranges of diets, it is reasonable to hypothesize that these species may compete with RASU for food. The literature provides no information on this possible relationship, but any macroinvertebrate species competing with RASU in this life stage for food will be spatially ubiquitous, highly persistent, and active year round.

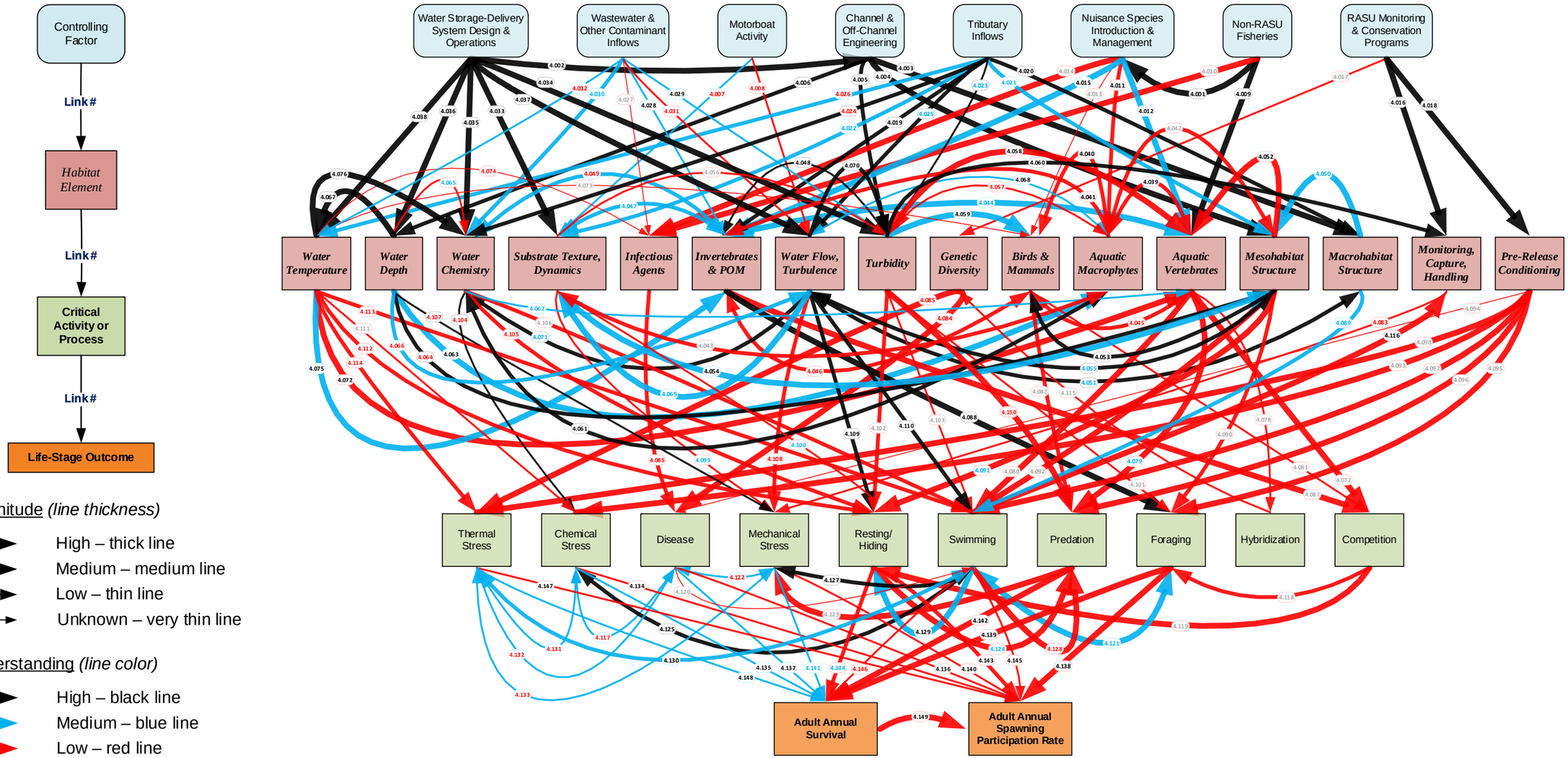
- As in the preceding life stage, RASU in this life stage can detect and swim away from other aquatic vertebrates, and the speed of such an avoidance behavior – the distances of movement achievable per second – presumably increases as their body size increases. The relationship between body size and swimming performance has not been tested for RASU, but tests on the closely related FLSU do show a strong positive relationship (Ward et al. 2002). At the same time, the aquatic vertebrates they might seek to avoid would likely be ubiquitous, and RASU in this life stage may have only limited ability to detect and escape attacks by swimming, given the range of avian and aquatic predators present.

- Swimming ability and strength among RASU in this life stage, as in the preceding life stage, probably have only moderate effect on their success in avoiding or escaping predator attack because of the abundance of strong, agile aquatic vertebrate predators in the system (except where these have been removed) and RASU vulnerability to avian predators. The major determining factors appear to relate to mesohabitat conditions that afford cover/protection. RASU in this life stage may identify suitable or unsuitable resting/hiding locations based in part on mesohabitat form, especially the availability of turbidity, gravel/cobble interstices, aquatic macrophytes, and deeper (darker) water (see chapters 3 and 4). The apparent contrast in RASU survival in this life stage, between Lake Mead and Lake Mohave, may be particularly informative: smaller RASU survive in the former, but not the latter, which provides more protective cover (turbidity, aquatic vegetation, etc.) in places such as the Colorado River inflow. Further, the spatial distribution of mesohabitat types and associated cover among these types will affect the distances over which RASU in this life stage may swim (e.g., during seasonal movement, the amount of open-water they will be exposed to during movement, and the density of cover available among mesohabitats). The latter variables may also affect the likelihood that RASU in this life stage will aggregate ("school") versus disperse as they move over longer distances.

- Reared RASU may acquire little experience with the range of flow velocities and levels of turbulence that they might encounter after release during their time in the rearing environment. They may also be subjected to adaptive pre-release conditioning to help them develop the strength, stamina, and agility they will need to respond to predator interactions and to the range of flow velocities and levels of turbulence that they will encounter after release. Both types of conditioning affect the ability of the repatriated RASU to move and avoid hazards after their release. In addition, RASU in hatcheries may become pre-conditioned to aggregating, including aggregating near the surface during feeding. Near-surface aggregation may not be adaptive after release because near-surface RASU are vulnerable to avian predation, but aggregating in deeper waters to avoid predators might be a beneficial behavior.

Finally, the present CEM identifies one habitat element that potentially could directly affect one of the other habitat elements with a high-magnitude effect on a critical biological activity or process which, in turn, has a high-magnitude effect on survival, but for which there is not sufficient information available to estimate the magnitude of the effect. As noted for earlier life stages, water temperature presumably affects the activity of all birds and mammals that may feed in or along the shorelines of LCR waters. However, as noted for the preceding life stage, this suite of relationships has not been studied for the LCR ecosystem.

The information reviewed for the present CEM (figure 6) indicates a low level of understanding of most of the high-magnitude causal linkages described in the preceding paragraphs that affect RASU adult annual survival and participation in spawning. The poorly understood causal relationships include (1) the effects of foraging and predation on adult survival, (2) the effects of foraging on spawning participation, (3) the effects of swimming and resting/hiding behaviors on predation, (4) the effects of competition on resting/hiding behaviors, (5) the effects of aquatic vertebrate and aquatic invertebrate abundance and activity on competition, (6) the effects of aquatic vertebrate abundance and activity on RASU swimming behaviors, (7) the effects of pre-release conditioning on foraging success, predation, and swimming behaviors among released RASU, (8) the effects of turbidity on predation, and (9) the effects of mesohabitat structure on RASU resting/hiding and swimming behaviors in this life stage. That is, the literature presents insufficient information or shows little agreement concerning the character, magnitude, and/or predictability of these proposed causal relationships.



Link Magnitude *(line thickness)*

- High – thick line
- Medium – medium line
- Low – thin line
- Unknown – very thin line

Link Understanding *(line color)*

- High – black line
- Medium – blue line
- Low – red line

Link Predictability *(link label color)*

- 0.000 High – black text
- 0.000 Medium – blue text
- 0.000 Low – red text
- 0.000 Unknown – grey text

Figure 6.—RASU life stage 4 – adult life stage, showing the relevant controlling factors, habitat elements, and critical biological activities and processes.

RASU LIFE STAGE 5 – SPAWNING ADULT LIFE STAGE

As described in chapter 2, this life stage covers adult RASU during the times in which they participate in spawning. This life stage begins when would-be spawners leave their home areas to move toward spawning sites and ends when these individuals return to their home areas. This life stage thus encompasses the time RASU spend at spawning sites and the time they spend traveling to and from these sites. This life stage has two life-stage outcomes: (1) spawning adult survival and (2) spawning adult fertility.

The information reviewed for the present CEM identifies 12 (of 14) critical biological activities or processes affecting the 2 outcomes for this life stage as shown on figure 7 (see also table 2). The present CEM diagram for this life stage (figure 7) contains more linkages than the diagram for any other life stage. This reflects the large number of critical biological activities and processes that affect the two life stages with at least low magnitude. However, the present CEM identifies only three critical biological activities or processes – predation, staging and spawning, and swimming – that have direct, high-magnitude effects on spawning adult survival and/or spawning adult fertility. Between the two life-stage outcomes, survival also affects fertility with high magnitude. As noted above (see also attachment 1), magnitude refers to the degree to which a given factor controls some condition relative to other factors affecting that same condition. In the present instance, the CEM proposes that predation, staging and spawning, and swimming have greater direct effects on the two outcomes for this life stage than do any other critical biological activities or processes. Foraging behaviors also may directly affect survival, but with medium magnitude, as discussed below.

Predation by non-native fishes and birds is the most commonly proposed cause of the observed poor survival among RASU of all life stages, as discussed above (chapters 3, 4, and 5; see “RASU Life Stage 4 – Adult Life Stage” above, this chapter). Spawning has only been observed at sites that lack turbidity and aquatic vegetation – the clear, shallow waters of which provide no protection to spawning RASU from either aquatic or avian predators. RASU that spawn in the daytime would be particularly vulnerable to predation from sight-feeding aquatic predators and from predatory birds. Nighttime spawning could reduce vulnerability to predation (see the discussion of the effects of swimming behaviors on predation, below).

Staging and spawning are the final two steps in the three-step process – ripening, staging, and spawning – that comprise this life stage. Any disruptions to staging or spawning behaviors necessarily have the potential to reduce fertility.

The present CEM hypothesizes that the swimming agility, strength, and stamina of spawning RASU, and their use of defensive or avoidance behaviors (e.g., "schooling"), all affect survival for this life stage. Spawning RASU must at least begin their participation in spawning with high levels of swimming agility, strength, and stamina in order to survive the demands of spawning, including staging. The literature indicates that RASU in fact become emaciated during spawning, a condition that would involve a loss of strength and stamina. The emaciation may be exacerbated by a lack of investment in foraging during the spawning cycle (see below). It should also be noted that RASU aggregation at spawning sites may make them more vulnerable to predation.

The present CEM identifies four critical biological activities or processes that affect one or both outcomes for this life stage indirectly by having direct, high-magnitude effects on staging and spawning, swimming behaviors, and/or predation.

- In addition to directly affecting survival in this life stage, which in turn affects fertility, predator activity also affects fertility indirectly by having a high-magnitude effect on staging and spawning activity. Predator activity may disrupt RASU movement to/from spawning sites and at the spawning sites, including directly at the time of spawning, thereby reducing the rate of success of staging and spawning. However, there are no studies specifically on predator activity at spawning sites during staging and spawning. Staging and spawning behaviors, in turn, may affect predation rates: The frequency of predator attacks on RASU traveling to/from staging sites presumably would be the same the frequency of attacks on adult RASU in general, with four possible differences: (1) spawners may be less cautious when heading toward staging sites, (2) RASU emaciation during and following spawning may make them more vulnerable, (3), as noted above, aggregation of RASU at spawning sites may increase their vulnerability to predation, and (4), as also noted above, the clear, shallow waters at RASU spawning sites may make them more vulnerable to attacks from some predators.

- Spawning RASU must find protected resting/hiding locations and water conditions in the areas around spawning sites and along their travel routes to/from these sites to avoid predation. Suitable resting/hiding sites may not be widely available along these routes or at these locations. The relationship has not specifically been studied.

- The rate of ripening necessarily has a high-magnitude effect on staging and spawning: The number of ripe RASU present in a connected set of reaches along the LCR presumably directly and positively affects the number of RASU able to participate in staging and spawning. The present CEM assessment of the magnitude of this effect assumes that only ripe individuals participate in staging and spawning activity. If this is not the

case, then spawning success will be diminished to the extent that unripe individuals participate. No study has documented such interference.

- As adult RASU become stronger and more agile swimmers, presumably they can maneuver increasingly well to avoid predation, as discussed above for adult RASU in general. They may also potentially engage in behaviors such as aggregation that may help with mutual detection and avoidance of predators, as also discussed above. However, RASU aggregate to spawn, and this swimming behavior may increase their vulnerability to predation, particularly when the aggregation takes place in clear, shallow water, where the RASU are additionally vulnerable to predation, as discussed above.

- RASU swimming behaviors during the spawning cycle – specifically the ways in which they navigate to and from spawning sites, avoiding hazards and finding resting/hiding and foraging opportunities along the way – directly affect staging success. Variation in RASU swimming behaviors at staging areas, in turn, may indirectly affect spawning by determining how RASU respond to potential disturbances (i.e., whether they swim away [disrupting spawning] or not, and whether the RASU aggregate in or near the water surface, both of which could affect their vulnerability to predation).

Additionally, the present CEM hypothesizes that three critical biological activities or processes for this life stage – competition, foraging, and swimming – affect survival and/or fertility indirectly by having direct, high-magnitude effects on resting/hiding or ripening:

(1) The abundance and range of species competing with spawning RASU for habitat, particularly cover, conceivably could constrain the success of these RASU in finding suitable resting/hiding habitat around spawning sites or along their travel routes to/from these sites. Competitors with RASU in this life stage for cover habitat may be abundant and ubiquitous in the LCR and associated off-channel sites. There is no literature on the topic.

(2) RASU that forage more successfully may be more likely to ripen successfully. The literature does not address this likely biological relationship.

(3) As spawning RASU become stronger and more agile, they can maneuver increasingly well to seek and move to/from resting/hiding locations around spawning sites and along their travel routes to/from the sites. RASU become increasingly strong and agile as they mature. These changes affect their ability to seek and move to/from suitable resting/hiding locations over increasingly large distances.

The present CEM also identifies two critical biological activities or processes, disease and staging and spawning, which may affect one or both outcomes for this life stage indirectly through other high-impact causal relationships for which there is not sufficient information available to estimate the magnitude of the effect.

(1) As with the adult life stage, spawning RASU weakened or potentially otherwise impaired by disease conceivably will have reduced swimming strength and stamina. No data were found that could be used to assess any of the variables affecting the magnitude of this potential relationship. Further, both disease and impaired swimming ability could arise as consequences of some other factor, such as reduced condition due to poor foraging or low temperature.

(2) Male and female RASU actively engaged in spawning encounters can move energetically against the substrates during these encounters, resulting in mechanical abrasion and stress. Conversely, it is logically possible that highly abraded individuals may withdraw from or engage less in subsequent spawning encounters in the same season. Bozek et al. (1984) report injuries from mechanical abrasion during spawning in Lake Mohave. The incidence and consequences of this relationship are otherwise unstudied in the LCR ecosystem.

The present CEM also identifies two critical biological activities or processes, hybridization and ripening, that may directly affect one or both outcomes for this life stage but for which there is not sufficient information available to estimate the magnitude of the effect.

(1) RASU hybrids with FLSU potentially have different fertility rates from genetically pure RASU (see “Hybridization,” chapter 3,). Data are only recently starting to emerge on the proportion of RASU-FLSU hybrids along the LCR below Hoover Dam that participate in spawning and on whether they exhibit differences in fertility compared to pure RASU (Wolters et al. 2017).

(2) Only ripe RASU participate successfully in spawning. However, the bioenergetic costs of devoting resources to ripening conceivably could reduce survival by leaving the ripe RASU vulnerable to various causes of mortality that stronger RASU are more able to avoid. The literature does not indicate whether this hypothesized relationship has any effect on this life-stage outcome.

The present CEM identifies six habitat elements with high-magnitude direct effects on predation, staging and spawning, and swimming – the taxonomic compositions, spatial and temporal distributions, abundances, and activity levels of the aquatic vertebrate and bird assemblages; mesohabitat structure; substrate texture/ dynamics; turbidity; and water temperature.

- The present CEM hypothesizes that both aquatic vertebrates and birds may prey on spawning RASU, based on the evidence for their preying on adult RASU in general (see above, this chapter, "RASU Life Stage 4 – Adult Life Stage"). Avoidance of aquatic vertebrate predators may also cause spawning RASU to swim out of spawning areas, disrupting staging and spawning.

- As discussed above (chapter 3), spawning RASU appear to select for a specific, limited suite of mesohabitat types for spawning. However, they do sometimes spawn on seemingly unexpected mesohabitats such as the boat ramp at the IPCA (LCR MSCP biologists 2013, personal communications) and in isolated off-channel ponds (Saltzgiver et al. 2015; Dowling et al. 2016a). Thus, spatially they may have some flexibility, but they must find mesohabitat settings that meet at least some criteria to serve as spawning habitat during the narrow window of the spawning period.

- RASU in fact may select spawning sites in part based not on overall mesohabitat type but on substrate characteristics such as texture and stability. Substrate disruption during actual spawning would disrupt the spawning activity, which may be why RASU appear to select stable settings for spawning, as discussed above (chapters 3 and 4). The 2016 LCR MSCP Species Account (LCR MSCP 2016a) states, with a long list of citations, "Spawning razorback suckers have . . . been collected over a variety of substrates, although the majority of spawning individuals tend to be captured over clean gravel and cobble-sized or rocky substrates." Similarly, Mueller (2006) notes that "the single commonality [among RASU spawning sites] appears to be appropriate substrate, a mixture of large gravels and small cobble . . . that have been flushed of [fine] sediments." Such substrates are self-stabilizing (i.e., resistant to erosion) because they consist of materials with high inertia. However, sites must experience at least moderate flow velocities or turbulence to be kept free of finer sediment that might discourage use of a site for spawning. Finning by spawning RASU also may remove fines from these surfaces during spawning. At the same time, as noted in the discussion of the possible effects of mesohabitat structure on staging and spawning, spawning RASU also show flexibility in substrate selection, such as the boat ramp at the IPCA (LCR MSCP biologists 2013, personal communications) and in isolated off-channel ponds (Saltzgiver et al. 2015; Dowling et al. 2016a). In any case, substrate instability is generally low in the present-day LCR and its refuges, or spatially limited and/or not highly persistent, given the limited range of mechanisms that can disturb substrates along the regulated river or in the refuges.

- RASU in this life stage, as in all life stages, are vulnerable to attack by sight-feeding predators. As in the preceding three life stages, RASU in this life stage may find it increasingly difficult to detect predators in turbidities above some threshold of reduced clarity, but potential sight-feeding predators conversely may find it increasingly difficult to detect RASU at higher turbidities as well. The benefits of turbidity for RASU in suppressing predator activity may outweigh the effects of elevated turbidity on the ability of RASU to detect predators particularly because RASU may have other behaviors that help reduce their vulnerability to detection in turbid water, including moving into cover habitat. At the same time, the present CEM does not propose that turbidity levels strongly affect staging and spawning, based on an absence of indications for such a relationship in the literature.

- A change in water temperature could be one of the cues that trigger staging and spawning, as noted in chapters 3 and 4. Most discussions of the cues for RASU staging and spawning focus on changes in flow conditions and water temperature. The interaction of these cues is perhaps better understood in the UCRB, where more natural flows and associated changes in water temperature still occur. However, changes in temperature alone, and perhaps also changes in water levels and indicators of season, may continue to provide cues in the LCR ecosystem (Minckley et al. 1991; Modde and Irving 1998; USFWS 1998, 2002a; Mueller 2006; LCR MSCP 2008, 2016a; Schooley et al. 2008; Albrecht et al. 2010b; Bestgen et al. 2011, 2012; Kegerries and Albrecht 2011; Patterson et al. 2012). Whether pheromones are also involved in triggering spawning is not known. On the other hand, RASU staging and spawning in the LCR ecosystem have been observed to take place in both lentic and lotic settings, and in isolated, hydrologically controlled ponds, as well as in open environments – a range of settings likely to exhibit a range of temperature averages and patterns of seasonal and diel variation. These facts suggest alternatively that water temperature may not have a consistently strong bearing on staging and spawning in the LCR ecosystem.

The present CEM identifies four habitat elements with high-magnitude direct effects on competition, foraging, resting/hiding, and ripening, the four critical biological activities and processes with high-magnitude indirect effects on the outcomes of this life stage. The four habitat elements in this case are the taxonomic compositions, spatial and temporal distributions, abundances, and activity levels of the (1) aquatic vertebrate assemblage, (2) aquatic invertebrate assemblage, (3) mesohabitat structure, and (4) water temperature (see chapters 3 and 4 for details).

- Spawning RASU may experience competition from other aquatic vertebrates not only for food items but also for habitat, especially for cover.

- Adult RASU feed primarily on benthic organisms and POM but may also consume zooplankton and POM in the water column. The abundance and composition of the planktonic and benthic communities and the abundance and composition of POM therefore shape the availability of suitable foods for spawning RASU during staging and resting. At the same time, some aquatic macroinvertebrates may feed on the same types of aquatic invertebrates and fine POM, on which RASU feed during this life stage, during staging and resting/hiding, thus competing with spawning RASU for these foods.

- RASU participating in a spawning cycle rest at staging sites and in the vicinity of their spawning sites. They may use resting/hiding sites in the vicinity of their spawning sites for some time after completing spawning. Mesohabitat structure determines the types and abundance of cover at resting/hiding sites and along movement pathways between them and the spawning sites. Spawning RASU may identify suitable or unsuitable resting/hiding locations based in part on mesohabitat form, including the availability of cover, deeper (darker) water (LCR MSCP 2016b), or elevated turbidity.

- A change in water temperature could be one of the cues that trigger ripening. However, RASU individuals may exhibit external reproductive traits for many months without becoming ripe (Minckley et al. 1991), indicating that sexual maturation and ripening are at least partially independent, making it difficult to determine what factors affect ripening. Conceivably, water temperature might affect ripening only indirectly via effects on health and foraging success.

Finally, the present CEM identifies one habitat element, the bird and mammal assemblage, that may affect one or both outcomes for this life stage indirectly, through some other high-impact causal relationship, but for which there is not sufficient information available to estimate the magnitude of the effect. Specifically, as noted for earlier life stages, water temperature presumably affects the activity of all birds and mammals that may feed in or along the shorelines of LCR waters. However, as noted for the preceding life stage, this suite of relationships has not been studied for the LCR ecosystem.

The information reviewed for the present CEM (figure 7) indicates a low level of understanding of most of the high-magnitude causal linkages described in the preceding paragraphs that affect spawning RASU survival and fertility. The poorly understood causal relationships include (1) the effects of predation on

survival among spawning RASU, (2) the effects of competition on resting/hiding behaviors, (3) the effects of foraging success on ripening, (4) the effects of predation, ripening, and swimming behaviors on staging and spawning, (5) the effects of resting/hiding and swimming behaviors on predation rates, (6) the effects of the abundance and activity of aquatic vertebrates on competition, predation, and RASU swimming behaviors, (7) the effects of the abundance and activity of predatory birds on predation, (8) the effects of the abundance and activity of aquatic invertebrates on competition, (9) the effects of mesohabitat structure on resting/hiding behaviors and on staging and spawning itself, (10) the effects of substrate texture/dynamics on staging and spawning, (11) the effects of turbidity on predation, and (12) the effects of water temperature on both ripening and staging and spawning. That is, the literature presents insufficient information or shows little agreement concerning the character, magnitude, and/or predictability of these proposed causal relationships.

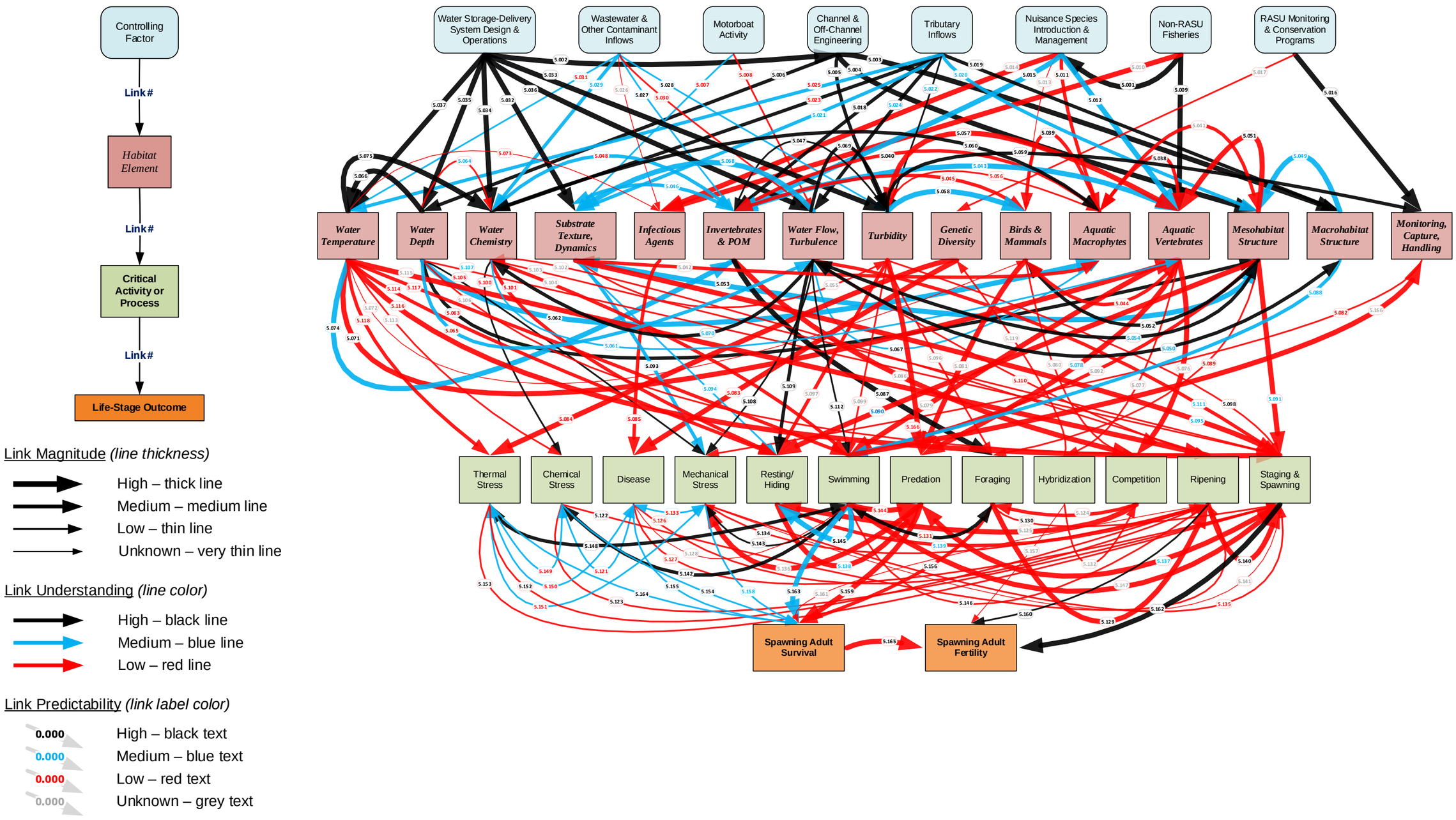


Figure 7.—RASU life stage 5 – spawning adult life stage, showing the relevant controlling factors, habitat elements, and critical biological activities and processes.

Chapter 7 – Causal Relationships Across All Life Stages

This chapter examines the information assembled for the present 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

Table 15 shows which critical biological activities and processes directly affect each life-stage outcome, the estimated magnitude of each effect, and the estimated level of understanding of the effect. Five critical biological activities or processes – chemical stress, disease, mechanical stress, predation, and thermal stress – directly affect at least one life-stage outcome for every life stage. Two critical biological activities or processes – foraging and swimming – directly affect at least one life stage for every life stage except the first, eggs and pre-dispersal larvae. Resting/hiding directly affects at least one life-stage outcome for every life stage except the first and last – eggs and pre-dispersal larvae, and spawning. However, it strongly affects spawning indirectly through its direct effects on predation and ripening. Several critical biological activities or processes affect life-stage outcomes for only a single life stage – egg settling and

Table 15.—Direct effects of critical biological activities and processes on life-stage outcomes

Key: Cell colors indicate the potential magnitude of the effect: High = ; Medium = ; Low = ; Unknown = .
Letters in cells indicate the level of understanding of the effect: High = ***H***; Medium = ***M***; Low = ***L***.

Life-stage outcome ➔ / **Critical biological activity or process 🡻**	Egg and pre-dispersal larval survival rate	Post-dispersal larval and younger juvenile survival rate	Older juvenile and subadult survival rate	Adult annual survival rate	Adult annual spawning participation rate	Spawning adult survival rate	Spawning adult fertility rate
Chemical stress	***M***	***M***	***M***	***M***	***L***	***M***	
Competition							
Disease	***M***	***M***	***M***	***M***	***L***	***M***	
Drifting		***L***					
Egg settling and adhesion	***H***						
Foraging		***L***	***L***	***L***	***L***	***L***	
Hybridization							***L***
Mechanical stress	***L***	***M***	***M***	***M***	***L***	***M***	
Predation	***L***	***L***	***L***	***L***		***L***	
Resting/hiding		***L***	***L***	***L***	***L***		
Ripening						***L***	***H***
Staging and spawning							***H***
Swimming		***L***	***L***	***L***	***L***	***M***	
Thermal stress	***M***	***M***	***M***	***M***	***L***	***M***	

adhesion for eggs and pre-dispersal larvae, drifting for post-dispersal larvae and younger juveniles, and hybridization, ripening, and staging and spawning for spawning adults. Finally, one critical activity or process, competition, has no direct effect on any life-stage outcome in any life stage. However, competition indirectly affects life-stage outcomes in every life stage except the first through its effects on two other critical biological activities and processes, foraging and resting/hiding, as discussed later in this chapter.

Table 15 indicates the following important (medium- or high-magnitude) direct effects of critical biological activities or processes on life-stage outcomes. As noted above (see also attachment 1), magnitude refers to the degree to which a given causal factor controls some condition relative to other factors affecting that same condition. It refers to the potential for the causal factor to have a stated effect. Specifically, the present CEM proposes that:

- Drifting has a direct, medium-magnitude potential effect on post-dispersal larval and younger juvenile survival. The present CEM identifies this as a medium- rather than a high-magnitude relationship because some settings provide nursery habitat immediately adjacent to spawning areas, allowing the dispersing larvae to move directly into nursery habitat essentially without drifting. However, the present CEM proposes that the relationship is not well understood.

- Egg settling and adhesion has a direct, high-magnitude potential effect on egg and pre-dispersal larval survival, and notes that this relationship appears to be well understood.

- Foraging has a direct, high-magnitude potential effect on older juvenile and subadult survival and adult survival; a direct, high-magnitude potential effect on the annual spawning participation rate among adults; and a direct, medium-magnitude potential effect on post-dispersal larval and younger juvenile survival, and spawning adult survival. However, the present CEM proposes that these relationship are not well understood.

- Mechanical stress has a direct, medium-magnitude potential effect on egg and pre-dispersal larval survival. However, the present CEM also proposes that the relationship is not well understood.

- Predation has a direct, high-magnitude potential effect on survival in every life stage. However, the relationship is not well understood. A few studies document predation on RASU in one or more life stages by individuals of several predatory invertebrate, vertebrate, and bird species. However, the present CEM identifies significant gaps in knowledge of the rates of predation by different predators, the overall effects of predation on survival in different life stages in different environments, or the factors that help RASU avoid or escape predation.

- Resting/hiding behaviors, particularly the ability to find suitable protective cover, have a direct, medium-magnitude potential effect on survival in all motile life stages except spawning. As noted above, the effects of resting/hiding behaviors on survival among spawning adults are indirect,

resulting from the effects of resting/hiding behaviors on ripening success and vulnerability to predation. The present CEM also proposes that these relationships are not well understood.

- The success of staging and spawning activities necessarily has a direct, high-magnitude effect on spawning adult fertility – a well understood relationship.

- Swimming behaviors have a high-magnitude potential effect on spawning adult survival because of the additional demands that spawning activities place on adult stamina. The present CEM estimates that this relationship is at least moderately well understood.

- Thermal stress has a direct, high-magnitude potential effect on egg and pre-dispersal larval survival and post-dispersal larval and younger juvenile survival. Temperature can significantly affect growth rates in these two life stages, with excessively low temperatures (recognized by the present CEM as a form of thermal stress) significantly suppressing growth. The present CEM estimates that these relationships are at least moderately well understood.

EFFECTS OF CRITICAL BIOLOGICAL ACTIVITIES AND PROCESSES ON EACH OTHER

Table 16 shows which critical biological activities and processes directly affect other critical biological activities and processes, thereby influencing life-stage outcomes indirectly across the five RASU life stages, the estimated magnitude of these effects, and the estimated level of understanding of the effects.

Table 16 indicates the following important (medium- or high-magnitude) direct effects of critical biological activities or processes on each other. As noted above (see also attachment 1), magnitude refers to the degree to which a given causal factor controls some condition relative to other factors affecting that same condition. It refers to the potential for the causal factor to have a stated effect. Specifically, the present CEM proposes that:

- Competition has a direct, medium-magnitude potential effect on RASU foraging success and a direct, high-magnitude potential effect on RASU resting/hiding behaviors in all four motile life stages. The present CEM also proposes that these relationships are not well understood.

Table 16.—Direct effects of critical biological activities and processes on each other

Key: Cell colors indicate the potential magnitude of the effect: High = ; Medium = ; Low = ; Unknown = .

Numbers in cells indicate the number of life stages in which the present CEM recognizes this relationship.

Subscripted letters with each number indicate the level of understanding of the effect: High = ***H***; Medium = ***M***; Low = ***L***.

An asterisk (*) indicates the relationship is bi-directional.

Affected activity or process ➔ / **Causal activity or process ➔**	Chemical stress	Competition	Disease	Drifting	Foraging	Mechanical stress	Predation	Resting/hiding	Ripening	Staging and spawning	Swimming	Thermal stress
Chemical stress			5_M*						1_L	1_L		
Competition					4_L			4_L				
Disease									1_L	1_L	4_L	
Drifting					1_L		1_M	1_L				
Egg settling and adhesion							1_M					
Foraging									1_L	1_L	1_H3_M*	
Hybridization		1_L										
Mechanical stress			1_H4_M*						1_L	1_L		
Predation						5_L				1_L*		
Resting/hiding							4_L		1_L			
Ripening										1_L		
Staging and spawning						1_L*						
Swimming	3_H*			1_L		3_H*	4_L	1_L3_M	1_L	1_L		1_H2_M*
Thermal stress	5_M*		1_H4_M*			5_M*			1_L	1_L		

- Drifting has a direct, high-magnitude potential effect on predation among post-dispersal larvae and younger juveniles. The duration of drifting and the exposure of the drifting larvae to predators along the drift pathway both have high potentials to affect the predation rate. The present CEM also proposes that this relationship is likely moderately well understood.

- Egg settling and adhesion has a direct, high-magnitude potential effect on predation among eggs and pre-dispersal larvae. The length of time that elapses from egg release to adhesion has a high potential to affect the predation rate. The present CEM also proposes that this relationship is likely moderately well understood.

- Foraging has a direct, high-magnitude potential effect on ripening among spawning adults and on swimming behaviors in all four motile life stages. Foraging success determines whether RASU have sufficient nutrition to sustain their stamina for these activities. However, the present CEM proposes that the relationship between foraging and ripening is not well understood. The relationship between foraging and swimming is bi-directional: RASU must swim effectively to forage effectively, and vice versa.

- Predation has a direct, medium-magnitude potential effect on mechanical stress in all life stages. Unsuccessful predator attacks nevertheless may injure the attacked RASU. The present CEM also proposes that these relationships are not well understood.

- Predation also has a direct, high-magnitude potential to disrupt staging and spawning not simply by causing mortality but by scattering any RASU that detect and attempt to avoid the predators. However, the present CEM also proposes that this relationship is not well understood.

- Resting/hiding behaviors, particularly the ability to find suitably protective cover conditions, has a direct, high-magnitude potential effect on predation in all four motile life stages. The present CEM also proposes that these relationships are not well understood.

- Resting/hiding activity also has a direct, medium-magnitude potential effect on ripening among spawning adults. The present CEM posits that RASU that succeed in finding suitable resting/hiding locations during the weeks or months leading up to spawning are more likely to survive and maintain the health needed to ripen. However, the present CEM also proposes that this relationship is not well understood.

- Ripening necessarily has a direct, high-magnitude effect on staging and spawning among spawning adults. However, the present CEM also proposes that this relationship is not well understood.

- Swimming behaviors have a direct, medium-magnitude potential effect on chemical stress among older juveniles and subadults, adults, and spawning adults. Individuals in these life stages have increasing abilities to swim away from or out of potentially chemically stressful water, avoiding or reducing chemical stress. The present CEM proposes that this relationship is well understood.

- Swimming behaviors also have a direct, high-magnitude potential effect on drifting success because the dispersing larvae must swim to control their movement into and out of the drifting currents. Similarly, swimming behaviors have a direct, high-magnitude potential effect on staging and spawning success. However, the present CEM also proposes that these relationships are not well understood.

- Swimming activities have a direct, high-magnitude potential effect on predation and resting/hiding activities. Predator avoidance and movement in/out of protective resting/hiding habitat (cover) are crucial to RASU survival. The present CEM proposes that these relationships across the four motile life stages are weakly to moderately well understood.

- Swimming behaviors have a direct, medium-magnitude potential effect on thermal stress among older juveniles and subadults, adults, and spawning adults. Individuals in these life stages have increasing abilities to swim away from or out of potentially thermally stressful water, avoiding or reducing thermal stress. The present CEM proposes that this relationship is well to moderately well understood among these three life stages.

- Thermal and mechanical stress reciprocally potentially directly affect each other with medium magnitude in all five life stages. Individuals compromised by one form of stress are more likely to be vulnerable to the other form of stress. The present CEM proposes that this relationship is moderately well understood among these three life stages.

EFFECTS OF HABITAT ELEMENTS ON CRITICAL BIOLOGICAL ACTIVITIES AND PROCESSES

Table 3 (see chapter 4) identifies which habitat elements affect which critical biological activities and processes. These relationships are largely identical across all life stages in the CEM. However, some critical biological activities and processes – and therefore some habitat elements – only come into play for one or two life stages. Tables 2 and 15 identify which critical biological activities and processes matter for which life stages. Table 17 shows which habitat elements directly affect which critical biological activities and processes (as in table 3) and indicates the estimated average magnitude of these effects and estimated average level of understanding of these effects among the five RASU life stages.

Table 17 indicates the following important (medium- or high-magnitude) direct effects of habitat elements on critical biological activities or processes. As noted above (see also attachment 1), magnitude refers to the degree to which a

Table 17.—Direct effects of habitat elements on critical biological activities and processes

Key: Cell colors indicate the potential magnitude of the effect (average across all life stages): High = ; Medium = ; Low = ; Unknown = .
Letters in each cell indicate the level of understanding of the effect: High = ***H***; Medium = ***M***' Low = ***L***.
An asterisk (*) indicates the relationship is bi-directional.

Critical biological activity or process ➔ / **Habitat element ➓**	Chemical stress	Competition	Disease	Drifting	Egg settling and adhesion	Foraging	Hybridization	Mechanical stress	Predation	Resting/hiding	Ripening	Staging and spawning	Swimming	Thermal stress
Aquatic macrophytes														
Aquatic vertebrates		***L***					***L***		***M***				***L***	
Birds and mammals		***L***							***L***					
Genetic diversity			***L***											***L***
Infectious agents			***L***											
Invertebrates and POM		***L***				***H***			***L***					
Macrohabitat structure				***M***									***M***	
Mesohabitat structure				***M***		***M***				***L***		***L***	***L***	
Monitoring, capture, handling					***L***			***L***						
Pre-release conditioning	***L***		***L***			***L***			***L***				***L***	***L***
Substrate texture/dynamics					***L***			***L***		***L***		***L***		
Turbidity						***L***			***L***	***L***		***L***	***L***	
Water chemistry	***H***									***L***	***L****	***L****	***L***	
Water depth					***M***			***H***			***L***	***L***		
Water flow/turbulence				***M***	***M***			***M***		***H***	***X***	***L***	***H***	
Water temperature	***L***									***L***	***L***	***L***	***L***	***L***

given causal factor controls some condition relative to other factors affecting that same condition. It refers to the potential for the causal factor to have a stated effect. Specifically, the present CEM proposes that:

- The taxonomic composition, size range, spatial and temporal distributions, and abundance of the aquatic macrophyte assemblage have no direct impacts of any magnitude on any critical biological activities or processes. As discussed below, however, they do have direct, high-magnitude potential effects on other habitat elements, as a result of which they indirectly affect several critical biological activities or processes.

- The taxonomic composition, size range, spatial and temporal distributions, and abundance of the aquatic vertebrate assemblage on average have direct, high-magnitude potential effects on competition, predation, and RASU swimming activities. The present CEM proposes that these relationships are only poorly to moderately well understood.

- The taxonomic composition, size range, spatial and temporal distributions, and abundance of the bird and mammal assemblages on average have direct, medium-magnitude potential effects on predation. The present CEM proposes that these relationships are not well understood.

- Genetic diversity has direct, high-magnitude potential effects on disease and vulnerability to thermal stress. The present CEM proposes that these relationships are not well understood.

- Infectious agents on average have direct, medium-magnitude potential effects on disease. The present CEM proposes that these relationships are not well understood.

- The taxonomic composition, size range, spatial and temporal distributions, and abundance of the aquatic invertebrate assemblage on average have direct, high-magnitude potential effects on competition and foraging, and direct, medium-magnitude potential effects on predation. The present CEM proposes that the effects on foraging are well understood, while the effects on competition and predation are not well understood.

- Macrohabitat structure on average has direct, medium-magnitude potential effects on drifting during the post-dispersal larval and younger juvenile life stage and on swimming behaviors during all four motile life stages. The present CEM proposes that these relationships are moderately well understood.

- Mesohabitat structure on average has direct, medium-magnitude potential effects on drifting and foraging, and direct, high-magnitude potential effects on resting/hiding and swimming behaviors during all four motile life stages and on staging among spawning adults. The present CEM proposes that the medium-magnitude effects are moderately well understood while the high-magnitude effects are only poorly understood.

- Pre-release condition on average has direct, high-magnitude potential effects on chemical stress, foraging, predation, swimming, and thermal stress among repatriated subadult and adult RASU. The present CEM proposes that these relationships are only poorly understood.

- Substrate texture/dynamics have direct, high-magnitude potential effects on egg settling and adhesion and on staging and spawning. The present CEM proposes that these relationships are only poorly understood.

- Turbidity has direct, consistently high-magnitude potential effects on predation on all five life stages. Turbidity also has medium-magnitude potential effects on resting/hiding activities in all four motile life stages because turbidity potentially can provide protective resting/hiding habitat (cover) for RASU in these life stages. The present CEM proposes that these relationships are all poorly understood.

- Water chemistry on average has direct, medium-magnitude potential effects on resting/hiding and swimming activities in all four motile life stages. Variation in water chemistry potentially can provide cues to help RASU navigate and locate resting/hiding habitat. The present CEM proposes that these relationships are not well understood.

- Water depth on average has direct, medium-magnitude potential effects on egg settling and adhesion during the egg and pre-dispersal larval life stage and on mechanical stress in all five life stages. The greater the water depth at a spawning site, the greater the potential for release of the eggs at some distance above the substrate, increasing the chances for disruption of the process of egg settling. Changes in water depth, as a result of water supply system operations, potentially can create conditions that result in mechanical stress to RASU in the affected waters. The present CEM proposes that the potential effects on mechanical stress are well understood, while the potential effects on egg settling and adhesion are moderately well understood.

- Water flow/turbulence on average has direct, medium-magnitude potential effects drifting, egg settling and adhesion, mechanical stress, resting/hiding, and staging and spawning. Except for the effects on staging and spawning, these relationships appear to be well to moderately well understood. The present CEM proposes that the effects on staging and spawning are only poorly understood as a result of continuing uncertainty about the range of flow conditions that RASU find suitable at spawning sites and about the possible role of flow pulses in triggering spawning activity.

- Water temperature has direct, high-magnitude potential effects on ripening and on staging and spawning, including the potential role of changing water temperature as a trigger for spawning activity. The present CEM proposes that these relationships are only poorly understood.

- Water temperature on average also has direct, medium-magnitude effects on resting/hiding, swimming activities, and thermal stress. The present CEM proposes that these relationships are only poorly understood.

EFFECTS OF HABITAT ELEMENTS ON EACH OTHER

Table 4 (see chapter 4) identifies which habitat elements affect other habitat elements. These relationships are largely identical across all life stages in the CEM. However, some habitat elements only come into play for one or two life stages. Table 18 shows which habitat elements directly affect which other habitat elements (as in table 4) and indicates the estimated average magnitude of these effects and estimated average level of understanding of these effects among the five RASU life stages.

Table 18.—Direct effects of habitat elements on each other

Key: Cell colors indicate the potential magnitude of the effect: High = ; Medium = ; Low = ; Unknown = .
Letters in each cell indicate the level of understanding of the effect: High = H; Medium = M; Low = L.
An asterisk (*) indicates the relationship is bi-directional.

Affected habitat element ➔ / **Causal habitat element ➔**	Aquatic macrophytes	Aquatic vertebrates	Birds and mammals	Infectious agents	Invertebrates and POM	Macrohabitat structure	Mesohabitat structure	Monitoring, capture, handling	Substrate texture/dynamics	Turbidity	Water chemistry	Water flow/turbulence	Water temperature
Aquatic macrophytes		***L****	***L***		***L****		***L****		***L****				
Aquatic vertebrates					***M****								
Birds and mammals		***L****			***L***								
Invertebrates and POM									***M****	***H****	***M****		
Macrohabitat structure							***M***					***H****	
Mesohabitat structure		***L***	***H***						***M****			***H****	
Substrate texture/dynamics										***L***			
Turbidity	***L***	***L****	***M***					***H***					
Water chemistry	***H****	***M***											
Water depth	***M***						***H***				***L***	***M***	***H***
Water flow/turbulence	***M****								***M***	***H***	***H***		
Water temperature		***L***	***L***	***L***	***M***						***H***		

Table 18 indicates the following important (medium- or high-magnitude) direct effects of habitat elements on each other. As noted above (see also attachment 1), magnitude refers to the degree to which a given causal factor controls some condition relative to other factors affecting that same condition. It refers to the potential for the causal factor to have a stated effect. Specifically, the present CEM proposes that:

- The taxonomic composition, size range, spatial and temporal distributions, and abundance of the aquatic macrophyte assemblage have medium-magnitude potential effects on aquatic vertebrates, invertebrates and POM, mesohabitat structure, and substrate texture/dynamics, and vice versa. The taxonomic composition, size range, spatial and temporal distributions, and abundance of the aquatic macrophyte assemblage also have medium-magnitude potential effects on birds and mammals, but this set of relationships is unidirectional; there is no reciprocal, feedback relationship. The present CEM proposes that these relationships are only poorly understood.

- The taxonomic composition, size range, spatial and temporal distributions, and abundance of the aquatic vertebrate assemblage potentially affect the aquatic invertebrate assemblage with high magnitude. The relationship is bi-directional. The present CEM proposes that the relationships between aquatic vertebrates and invertebrates are moderately well understood.

- The taxonomic composition, size range, spatial and temporal distributions, and abundance of the bird and mammal assemblage have medium-magnitude potential effects on the aquatic vertebrate assemblage and the invertebrate assemblage. The effects on the aquatic vertebrate assemblage are reciprocal; this is a bi-directional set of relationships. The present CEM proposes that both sets of relationships are only poorly understood.

- The taxonomic composition, size range, spatial and temporal distributions, and abundance of the aquatic invertebrate and POM assemblage have medium-magnitude potential effects on substrate texture/dynamics and on water chemistry. Both sets of relationships are bi-directional. The present CEM proposes that both sets of relationships are moderately well understood.

- Macrohabitat structure has high-magnitude potential effects on mesohabitat structure and medium-magnitude potential effects on water flow/turbulence. The interrelationships between macrohabitat structure and water flow/turbulence are bi-directional. The present CEM proposes that the effects of macrohabitat structure on water flow/turbulence are well understood, while the effects on mesohabitat structure are only moderately well understood.

- Mesohabitat structure has high-magnitude potential effects on aquatic vertebrates and substrate texture/dynamics, and medium-magnitude potential effects on birds and mammals and on water flow/turbulence. The effects on substrate texture/dynamics and on water flow/turbulence are bi-directional. The present CEM proposes that the effects of mesohabitat structure on birds and mammals and on water flow/turbulence are well understood, the effects on substrate texture/dynamics are moderately well understood, and the effects on aquatic vertebrates are poorly understood.

- Turbidity has high-magnitude potential effects on aquatic vertebrates and on birds and mammals, and medium-magnitude potential effects on monitoring, capture, and handling. The effects on aquatic vertebrates are bi-directional. The present CEM proposes that the effects of turbidity on monitoring, capture, and handling are well understood, the effects on birds and mammals are moderately well understood, and the effects on aquatic vertebrates are poorly understood.

- Water chemistry has medium-magnitude potential effects on aquatic macrophytes, and vice versa. The present CEM proposes that both sets of relationships are well understood.

- Water depth has high-magnitude potential effects on aquatic macrophytes and water temperature, and medium-magnitude potential effects on mesohabitat structure and on water flow/turbulence. The present CEM proposes that the effects of water depth on mesohabitat structure and water temperature are well understood, while the effects on aquatic macrophytes and water flow/turbulence are moderately well understood.

- Water flow/turbulence has high-magnitude potential effects on substrate texture/dynamics, and medium-magnitude potential effects on turbidity and water chemistry. The present CEM proposes that the effects of water flow/turbulence on turbidity and water chemistry are well understood, while the effects on substrate texture/dynamics are moderately well understood.

- Water temperature has high-magnitude potential effects on aquatic vertebrates, aquatic invertebrates, and water chemistry. The present CEM proposes that the effects of water temperature water chemistry are well understood, the effects on aquatic invertebrates are moderately well understood, and the effects on aquatic vertebrates are not well understood.

EFFECTS OF CONTROLLING FACTORS ON HABITAT ELEMENTS

Table 14 (see chapter 5) identifies which controlling factors affect which habitat elements. These relationships are identical across all life stages in the CEM. Table 19 shows which controlling factors directly affect which habitat elements (as in table 14) and indicates the estimated average magnitude of these effects and estimated average level of understanding of these effects among the five RASU life stages.

Table 19.—Direct effects of controlling factors on habitat elements

Key: Cell color indicates the potential magnitude of the effect: High = ; Medium = ; Low = ; Unknown = .
Letters in each cell indicate THE level of understanding of the effect: High = ***H***; Medium = ***M***; Low = ***L***.

Habitat elements ➔ / **Controlling factors 🡻**	Aquatic macrophytes	Aquatic vertebrates	Birds and mammals	Genetic diversity	Infectious agents	Invertebrates and POM	Macrohabitat structure	Mesohabitat structure	Monitoring, capture, handling	Pre-release conditioning	Substrate texture/dynamics	Turbidity	Water chemistry	/Water depth	Water flow/turbulence	Water temperature
Channel and off-channel engineering							***H***	***H***				***H***		***H***		
Motorboat activity											***M***				***L***	
Non-RASU fisheries		***H***			***L***											
Nuisance species introduction and management	***L***	***M***	***L***		***L***	***M***										
RASU monitoring and conservation programs				***H***					***H***	***H***						
Tributary inflows						***H***	***H***	***M***			***M***	***H***	***H***		***H***	***M***
Wastewater and other contaminant inflows					***L***	***M***						***M***	***M***		***L***	***M***
Water storage-delivery system design and operations											***H***	***H***	***H***	***H***	***H***	***H***

Table 19 indicates the following important (medium- or high-magnitude) direct effects of habitat elements on each other. As noted above (see also attachment 1), magnitude refers to the degree to which a given causal factor controls some condition relative to other factors affecting that same condition. It refers to the potential for the causal factor to have a stated effect. Specifically, the present CEM proposes that:

- Channel and off-channel engineering have high-magnitude effects on macrohabitat structure and mesohabitat structure, and medium-magnitude effects on turbidity and water depth. The present CEM proposes that all four sets of effects are well understood.

- Non-RASU fisheries have high-magnitude effects on aquatic vertebrates and infectious agents. The present CEM proposes that the effects on the aquatic vertebrate assemblage are well understood, while the effects on infectious agents are not well understood.

- Nuisance species introduction and management have high-magnitude effects on the aquatic vertebrate assemblage, infectious agents, and the aquatic invertebrate assemblage, and medium-magnitude effects on the aquatic macrophyte assemblage. The present CEM proposes that the effects on the aquatic vertebrate and invertebrate assemblages are moderately well understood, while the effects on infectious agents and the aquatic macrophyte assemblage are not well understood. The present CEM also notes that nuisance species introductions and management could be affecting the bird and mammal assemblages, but the types and magnitude of these effects are unknown.

- RASU monitoring and conservation programs have high-magnitude effects on genetic diversity; monitoring, capture, and handling; and pre-release conditioning. The present CEM notes that these effects are well understood.

- Tributary inflows have medium-magnitude effects on aquatic invertebrates and POM, macrohabitat structure, mesohabitat structure, substrate texture/ dynamics, water chemistry, water flow/turbulence, and on water temperature. The present CEM proposes that the effects on the aquatic invertebrates and POM, macrohabitat structure, water chemistry, and on water flow/turbulence are well understood, while the effects on mesohabitat structure, substrate texture/dynamics, and on water temperature are moderately well understood.

- Wastewater and other contaminant inflows have medium-magnitude effects on water chemistry. The present CEM proposes that these effects are moderately well understood. The present CEM also notes that wastewater and other contaminant inflows could be affecting the diversity of infectious agents present in the system, but the types and magnitude of these effects are unknown.

- Water storage-delivery system design and operations have high-magnitude effects on substrate texture/dynamics, turbidity, water chemistry, water depth, water flow/turbulence, and water temperature. The present CEM notes that these effects are all well understood.

The present CEM also recognizes that two controlling factors affect two others. Specifically, non-RASU fisheries affect nuisance species introduction and management, and water storage-delivery system design and operations affect channel and off-channel engineering. In the first instance, past non-RASU fisheries activities introduced some nuisance species into the LCR ecosystem. Some species introduced as bait and as forage for sport fisheries have become nuisance species, and agency fishery management practices – at least in the past – may have tolerated or even encouraged unofficial introductions of other bait and forage species. Some nuisance species may be infectious agents carried by introduced bait, forage, and sport fishery species. In the second instance, the needs for water storage and delivery, system-wide, have long been the primary drivers of decisions on where, when, and how Reclamation and its partners have needed to modify (engineer) channel and off-channel geometry (LCR MSCP 2004).

POTENTIALLY INFLUENTIAL CAUSAL RELATIONSHIPS WITH LOW UNDERSTANDING

Many causal relationships proposed in the present CEM (see chapter 6) are rated as having low understanding. The present CEM proposes these relationships based on established ecological principles and suggestions in the literature on RASU. 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.

Table 20 identifies those direct causal relationships that the present CEM proposes have high magnitude but low understanding for which the causal agent is a habitat element. Table 20 indicates the number of life stages for which the present CEM proposes each relationship and indicates which relationships are hypothesized to be bi-directional.

Table 20.—Poorly understood high-magnitude direct effects of habitat elements

Key: Numbers indicate the number of life stages for which the present CEM proposes the effect.
An asterisk (*) indicates the relationship is bi-directional.

Affected factor ➔ / **Causal factor 🡻**	Aquatic vertebrates	Chemical stress	Competition	Disease	Egg settling and adhesion	Foraging	Predation	Resting/hiding	Ripening	Staging and spawning	Swimming	Thermal stress
Aquatic vertebrates			**4**				**4**				**4**	
Birds and mammals							**3**					
Genetic diversity				**5**								**5**
Invertebrates and POM			**4**				**2**					
Mesohabitat structure	**5**							**3**		**1**	**3**	
Pre-release conditioning		**1**				**1**	**1**				**1**	**1**
Substrate texture/dynamics					**1**					**1**		
Turbidity	**5***						**5**					
Water temperature	**5**								**1**	**1**		

Table 20 indicates consistently low levels of understanding of the ways in which three habitat elements – mesohabitat structure, turbidity, and water temperature – directly affect the taxonomic composition, size range, spatial and temporal distributions, and/or abundance of the aquatic vertebrate assemblage. The relationship between turbidity and the aquatic vertebrate assemblage is bi-directional. Some aquatic vertebrates, such as common carp, disturb substrates and thereby can generate turbidity themselves.

Table 20 further indicates low levels of understanding of:

- The ways in which the taxonomic composition, size range, spatial and temporal distributions, and/or abundance of the aquatic vertebrate assemblage affect competition with and predation on RASU, and affect RASU swimming behaviors (e.g., avoidance or defensive behaviors).

- The ways in which the taxonomic composition, size range, spatial and temporal distributions, and/or abundance of the bird and mammal assemblages affect predation on RASU.

- The ways in which genetic diversity among RASU may affect their susceptibility to disease or thermal stress.

- The ways in which the taxonomic composition, size range, spatial and temporal distributions, and/or abundance of the aquatic invertebrate assemblage affect competition with and predation on RASU.

- The ways in which mesohabitat structure affects the aquatic vertebrate assemblage, RASU resting/hiding activities (i.e., use of cover), staging and spawning activity, and swimming behaviors.

- The ways in which pre-release conditioning – both routine conditioning to normal facility conditions and adaptive conditioning to demands the RASU may face upon release – affects RASU sensitivity to chemical stress, foraging behaviors, vulnerability to predation, swimming strength and stamina, and sensitivity to thermal stress.

- The ways in which substrate texture/dynamics affect egg settling and adhesion, and staging and spawning behavior.

- The ways in which turbidity affects aquatic vertebrates and predation rates.

- The ways in which water temperature affects the aquatic vertebrate assemblage, ripening, and staging and spawning success.

Table 21, in turn, identifies those direct causal relationships that the present CEM proposes have high magnitude but low understanding, for which the causal agent is a critical biological activity or process. Table 21 also indicates the number of life stages for which the present CEM proposes each relationship and indicates which relationships are hypothesized to be bi-directional.

Table 21 identifies six critical biological activities or processes – competition, foraging, predation, resting/hiding, ripening, and swimming – that the present CEM proposes have high-magnitude but poorly understood direct effects either on other critical biological activities or processes or on particular life-stage outcomes. Specifically, table 21 indicates low levels of understanding of:

- The effects of competition on RASU resting/hiding activities (i.e., the degree to which RASU face competition for habitat space, including cover).

- The effects of foraging success on RASU ripening, older juvenile and subadult survival, adult annual survival, and the adult annual spawning participation rate.

Table 21.—Poorly understood high-magnitude direct effects of critical biological activities and processes

Key: Numbers indicate the number of life stages for which the present CEM proposes the effect.
An asterisk (*) indicates relationship is bi-directional.

	Affected critical biological activity or process						**Affected life-stage outcome**					
Causal factor ↓	Drifting	Mechanical stress	Predation	Resting/hiding	Ripening	Staging and spawning	Egg and pre-dispersal larval survival rate	Post-Dispersal larval and younger juvenile survival rate	Older juvenile and subadult survival rate	Adult annual survival rate	Adult annual spawning participation rate	Spawning adult survival rate
Competition				**4**								
Foraging					**1**				**1**	**1**	**1**	
Predation		**4**				**1***	**1**	**1**	**1**	**1**		**1**
Resting/Hiding			**4**									
Ripening						**1**						
Swimming	**1**		**4**	**1**		**1**						

- The effects of predation on mechanical stress due to injuries from predator attacks, on staging and spawning success, and on RASU survival in every life stage. The relationship between predation and staging and spawning, as noted earlier, is proposed to be bi-directional because predation can disrupt staging or spawning, while RASU that engage in staging and spawning behaviors may make themselves more vulnerable to predation.

- The effects of resting/hiding activities – specifically, the effects of use of cover – on predation rates.

- The effects of ripening on staging and spawning.

- The effects of swimming behaviors, strength, and stamina on drifting by larvae after dispersing from their natal sites, predation, resting/hiding behaviors, and staging and spawning success.

The present CEM also proposes that one critical activity or process – swimming – has high-magnitude but poorly understood direct effects on one habitat element, monitoring, capture, handling. The present CEM proposes specifically that swimming has high-magnitude but poorly understood direct

effects on monitoring, capture, and/or handling of post-dispersal larvae and younger juveniles, older juveniles and subadults, and adults.

Additionally, the present CEM recognizes two controlling factors that have hypothesized high-magnitude direct effects that are poorly understood. As noted earlier in this chapter, non-RASU fisheries and nuisance species introduction and management could both affect the incidence of infectious agents in the LCR ecosystem with high magnitude. However, the literature does not provide sufficient information to establish a firm understanding of the situation.

Finally, the present CEM proposes several causal relationships that appear reasonable based on established ecological principles but for which the literature on RASU does not provide sufficient information to estimate the magnitude of the effect. Table 22 identifies all relationships identified by the present CEM with unknown magnitude and low understanding, specifically:

- The possible effects of nuisance species introduction and management on the compositions of the bird and mammal assemblages.
- The possible effects of wastewater and other contaminant inflows on the types and abundance of infectious agents in the LCR ecosystem.
- The possible effects of birds and mammals on the rate of predation on one particular life stage, eggs and pre-dispersal larvae.
- The possible effects of pre-release conditioning on disease rates among repatriated RASU.
- The possible effects of water temperature on the activity levels of birds and mammals and on infectious agents.
- The possible effects of disease burden on RASU swimming strength and stamina.
- The possible effects of drifting behaviors on foraging and resting/hiding behaviors among post-dispersal larvae and younger juveniles.
- The possible effects of hybridization on the spawning adult fertility rate.
- The possible effects of predation on mechanical stress in one particular life stage, eggs and pre-dispersal larvae.
- The possible effects of ripening – specifically its bioenergetic demands – on the spawning adult survival rate.
- The possible effects of staging and spawning on mechanical stress, and vice versa.

Table 22.—Poorly understood causal relationships of unknown magnitude

Key: Numbers indicate number of life stages for which CEM proposes the effect.
An asterisk (*) indicates the relationship is bi-directional.

Affected factor ➔ / **Causal factor ➓**	Birds and mammals	Infectious agents	Disease	Foraging	Mechanical stress	Predation	Resting/hiding	Swimming	Spawning adult fertility rate	Spawning adult survival rate
Nuisance species introduction and management	**5**									
Wastewater and other contaminant inflows		**5**								
Birds and mammals						**1**				
Pre-release conditioning			**1**							
Water temperature	**5**	**5**								
Disease								**4**		
Drifting				**1**			**1**			
Hybridization									**1**	
Predation					**1**					
Ripening										**1**
Staging and spawning					**1***					

Chapter 8 – Discussion and Conclusions

This document presents a revised CEM for RASU for the LCR MSCP, superseding the original version from 2013 (Braun and McClure 2013). The purpose of this model is to help the LCR MSCP identify areas of scientific certainty versus uncertainty concerning RASU ecology, the effects of specific stressors, the effects of specific management actions aimed at species habitat restoration, and the indicators used to measure RASU habitat and population conditions. The present CEM addresses the RASU population along the river and the lakes of the LCR, including protected areas that currently provide or could provide RASU habitat under the auspices of the LCR MSCP Habitat Conservation Plan. The assessment of causal relationships in the present 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 survival and, where appropriate, outcomes related to reproductive output.

3. For each life-stage outcome, identify the critical biological activities and processes, the rates of which shape the rates of 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 and aspects of their abundance, composition, or other properties that shape the rates of these activities or processes. Habitat elements are features of the physical and biological environment.

5. Identify controlling factors, in this instance largely consisting of human activities and institutional actions, which 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 weather and climate.

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

CEM COMPONENTS

The RASU conceptual ecological model identifies five life stages. Life-stage outcomes consist of the survival rate for each life stage, the adult reproductive participation rate, and spawning adult fertility. The five life stages are as follows:

- Eggs and pre-dispersal larval
- Post-dispersal larvae and younger juvenile
- Older juvenile and subadult
- Adult
- Spawning adult

The RASU conceptual ecological model identifies 14 critical biological activities and processes that affect one or more of these life-stage outcomes. The 14 critical biological activities and processes are as follows, in alphabetical order:

- Chemical stress
- Competition
- Disease
- Drifting
- Egg settling and adhesion
- Foraging
- Hybridization
- Mechanical stress
- Predation
- Resting/hiding
- Ripening
- Staging and spawning
- Swimming
- Thermal stress

The RASU conceptual ecological model distinguishes 16 habitat elements that affect the rates, timing, magnitude, distribution, or other aspects of 1 or more critical biological activities or processes for 1 or more life stages. The 16 habitat elements are as follows, in alphabetical order:

- Aquatic macrophytes
- Aquatic vertebrates
- Birds and mammals
- Genetic diversity
- Infectious agents
- Invertebrates and POM
- Macrohabitat structure
- Mesohabitat structure
- Monitoring, capture, handling
- Pre-release conditioning

- Substrate texture/dynamics
- Turbidity
- Water chemistry
- Water depth
- Water flow/turbulence
- Water temperature

Finally, the RASU conceptual ecological model distinguishes 8 controlling factors that affect the distribution, quality, composition, abundance, and other features of one or more of these habitat elements. Because the LCR comprises a highly regulated system, the controlling factors almost exclusively concern human activities. The 8 controlling factors are as follows, in alphabetical order:

- Channel and off-channel engineering
- Motorboat activity
- Non-RASU fisheries
- Nuisance species introduction and management
- RASU monitoring and conservation programs
- Tributary inflows
- Wastewater and other contaminant inflows
- Water storage-delivery system design and operations

HIGH-MAGNITUDE CAUSAL RELATIONSHIPS

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:

- Five controlling factors have consistently high-magnitude direct potential effects on multiple habitat elements across all RASU life stages. These are, in alphabetical order: channel and off-channel engineering, non-RASU fisheries, nuisance species introduction and management, RASU monitoring and conservation programs, and water storage-delivery system design and operations.

- Eight habitat elements have high-magnitude direct potential effects on multiple critical biological activities and processes across all RASU life stages. These are, in alphabetical order: aquatic vertebrates, genetic diversity, invertebrates and POM, mesohabitat structure, pre-release conditioning, substrate texture/dynamics, turbidity, and water temperature.

- Seven habitat elements consistently have high-magnitude direct potential effects on other habitat elements and thereby have strong indirect effects on one or more critical biological activities or processes across all RASU life stages. These are, as follows, listed based on the number of affected habitat elements and then alphabetically: mesohabitat structure, turbidity, water temperature, water depth, aquatic vertebrates, macrohabitat structure, and water flow/turbulence. In two instances, the direct effects of one of these high-impact habitat elements on another are bi-directional (i.e., the "causal" and "affected" habitat elements strongly, reciprocally affect each other). Mesohabitat structure both directly affects and is directly affected by substrate texture/dynamics, with high magnitude. Similarly, turbidity both directly affects and is directly affected by the abundance and composition of the aquatic vertebrate assemblage. Five habitat elements – aquatic vertebrates, mesohabitat structure, turbidity, substrate texture/dynamics, and water temperature – thus have consistently high-magnitude direct *and indirect* potential effects on one or more critical biological activities or processes across all RASU life stages.

- Six critical biological activities or processes have high-magnitude direct potential effects on one or more life-stage outcomes across the five RASU life stages. Predation directly affects survival in all five life stages, with high magnitude. Foraging success is hypothesized to have the potential to directly affect survival among older juveniles and subadults, and among adults, and also to affect the adult annual spawning participation rate, all with high magnitude. Thermal stress is hypothesized to have the potential to directly affect survival among eggs and pre-dispersal larvae, and among post-dispersal larvae and younger juveniles, both with high magnitude. Egg settling and adhesion is hypothesized to have the potential to directly affect survival among eggs and pre-dispersal larvae with high magnitude. Staging and spawning is hypothesized to have the potential to directly affect spawning adult fertility, and swimming activities, strength, and stamina are hypothesized to have the potential to directly affect survival among spawning adults, all with high magnitude.

- Eight critical biological activities or processes have high-magnitude direct potential effects on other critical biological activities or processes and thereby have strong indirect effects on one or more life-stage outcomes across the five RASU life stages. Swimming activities, strength, and stamina are hypothesized to have the potential to directly affect drifting, predation, resting/hiding, and staging and spawning with high magnitude. Foraging success is hypothesized to have the potential to directly affect ripening and swimming strength and stamina, all with high magnitude. Competition is hypothesized to have a high-magnitude direct effect on resting/hiding activity (i.e., on the ability of RASU to find suitable cover habitat) in all four motile life stages. Drifting dynamics, egg settling and adhesion, and resting/hiding activities are all hypothesized to have

high-magnitude direct effects on predation in various life stages, and both predation and ripening are hypothesized to have to have high-magnitude direct effects on staging and spawning. The relationship between foraging and swimming is hypothesized to be bi-directional, as is the relationship between predation and staging and spawning. Four critical biological activities or processes – foraging, predation, staging and spawning, and swimming – thus have consistently high-magnitude direct *and indirect* potential effects on life-stage outcomes across the five RASU life stages.

HIGH-MAGNITUDE CAUSAL RELATIONSHIPS WITH LOW UNDERSTANDING

The assessment of causal relationships also identified those with high magnitude but low understanding. Proposed high-magnitude but poorly understood direct potential effects of habitat elements include:

- The potential effects of aquatic vertebrate assemblage composition and abundance on competition and swimming activities.
- The potential effects of genetic diversity on RASU vulnerability to disease and thermal stress.
- The potential effects of aquatic invertebrate assemblage composition and abundance on competition.
- The potential effects of mesohabitat structure on resting/hiding, staging and spawning, and swimming behavior.
- The potential effects of pre-release conditioning on RASU vulnerability to chemical stress, predation, and thermal stress, and on RASU foraging and swimming behaviors.
- The potential effects of substrate texture/dynamics on egg settling and adhesion and on staging and spawning dynamics.
- The potential effects of turbidity on predation on all five life stages.
- The potential effects of water temperature on ripening and on staging and spawning.

- The potential effects of mesohabitat structure, turbidity, and water temperature on the abundance and composition of the aquatic vertebrate assemblage in different locations within the LCR ecosystem.

Proposed high-magnitude but poorly understood direct potential effects of critical activities or processes include:

- The potential effects of foraging behaviors and success on survival among older juveniles, subadults, and adults, and on the adult annual spawning participation rate.

- The potential effects of predation on survival in all five life stages.

- The potential effects of competition on resting/hiding behaviors in all four motile life stages.

- The potential effects of foraging success on ripening.

- The potential effects of predation on staging and spawning, and vice versa.

- The potential effects of resting/hiding behaviors, specifically the use of cover, on predation.

- The potential effects of ripening on staging and spawning.

- The potential effects of swimming behaviors, strength, and/or stamina on drifting, predation, resting/hiding among post-dispersal larvae and younger juveniles, and staging and spawning.

Finally, the present CEM proposes several causal relationships based on basic ecological and biological concepts, for which the literature on RASU does not provide sufficient information to assess the possible magnitude of any effect. Table 22, above, identifies these possible causal relationships with unknown magnitude and low understanding.

RASU are among several native fishes of the LCR that have experienced massive reductions in abundance over the past several decades. Reviews of the status of RASU 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 present CEM did not turn up clear evidence that water pollution currently affects the overall distribution or health of the species. Similarly, RASU appear to be able to spawn in river sections (and possibly also off-channel ponds [Kretschmann and Leslie 2006]) with highly altered

temperature and flow regimes, although the present assessment did not evaluate the possible limits of this range of tolerance. On the other hand, the literature strongly suggests that predation by non-native species threatens the persistence of RASU wherever they occur, except apparently in settings where mesohabitat conditions with turbidity and/or good cover afford motile RASU with some measure of protection. A broad spectrum of birds, native and non-native aquatic vertebrates, and possibly also invertebrates (e.g., crayfish) are known or thought to prey on RASU. The present CEM also suggests that RASU numbers and distribution may be sensitive to other constraints, specifically the abundance and quality of food materials, and the availability of hydrologically and geomorphically suitable spawning, drifting, nursery, and other resting/hiding habitat, including habitat with aquatic macrophytes cover. Finally, the present CEM highlights continuing uncertainties concerning the effects of pre-release conditioning among RASU reared for repatriation – including both conditioning to ambient conditions at the rearing facilities and adaptive conditioning to prepare the reared RASU for the conditions they face upon release.

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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 Implementation Plan (DRERIP): https://www.dfg.ca.gov/ERP/conceptual_models.asp. The DRERIP is jointly implemented by the California Department of Fish and Wildlife, U.S. Fish and Wildlife Service, and the National Marine Fisheries Service. The Bureau of Reclamation participates in this program.

The DRERIP 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 survival 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 DRERIP 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 operations (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* (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 distribution, 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 distribution, 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 DRERIP 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 DRERIP methodologies for assessing causal linkages differ in three ways. First, the DRERIP 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 DRERIP methodology treats spatial and temporal scales 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 DRERIP 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 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. Each causal link – and therefore each arrow – is labeled with a unique identification number, indexed in the CEM spreadsheet. 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 DRERIP 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 $\geq$ 2.67
Medium	Numerical average $\geq$ 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

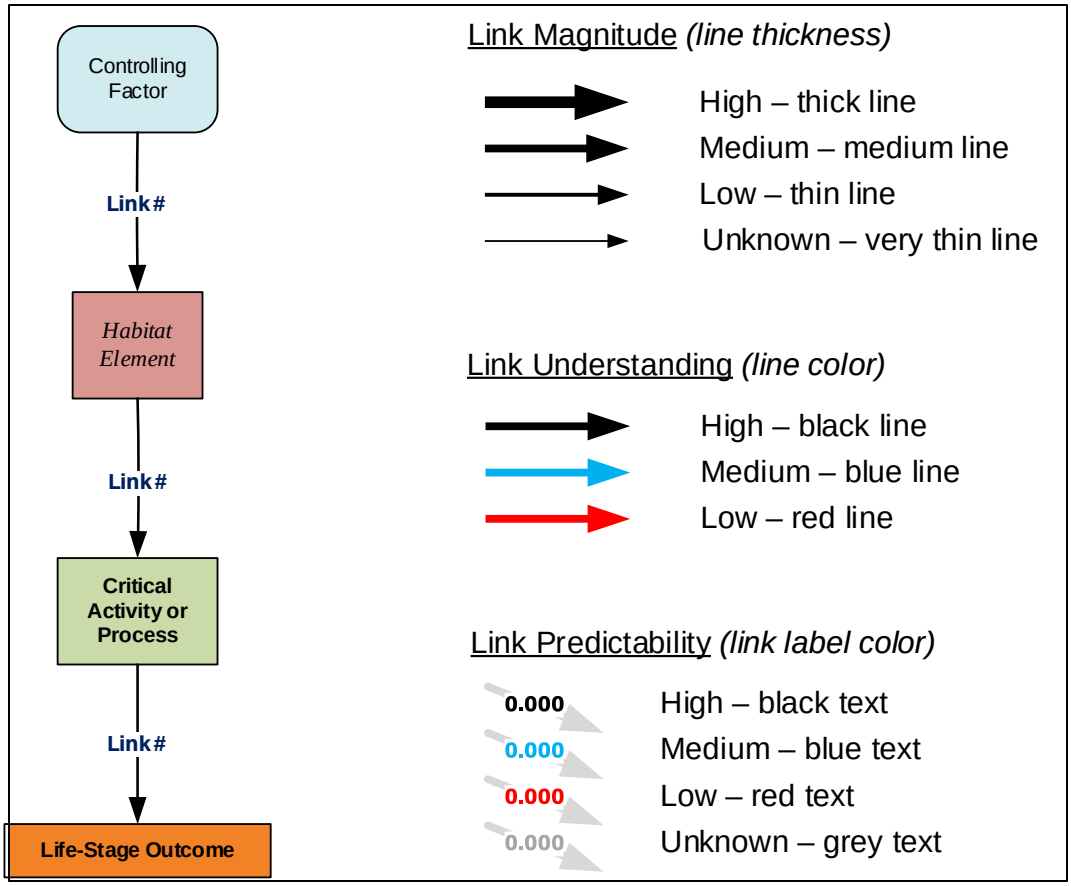

Figure 1-1.—Conventions for displaying cause and effect nodes, linkages, link magnitude, link understanding, and link predictability

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ATTACHMENT 2

Razorback Sucker (*Xyrauchen texanus*) (RASU) 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.—RASU river gradient associations by life stage, after Valdez et al. (2012a)
Usage (association) ratings: H = high use; M = moderate use; L = little use; "-" = no use; X = historic but not current use; "?" = suspected.

River and reach ↓	Gradient ↓ / Life stage →	Egg and pre-dispersal larval	Post-dispersal larval and younger juvenile	Older juvenile and subadult	Adult	Spawning adults
Green River						
Flaming Gorge Dam to Split Mountain	5.2–20.1 ft/mi*	**-**	**-**	**L**	**L**	**-**
Split Mountain to Sand Wash	1.1–4.8 ft/mi	**H**	**H**	**H**	**H**	**H**
Desolation Canyon (Sand Wash to Green River)	9.8 ft/mi	**L?**	**-**	**L**	**L**	**L?**
Green River to Colorado River confluence	1.1–2.1 ft/mi	**L?**	**H**	**L**	**L**	**L?**
Upper Colorado River						
Rifle to Palisade	7.7 ft/mi	**-**	**-**	**-**	**M**	**-**
Palisade to Moab	5.1 ft/mi	**L?**	**H**	**L**	**H**	**L?**
Moab to Green River confluence	2.3 ft/mi	**-**	**-**	**-**	**L**	**-**
Cataract Canyon	10 ft/mi	**-**	**-**	**-**	**-**	**-**
Lake Powell	Impoundment	**-**	**L**	**L**	**L**	**-**
San Juan River						
Navajo Dam to Animas River	9.2 ft/mi	**-**	**-**	**-**	**-**	**-**
Animas River to Bluff	7.4 ft/mi	**H**	**L**	**M**	**H**	**H**
Bluff to Clay Hills (Lake Powell inflow)	8.3 ft/mi	**-**	**H**	**L**	**L**	**-**
Lower Colorado River						
Grand Canyon (Glen Canyon Dam to Lake Mead inflow)[1]	15.4 ft/mi	**L**	**L**	**L**	**L**	**L**
Lake Mead	Impoundment	**H**	**H**	**H**	**H**	**H**
Lake Mohave	Impoundment	**H**	**H**	**H**	**H**	**H**
Lake Havasu	Impoundment	**H**	**H**	**H**	**H**	**H**
Parker Dam to Gulf of California[2]	1.0-1.5 ft/mi	**X**	**X**	**X**	**X**	**X**
Gila River						
Arizona/New Mexico line to San Carlos Lake[2]	12.4 ft/mi	**X**	**X**	**X**	**X**	**X**
Coolidge Dam to Salt River[2]	8.7 ft/mi	**X**	**X**	**X**	**X**	**X**
Salt River to Colorado River confluence[2]	3.5 ft/mi	**X**	**X**	**X**	**X**	**X**
Salt River	–	**-**	**-**	**L**	**M**	**-**
Verde River	–	**-**	**-**	**L**	**M**	**-**

* ft/mi = channel gradient, in feet of elevation change per river mile of channel length.
Note 1: Usage ratings updated with recent information on RASU occurrence in all life stages in western Grand Canyon (Bureau of Reclamation 2017).
Note 2: Usage ratings updated to indicate historic use (see also chapter 1).

Table 2-2.—RASU mesohabitat associations by life stage and, for adults, by season, after Valdez et al. (2012a)

Life stage ➔ / Mesohabitat type ➓	Egg and Pre-dispersal larval	Post-dispersal larval and younger Juvenile	Older juvenile and subadult	Adults in spring	Adults in summer	Adults in fall	Adults in winter	Spawning adults
Cobble/gravel bars	X				X			X
Cobble/gravel shore, bays/coves	X							X
Cobble/gravel shore, tributary inflows	X							X
Deep eddies			X					
Deep pools			X			X		
Flood plain wetlands	X	X	X					X
Gravel pit ponds	X		X	X	X			X
High-velocity runs					X	X		
Inundated vegetation				X				
Low-velocity backwaters		X	X	X	X	X	X	
Low-velocity cove shallows		X						
Low-velocity eddies			X	X	X	X	X	
Low-velocity main stem shallow shores		X	X					
Low-velocity pools			X	X	X	X	X	
Low-velocity runs			X	X	X	X	X	
Low-velocity tributary-mouth shallows		X	X					
Pool edges							X	
Riffles					X			
Side channels				X	X	X	X	
Slackwaters							X	

Table 2-3.—RASU substrate associations by life stage, after Valdez et al. (2012a)
(X = frequent use; x = occasional use)

Life stage ➔ / ➓ Substrate type	Egg and pre-dispersal larval	Post-dispersal larval and younger juvenile	Older juvenile and subadult	Adult	Spawning adults
Bedrock			x	x	
Boulder			x	x	
Cobble	X				X
Cobble/gravel	X				X
Cobble/gravel/sand	X		X	X	X
Gravel	X				X
Gravel/sand		X			
Gravel/sand/silt	X		X	X	X
Sand/silt			X	X	
Silt dominant		X	X	X	

Table 2-4.—RASU depth (meters) associations by life stage and, for adults, by season, after Valdez et al. (2012a)
(Values in parentheses are extreme outliers.)

Life stage ➔ / Value ➓	Egg and pre-dispersal larval; spawning adults	Post-dispersal larval and younger juvenile	Older juvenile and subadult; sudults in spring	Older Juvenile and subadult; adults In summer	Older juvenile and subadult; adults in fall	Older juvenile and subadult; adults In winter	Older juvenile and subadult; adults year round
Minimum depth, meters	0.2–0.8 (2.75)	0.1–1.4	0.2–1.5	0.2–1.2 (9.1)	0.2–1.2 (9.1)	0.4–1.9	0.4–0.6
Maximum depth, meters	1.0–5.5	0.2–6.1	0.8–6.1	1.9–3.0 (18.3)	1.2–3.0 (18.3)	1.1–6.1	0.4–3.4

Table 2-5.—RASU velocity (meters per second [m/sec]) associations by life stage and, for adults, by season, after Valdez et al. (2012a)

Life stage ➔ / Value ⬇	Egg and pre-dispersal larval; Spawning adults	Post-dispersal larval and younger juvenile	Older juvenile and subadult; adults in spring	Older juvenile and subadult; adults in summer	Older juvenile and subadult; adults in fall	Older juvenile and subadult; adults in winter	Older juvenile and subadult; adults year round
Minimum velocity, m/sec	0–0.9	0–0.06	0–0.3	0–0.5	0–0.5	0–0.2	0.1
Maximum velocity, m/sec	0.4–1.4	0–0.06	0.3–0.7	0.5–0.7	0.5–0.7	0.4–0.5	0.1–0.2

Table 2-6.—RASU temperature (degrees Celsius [°C]) associations by life stage and, for adults, by season, after Valdez et al. (2012a)

(Values in parentheses are extreme outliers.)

Life stage ➔ / Value ⬇	Egg and pre-dispersal larval; spawning adults	Post-dispersal larval and younger juvenile	Older juvenile and subadult; adults in spring	Older juvenile and subadult; adults in summer	Older juvenile and subadult; adults in fall	Older juvenile and subadult; adults in winter
Minimum temperature, °C	6.0–14.4	11–21.7 (34.0)	7.8–10.9	7.8–15.0	0.0–11.5	0.0–1.3
Maximum temperature, °C	14.8–27.0	15.0–29.0 (34)	14.8–27.0	12.5–27.0	10.5–27.0	4.3–10.5

Literature Cited

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