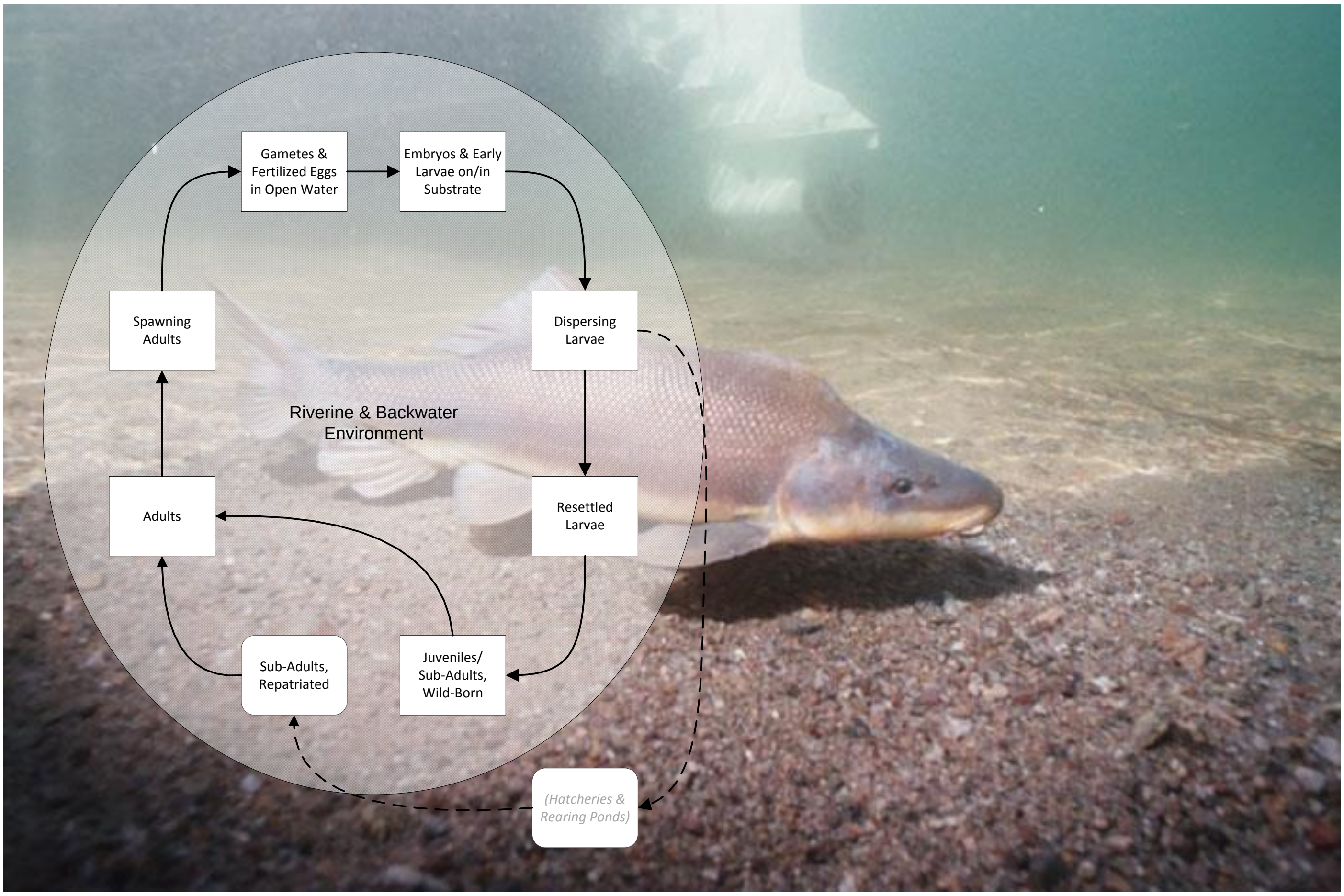
Lower Colorado River Multi-Species Conservation Program

Balancing Resource Use and Conservation

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



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November 2013

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U.S. DEPARTMENT OF THE INTERIOR

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

CEM	conceptual ecological model
DO	dissolved oxygen
HCP	Habitat Conservation Plan
km	kilometer(s)
LCR	lower Colorado River
LCR MSCP	Lower Colorado River Multi-Species Conservation Program
mm	millimeter(s)
POM	particulate organic matter
RASU	razorback sucker
Reclamation	Bureau of Reclamation
TL	total length
UCRB	Upper Colorado River Basin
USFWS	U.S. Fish and Wildlife Service

Symbols

>	greater than
<	less than

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Executive Summary

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 habitat and species restoration, and the methods used to measure RASU habitat and population conditions.

CONCEPTUAL ECOLOGICAL MODELS

Conceptual ecological models 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 the 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 shape the abundance, distribution, and persistence of the species in that area.

Specifically, the RASU conceptual ecological model has four core components:

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

  Critical biological activities and processes – These consist of the activities in which the species must engage and the biological processes that must take place during each life stage to sustain an acceptable rate of transition (recruitment) to the next life stage.

- **Habitat elements** – These consist of the specific habitat conditions that are necessary or sufficient for the critical activities and processes to take place or that interfere with critical activities or processes. The abundance and distribution of habitat elements control the rates (intensities) of the activities and processes that they affect.

- **Controlling factors** – These consist of environmental conditions and dynamics – including human actions – that determine the abundance, spatial and temporal distribution, and quality of important habitat elements. Controlling factors are also called "drivers."

The CEM identifies the causal relationships among these components that affect the rate at which individuals of a species survive and transition (recruit) from one life stage to the next. Further, the model 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 status (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.

STRUCTURE OF THE RASU CONCEPTUAL ECOLOGICAL MODEL

The RASU conceptual ecological model addresses the RASU population along the river and lakes of the lower Colorado River (LCR) and in wildlife refuges and other protected areas along the LCR managed as RASU habitat under the auspices of the LCR MSCP Habitat Conservation Plan. It does not include facilities managed exclusively for rearing RASU larvae into subadults, but does include protected areas into which RASU subadults are repatriated as part of the augmentation program.

The basic sources of the information for the RASU conceptual ecological model are Minckley et al. (1991), U.S. Fish and Wildlife Service (1998, 2002a), Reclamation (2004, 2008), Mueller (2006), and Valdez et al. (2012). These publications summarize and cite large bodies of earlier studies. The model also integrates numerous additional sources, particularly reports and articles completed since these publications; information on current research projects; and the expert knowledge of LCR MSCP fish biologists. Our purpose is not to provide an updated literature review, but to integrate the available information and knowledge into a CEM. The review of RASU habitat requirements by Valdez et al. (2012) strongly complements the present document.

The RASU conceptual ecological model distinguishes and assesses eight life stages as follows:

1. Gametes and eggs in open water
2. Embryos and early larvae on/in the substrate
3. Dispersing larvae
4. Resettled larvae
5. Juveniles/subadults, wild born
6. Subadults, repatriated
7. Adults
8. Spawning adults

The model distinguishes 13 critical biological activities or processes relevant to 1 or more of these 8 life stages, 16 habitat elements relevant to 1 or more of these 13 critical biological activities or processes for 1 or more life stages, and 7 controlling factors that affect 1 or more of these 16 habitat elements. Because the LCR and its refuges comprise a highly regulated system, the controlling factors exclusively concern human activities.

The 13 critical biological activities and processes identified across all life stages are: chemical stress, disease, drifting, egg descent, egg settling/adhesion, foraging, mechanical stress, predation, resting, ripening, staging and spawning, swimming, and thermal stress. The 16 habitat elements identified across all life stages are: competitor activity, depth, flow/turbulence, genetic diversity, infectious agents, macrohabitat geometry, mesohabitat geometry/cover, plankton-benthos-particulate organic matter (POM), predator activity, pre-release conditioning, scientific study, substrate texture/dynamics, transport/release, turbidity, water chemistry, and water temperature. The seven controlling factors identified across all habitat elements are: nuisance species introduction and management; management of channel, lake, and pond geometry; motorboat activity; non-RASU fishery management; tributary inflow; wastewater and other contaminant inflow; and water storage-delivery management.

RESULTS

The analysis of the causal relationships shows which critical biological activities and processes most strongly support or limit the success of each life stage in the present system, which habitat elements most strongly affect the rates of these critical activities and processes, and which controlling factors most strongly affect the abundance, distribution, or condition of these habitat elements.

The analysis identifies several critical biological activities and processes that significantly affect survivorship across multiple life stages. Highlights of the results include the following:

- The rate of predation strongly affects the success rate of every life stage.

- The rate of foraging success moderately or strongly affects the success rate of all six mobile life stages.

- The effectiveness of swimming behaviors in allowing RASU to navigate among habitats and avoid predation strongly affects the success rate for all juveniles, subadults, and adults, including during spawning.

- The rate of occurrence of mechanical stress moderately affects the success of embryo and protolarval development on/in the substrate at spawning sites.

- The dynamics of drifting moderately affect the success rate for dispersing larvae, at least in the river and its reservoirs.

These findings concerning salient biological activities and processes are noteworthy for not highlighting disease, chemical stress, or thermal stress as significant factors affecting RASU survivorship and reproduction. The literature identifies all three as matters worthy of consideration, but also presents no clear evidence that they presently affect or have recently affected RASU survivorship along the LCR relative to other more potent factors.

Further, the analysis identifies several habitat elements that strongly affect the most salient biological activities across all life stages. Highlights of the results include the following *direct* effects of habitat element abundance and condition on critical biological activities and processes (the analysis identifies numerous indirect effects as well):

- Mesohabitat geometry/cover directly strongly or moderately influences 6 of the 10 most influential critical biological processes or activities.

- Flow/turbulence also directly strongly or moderately influences 6 of the 10 most influential critical biological processes or activities at multiple spatial scales.

- Substrate texture/dynamics strongly or moderately influence 4 of the 10 most influential critical biological processes or activities at the scale of individual habitat sites.

- Pre-release conditioning strongly or moderately influences three critical biological processes or activities for life stage 6 – repatriated subadults: foraging behaviors, swimming behaviors, and predator avoidance.

- Water temperature strongly or moderately influences two critical biological processes or activities for life stage 8 – spawning adults: the cueing of reproductive ripening and participation in spawning itself.

- Macrohabitat geometry shapes drifting and swimming distances among habitats.

- Competitor activity and predator activity both strongly or moderately influence 2 of the 10 most influential critical biological processes or activities: predation and swimming behaviors.

- Changes in depth during the short period of embryo development can cause mechanical stress to RASU embryos by exposing them to desiccation or inundating them to excessive depths.

- The abundance and composition of plankton-benthos-POM resources strongly influence foraging, 1 of the 10 most influential critical biological processes or activities for all RASU mobile life stages.

- Turbidity strongly affects predation, possibly the most influential critical biological process or activity for all RASU life stages, by shaping the ability of different predators to forage.

- Water chemistry may affect primary productivity along the LCR and in its refuges and therefore moderately shape the abundance and composition of the planktonic and benthic biological assemblages and the abundance and distribution of POM.

The analysis also identifies which controlling factors had the greatest effect on which habitat elements across all eight life stages. Highlights of these findings include:

- Management of channel, lake, and pond geometry strongly affects macrohabitat geometry and mesohabitat geometry/cover, and it moderately affects water depth.

- Non-RASU fishery management strongly affects competitor activity, the abundance and composition of the assemblage of infectious agents in the water, the abundance and composition of plankton-benthos-POM resources, and predator activity.

- Nuisance species introduction and management also strongly affects competitor activity, the abundance and composition of the assemblage of infectious agents in the water, the abundance and composition of plankton-benthos-POM resources, and predator activity.

- Tributary inflows have a medium-magnitude impact on macrohabitat geometry and mesohabitat geometry/cover as well as water chemistry.

- Wastewater and other contaminant inflows have a medium-magnitude impact on water chemistry.

- Water storage-delivery management has a strong impact on water depth, flow/turbulence, macrohabitat geometry, substrate texture/dynamics, water chemistry, and water temperature.

- Motorboat activity has only localized, temporary effects on substrate texture/dynamics and turbulence.

Finally, the analysis highlights several potentially important causal relationships about which scientific understanding remains low. These may warrant attention to determine if improved understanding might provide additional management options for improving RASU survivorship and recruitment in the LCR and its refuges. Specifically, the findings suggest a need to improve the understanding of:

- The ecology of predation on RASU, how this may vary among predator species and across different macro and mesohabitat settings, and whether it may be possible to manipulate these habitat conditions to improve RASU survival even in the presence of predators.

- The ways in which mesohabitat conditions and substrates shape RASU behaviors and survivorship in all life stages based on quantifiable habitat and substrate characteristics.

- The possible effects of food availability and the ecology of intra and interspecific competition affecting RASU survival and recruitment.

- The conditions that can trigger or cue RASU ripening and staging for spawning.

- The relative importance of lack of conditioning to flow velocities and available foods, and the lack of experience with predators to high rates of stress and mortality after release of repatriated subadults. Whether repatriated subadults experience high rates of stress and mortality due to their lack of conditioning to the foods available and flow velocities they experience after release or due to a lack of experience with predators.

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 habitat and species restoration, and the methods 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 (DiGennaro et al. 2012) with modifications.

The model addresses the RASU population along the river and lakes of the lower Colorado River (LCR) and in wildlife refuges and other protected areas along the LCR managed as RASU habitat under the auspices of the LCR MSCP Final Habitat Conservation Plan (HCP). It does not include facilities managed exclusively for rearing RASU larvae into subadults, but does include protected areas into which hatchery-reared RASU subadults are repatriated as part of the augmentation program (Reclamation 2006). The model thus addresses the landscape as a whole rather than any single reach or managed area.

The basic sources of the information for the RASU conceptual ecological model are Minckley et al. (1991), (U.S. Fish and Wildlife Service [USFWS] 1998, 2002a), Reclamation (2004, 2008), Mueller (2006), and Valdez et al. (2012). These publications summarize and cite large bodies of earlier studies. The model also integrates numerous additional sources, particularly reports and articles completed since the aforementioned publications; information on current research projects; and the expert knowledge of LCR MSCP fish biologists. Our purpose is not to provide an updated literature review, but to integrate the available information and knowledge into a CEM. The review of RASU habitat requirements by Valdez et al. (2012) strongly complements the present document.

This document is organized as follows: The remainder of chapter 1 provides an overview of the reproductive ecology of the razorback sucker, specifically its adaptation to the pre-regulation LCR hydrogeomorphic environment, and introduces the underlying concepts and structure of the CEM. Succeeding chapters present and explain the model for the RASU in the LCR and evaluate the implications of this information for management, monitoring, and research needs.

RAZORBACK SUCKER REPRODUCTIVE ECOLOGY

The razorback sucker 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.

RASU have a distinctive reproductive strategy, characterized by the production of huge numbers of eggs during each spawning season with low parental investment and extremely low larval survivorship, coupled with a large adult body size and long adult lifespan (Mueller 2006). The species thus strongly matches the criteria for a "periodic" reproductive strategist (per 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 total pre-regulation population size cannot be estimated, but 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). Only a portion of the females spawn in any given year (see chapters 2, 3, and 6), but even a 10-percent rate of participation among the females in Lake Mohave in 1988 would have produced roughly 225–600 million eggs for fertilization each year. Adults spawn multiple times over their lifetimes as evidenced by repeated annual returns to individual spawning sites (see chapters 2, 3, and 6). A hypothetical female that spawns only five times over a 40-year lifespan thus might produce roughly 500,000 eggs, only 2of which need grow into sexually mature offspring for the parents to replace themselves in the population. RASU thus have extremely low natural rates of survivorship and fertility – an average lifetime reproductive success rate of perhaps only four in a million.

The timing of spawning in the LCR 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). Spawning sites must provide substrates that remain stable over the course of the spawning season so that the deposited eggs do not get churned up, buried, or exposed during the rise and fall of flood pulses. A flood pulse must arrive with the right timing and right magnitude to disperse the newly emerged larvae into shallow-water environments, and these nursery environments must persist long enough to support larval maturation at least into juvenile body form and size (>25-millimeter [mm] body length). However, the flood pulse may just as easily occur too early before or too late after larval emergence to disperse the larvae across flood-shaped shallow-water environments, provide insufficient water to inundate the flood plain, or carry the larvae far downstream rather than shunt them off into low-velocity environments even during a well-timed flood pulse.

For those larvae that do reach suitable shallow-water habitat, maturation to the juvenile stage may take approximately 30–100 days (Gustafson 1975; Clarkson and Childs 2000; Bestgen 2008). Suitable nursery environments include 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 drying of flood plain ponds may render them inhospitable to larval RASU before they completely dry out due to rising water temperatures and salinity (another consequence of evaporation). The mechanisms by which RASU larvae disperse into their growth habitats following emergence therefore involve several additional risks to larval survival.

Further, the timing and magnitude of the Colorado River flood pulse 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 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. In fact, the drought in 2000–2004 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). 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 varies with the timing of onset of snowmelt in different parts of the Rocky Mountains and the timing of spring rainstorms, including rain-on-snow events. Extreme 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 the flannelmouth sucker (*Catostomus latipinnis*) 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 same drought would have affected RASU as well (see also Douglas and Douglas 2007; Hopken et al. 2012).

RASU thus evolved in an ecosystem prone to extreme variations in the availability of water. This variation affected the spatial pattern, extent, timing, and duration of flooding, pre-regulation; 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, in this case, specific to the LCR valley itself.

Not surprisingly, therefore, the evidence suggests that most of the mortality experienced by RASU under natural conditions would have occurred during the first few days and weeks following spawning; but, their vulnerability to the natural hydroclimatic variation is only part of the reason. Numerous native species consume RASU eggs, including adult RASU and bonytail (*Gila elegans*) (Mueller 2006; see chapter 6). The concentration of eggs at spawning sites makes them particularly vulnerable to consumption, and their availability during the late winter or early spring would provide a food resource during a season of otherwise low productivity (Mueller 2006). Numerous native species also prey on the larvae and smaller juveniles as they mature after dispersal, including the carnivorous 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 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 that has accumulated over years of investigations and management actions. Conceptual ecological models capture and synthesize this knowledge into a transparent, flexible framework (Fischenich 2008; DiGennaro et al. 2012).

Conceptual ecological models 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 we expect the characteristics of the resource to change as a result of altering its shaping/controlling factors, including those resulting from management actions.

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

CONCEPTUAL ECOLOGICAL MODEL STRUCTURE FOR THE RAZORBACK SUCKER

The CEM methodology used here expands on that developed for the Sacramento-San Joaquin River Delta Regional Ecosystem Restoration Implementation Plan (DiGennaro et al. 2012). The expansion incorporates recommendations of Wildhaber et al. (2007, 2011), Kondolf et al. (2008), and Burke et al. (2009) to provide greater detail on causal linkages and outcomes. Attachment A provides a detailed description of the methodology. The model is a "life history" model, as is common for CEMs focused on individual species (Wildhaber et al. 2007, 2011). That is, it distinguishes the major life stages or events through which the individuals of a species must pass to complete a full life cycle, including reproducing. 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 shape the abundance, distribution, and persistence of the species in that area.

The RASU conceptual ecological model has four core components as explained further in attachment A:

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

- **Critical biological activities and processes** – These consist of the activities in which the species must engage and the biological processes that must take place during each life stage to sustain an acceptable rate of transition (recruitment) to the next life stage. Examples of activities and processes for a bird species may include nesting, foraging, avoiding predators, and avoiding other specific hazards. Activities and processes may be considered "rate" variables; the rate (intensity) of the activities and processes, taken together, determine the rate of recruitment of individuals to the next life stage.

- **Habitat elements** – These consist of the specific habitat conditions that are necessary or sufficient for the critical activities and processes to take place or that interfere with critical activities or processes. The abundance and distribution of habitat elements control the rates (intensities) of the activities and processes that they affect. Taken together, the suite of habitat elements for a life stage is called the "habitat template" for that life stage. Defining the habitat template also 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 begin to fail – if the state of the science supports such estimates.

- **Controlling factors** – These consist of environmental conditions and dynamics – including human actions – that determine the abundance, spatial and temporal distribution, and quality of important habitat elements. Controlling factors are also called "drivers." There may be a hierarchy of such factors affecting the system at different scales of time and space (Burke et al. 2009). For example, the availability of breeding territories may depend on factors such as river flow rates and flow-path morphology, which in turn may depend on factors such as watershed geology, vegetation, and climate.

The conceptual ecological model identifies these four components and the causal relationships among them that affect the rate at which individuals of a species survive and transition (recruit) from one life stage to the next. Further, the CEM assesses each causal linkage based on four variables 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 rate of success of the life stage, support or limit the rate of each critical biological activity or process, and support or limit the quality of each habitat element (as it affects other habitat elements or affects critical biological activities or processes). In addition, the model 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 A 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. The last two parts of this definition – concerning habitats and ecological interactions – are the most crucial for the purposes of the present RASU conceptual ecological model for the LCR MSCP.

This chapter proposes a life stage model for the RASU in the LCR on which to build the conceptual ecological model. 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), Reclamation (2008), and Albrecht et al. (2010a). Zelasko et al. (2009) and Valdez et al. (2011) present conceptual life history models for the Upper Colorado River Basin (UCRB). The CEM in Valdez et al. (2011) includes an explicit designation of life stages and lists of biotic controlling factors and abiotic controlling factors.

EMBRYOS AND LARVAE

Snyder and Muth (2004) identify four larval phases – protolarva, flexion mesolarva, postflexion metalarva, and metalarva – and seem to imply that these phases have different ecological requirements. However, they do not make clear these differences in ecological requirements. In contrast, Valdez et al. (2011) lump the larval phases into three behavioral categories:

1. Larvae that remain embedded in the substrate until they swim up and disperse. Snyder and Muth (2004) state that RASU larvae remain in the substrate after hatching until they are able to “swim up” (remain in the substrate until ready to migrate). (Valdez et al. (2011) state that newly hatched larvae stay in the substrate where they hatched 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.)

2. Dispersing larvae in the main channel and channel margins.
3. Post-dispersal larvae that have migrated into flood plain wetlands and riverine backwaters where they mature into juveniles.

The present CEM adopts the classification from Valdez et al. (2011) rather than from Snyder and Muth (2004) because the former focuses on larval behaviors in their environmental context while the latter focuses on morphology alone. Embryo development to hatching typically requires approximately 6–7 days and swim up another 4–7 days. The transition from larva to juvenile involves changes in both behavior and morphology during the first year of life, including 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; Mueller 2006; Reclamation 2008; Albrecht et al. 2010a; Bestgen et al. 2011, 2012).

JUVENILES AND SUBADULTS

The literature on RASU does not use the terms “juvenile” versus “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; Reclamation 2008). This lack of firm definitions for juvenile versus subadult appears to result from a lack of distinct biological milestones between the development of juvenile morphology on the one hand (see above) and sexual maturation on the other. Nevertheless, it is important to consider whether a life stage model for RASU should distinguish more than one life stage along the juvenile-subadult continuum.

The massive mortality observed for stocked RASU during the first several years of the augmentation program led to studies of what factors contributed to this mortality (Minckley et al. 1991; USFWS 1998, 2002a; Marsh et al. 2005; Reclamation 2008; Schooley and Marsh 2007; Patterson et al. 2012). These studies identify the size of the released fish as a critical variable affecting post-release survivorship, with a threshold of 300 mm total length (TL) for likely survival.[1] 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; Reclamation 2008; Schooley and Marsh 2007). However, Bestgen (1990), Reclamation (2008), and Valdez et al. (2011) indicate that RASU are not sexually

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[1] However, Kesner et al. (2012) found that survival of repatriated RASU in Lake Mohave improved significantly for fish with TL >450 mm and recommended shifting the minimum size for released fish accordingly. Investigations are underway to assess whether repatriating fish with TL >500 mm might significantly change survivorship (http://www.lcrmscp.gov/fish/fish_res_mon.html).

mature at 300 mm TL, but rather become ready and able to spawn on average roughly at age 4, corresponding roughly to an average length ≥350–400 mm TL. This information would seem to suggest that the RASU conceptual ecological 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.

This assessment also considers the possibility that "juveniles," too, may fall into different classes that warrant separate treatment in the CEM. 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; Reclamation 2008). For example, UCRB studies (Bestgen et al. 2011; Valdez et al. 2011) indicate that post-dispersal larval and juvenile *wild-born* RASU often concentrate in flood plain wetlands with limited access to the main channel. In these settings, they are vulnerable to summer heat and drying, winter freezing, and flushing by annual floods. These particular forms of vulnerability do not apply to the LCR due to the massive regulation of water levels along the LCR, channelization, and higher winter temperatures. However, the basic biology of the species is the same in the two subbasins. Thus, these 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. Age-1 wild-born juveniles have been caught in a wide variety of settings both in the UCRB and along the LCR (Minckley et al. 1991; Reclamation 2008; Bestgen et al. 2011, 2012). This distribution also suggests that, as they mature into their second year, RASU wild-born juveniles range more widely among macrohabitat settings, and their swimming abilities allow them to move more effectively out of harm's way from fluvial disturbances. Further, RASU develop their characteristic bony nuchal hump beginning when they are approximately 200 mm TL (Portz and Tyus 2004), potentially affecting their vulnerability to predation by Colorado pikeminnow (*Ptychocheilus lucius*), their dominant native predator (see chapter 4).

Nevertheless, neither age nor changes in size or morphology correlate with any distinctive changes 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 UCRB (Minckley et al. 1991; Reclamation 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, the pikeminnow is no longer the major (or even a minor) predator on RASU in the LCR (see chapters 4 and 6). The larger non-native predators do not need to swallow their prey whole, as do pikeminnow, and have different gape sizes than the pikeminnow. As a result, development of the nuchal hump in growing RASU may no longer mark a change in vulnerability to predation.

For these reasons, wild-born juveniles and subadults in the LCR appear better addressed in the CEM as a single life stage with a continuum of habitat conditions and constraints – a life stage beginning with the change from larval to adult skeletal morphology and ending with the development of sexual maturity. Hatchery-reared subadults, on the other hand, require separate treatment in the life stage model.[2]

HATCHERY-REARED VERSUS WILD-BORN SUBADULTS

The RASU raised in hatcheries for later repatriation to the LCR originate as wild-born dispersing larvae captured via night netting along the shores of Lake Mohave (Delrose 2011). The program repatriates these fish only when they attain a minimum size of 300 mm TL. As with wild-born RASU, they are rarely sexually mature at this size. This pattern of size-based selection of reared RASU for release places them in the subadult category noted above.

Studies in both the LCR and UCRB (Minckley et al. 1991; Brandenburg and Farrington 2007; Schooley and Marsh 2007; Schooley et al. 2008; Reclamation 2008; Zelasko et al. 2011; Bestgen et al. 2012; Kesner et al. 2012) indicate that repatriated RASU suffer very high rates of mortality within the first year (or less) following their release. The LCR MSCP HCP needs to address this high mortality to ensure greater survivorship among the repatriated RASU, and several research projects are underway that address this concern (http://www.lcrmscp.gov/fish/fish_res_mon.html). For example, repatriated RASU may be naïve (unconditioned) with respect to predation and the behaviors they need to learn in order to better avoid predators (Mueller et al. 2007). 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), and the process of transporting and releasing hatchery-raised fish may itself cause them stress that affects their

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[2] The conceptual ecological model does not address RASU larval and juvenile development in the hatchery system per se. It only concerns RASU survivorship and reproduction in the LCR aquatic (river and backwater) system itself, covering all wild-born RASU and hatchery-reared RASU after their repatriation, including repatriation into artificially maintained backwater habitats.

ability to assimilate (Schooley et al. 2008). The repatriated RASU thus differ behaviorally in a sufficient number of ways from subadults that have matured in situ in the LCR and its backwater habitats to warrant distinguishing them as a distinct life stage in the CEM.

It should be noted, however, that monitoring efforts for many years have detected few or no wild-born subadult RASU along the LCR outside of Lake Mead (Kesner et al. 2007, 2008, 2010, 2012). Further, the augmentation program has only minimal release goals for Lake Mead (Reclamation 2006; Albrecht et al. 2010a, 2010b). As a result, it is not possible to assess whether wild-born and repatriated subadults suffer different rates of mortality.

ADULTS

Adulthood among RASU begins with the completion of sexual maturation. The adult population of RASU in the LCR consists of two types of survivors in the LCR and its backwater habitats: (1) repatriated subadults that have survived following release and (2) subadults that have matured in situ from birth. The latter may exist only in Lake Mead. The relative contributions of the wild-born versus repatriated subpopulations to the adult population in each reach is a matter of great research interest (Minckley et al. 1991; Schooley and Marsh 2007; Schooley et al. 2008; Reclamation 2008; Zelasko et al. 2009, 2011; Albrecht et al. 2010a; Bestgen et al. 2012; Kesner et al. 2007, 2008, 2010, 2012). Adults can live up to 40+ years (reports range up to 44 years).

SPAWNING ADULTS

Spawning involves a biologically distinct suite of behaviors within the RASU life cycle. RASU adults aggregate to spawn, migrating 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; Reclamation 2008; Albrecht et al. 2010a, 2010b; Valdez et al. 2012). 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; Reclamation 2008; Albrecht et al. 2010a; Wydoski et al. 2010; Wydoski and Lantow 2012). Reports indicate that only a fraction of the adults spawn in any single year, and that spawning aggregations contain more males than females (Minckley et al. 1991; Reclamation 2008). Spawning RASU apparently may remain in the area of their spawning site for weeks, resting and feeding before and after spawning events, which involve a distinct suite of behaviors (Minckley et al. 1991; Mueller 2006; Reclamation 2008). Some of these behaviors appear aimed at – or at least 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).

GAMETES AND FERTILIZED EGGS

Finally, the spawning process involves the release of gametes into the water above the selected spawning site. Once fertilization takes place, the eggs harden and settle onto or into the substrate where they become adhesive over the course of 3–4 hours (Minckley and Gustafson 1982; Bozek et al. 1990; Minckley et al. 1991; Reclamation 2008). The eggs are subject to intense predation, including that by adult RASU, before apparently becoming less vulnerable once they adhere to, and sometimes become embedded in, the substrate (as summarized by Bozek et al. 1984; Minckley et al. 1991; USFWS 1998, 2002a; Mueller 2006; Reclamation 2008). Sources sometimes refer to the fertilized eggs as lying “in” rather than simply “on” the substrate (Bozek et al. 1984).

The events involving the gametes take place very quickly following their release and so might not qualify as a distinct life stage separate from spawning itself. However, “spawning” refers to the behavior of the adults. Other than potentially feeding on the eggs as they settle, adult RASU abandon their gametes after release. This abandonment leaves the gametes subject to environmental conditions that have little or nothing to do with adult RASU behavior other than their selection of the spawning sites. Consequently, the stresses (affecting the likelihood of survival) experienced by the gametes following their release differ from the stresses experienced by the spawning adults. For this reason, the present assessment distinguishes “gametes and fertilized eggs in open water” as a separate, but brief, life stage.

LIFE STAGE MODEL SUMMARY

Based on this information, the RASU conceptual ecological model distinguishes eight life stages as shown in table 1 and figure 1. Figure 1 also indicates the hatchery rearing pathway, which is not a subject of the present CEM, but is indicated here for completeness. The life stages are numbered sequentially beginning with the gametes and eggs.

Table 1.—RASU life stages in the LCR ecosystem

1. Gametes and fertilized eggs in open water	5. Juveniles/subadults, wild born
2. Embryos and early larvae on/in the substrate	6. Subadults, repatriated
3. Dispersing larvae	7. Adults
4. Resettled larvae	8. Spawning adults

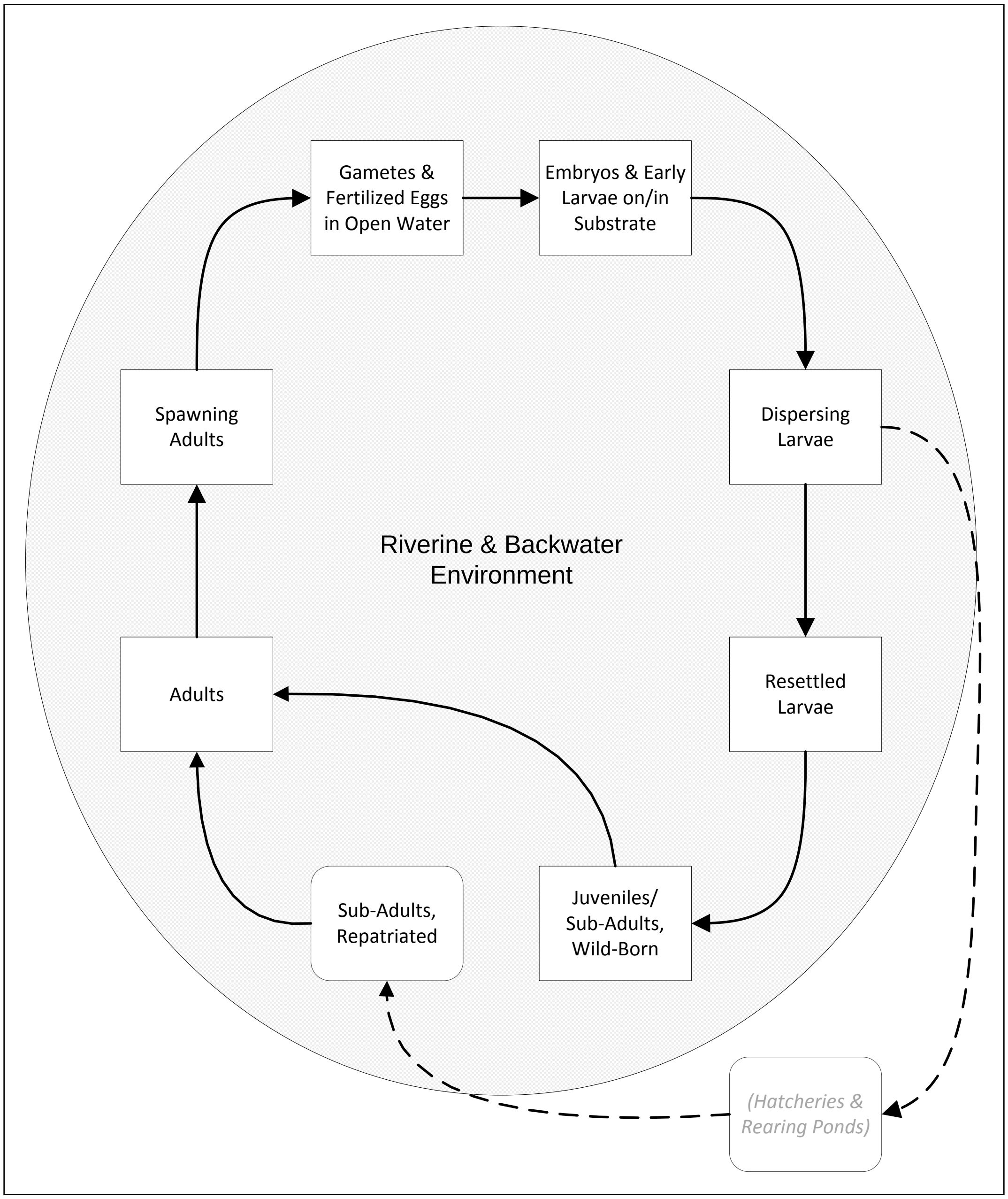

Figure 1.—Proposed RASU life history model.

Chapter 3 – Critical Biological Activities and Processes

Critical biological activities and processes consist of the activities in which the species engages and the biological processes that take place during each life stage that shape the rate of recruitment to the next life stage. Critical activities and processes are "rate" variables. The rate (intensity) of these activities and processes, taken together, determine the rate of recruitment of individuals from one life stage to the next.

The model identifies 13 critical 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 agility, strength, and stamina. However, grouping activities or processes across all life stages into broad types makes it easier to compare the individual life stages to each other across the entire life cycle. Table 2 lists the 13 critical activities and processes and their distribution across life stages.

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

Life stage ➔ **⬇ Critical biological activity or process**	**Gametes and fertilized eggs in open water**	**Embryos and early larvae on/in the substrate**	**Dispersing larvae**	**Resettled larvae**	**Juveniles/subadults, wild born**	**Subadults, repatriated**	**Adults**	**Spawning adults**
Chemical stress	X	X	X	X	X	X	X	X
Disease	X	X	X	X	X	X	X	X
Drifting			X	X				
Egg descent	X							
Egg settling/adhesion	X							
Foraging			X	X	X	X	X	X
Mechanical stress	X	X	X	X	X	X	X	X
Predation	X	X	X	X	X	X	X	X
Resting		X	X	X	X	X	X	
Ripening								X
Staging and spawning								X
Swimming			X	X	X	X	X	X
Thermal stress		X	X	X	X	X	X	X

The basic sources of the information used to identify the critical activities and processes are Minckley et al. (1991), USFWS (1998, 2002a), Reclamation (2004, 2008), Mueller (2006), Albrecht et al. (2010a), Zelasko et al. (2009), and Valdez et al. (2011) for the UCRB. The identification also integrates information from both older and more recent works as well as the expert knowledge of LCR MSCP fish biologists. The following paragraphs discuss the 13 critical activities and processes in alphabetical order. The 8 core reference works noted above are implicit citations for all 13 definitions.

CHEMICAL STRESS

RASU in every life stage 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, possibly including selenium (Hamilton et al. 2005a; Stolberg 2009, 2012). 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. However, as RASU mature, they become increasingly able to avoid or remove themselves from settings in which they may sense chemically unsuitable conditions – if these conditions are sufficiently localized to permit such avoidance or escape.

DISEASE

RASU in every life stage are vulnerable to infection, including that by fungi and parasites (see also Clarkson et al. 1997; Robinson et al. 1998; Mueller 2006; Marsh 1987; Ward et al. 2007; Ward and Finch 2009). Non-lethal infections may make the affected individuals vulnerable to mortality from other causes.

DRIFTING

RASU dispersing larvae move over short (<10 meters) to larger distances (1–10 kilometers [km] or more) primarily passively by the force of water currents, although they may try control the timing of drift by swimming in/out of currents (Modde and Irving 1998; Tyus et al. 2000). A preference for night drifting may be an adaptation for avoiding predation (see also Johnson et al. 1993; Horn et al. 1994; Johnson and Hines 1999). RASU resettled larvae also may move passively by the force of water currents, but this mode of movement presumably is less important than swimming for this later larval stage (Modde and Irving 1998; Tyus et al. 2000). They also may preferentially drift at night.

EGG DESCENT AND EGG SETTLING/ADHESION

Spawning RASU males and females release gametes into the open water above sites selected for spawning, and fertilization takes place in the open water (Minckley and Gustafson 1982; Bozek et al. 1984; Langhorst and Marsh 1986; Snyder and Muth 2004). The spawning activity itself helps prepare the selected sites to receive and protect the eggs by agitating the surface of the benthic substrate, thereby removing fine sediment and/or excavating nest-like depressions (Bozek et al. 1984; Snyder and Muth 2004; Mueller 2006). 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. Spawning RASU "finning" during the spawning act not only may remove fine sediment and excavate depressions in the substrate, but may also drive the eggs into the substrate, eliminating the "descent" step altogether (Mueller 2006). Success for the gametes consists of their combining to produce fertilized eggs, and success for the fertilized eggs consists of their surviving in the open water to adhere to or become embedded in the substrate and begin embryological development. Although the process encompasses several distinct phases, the habitat conditions affecting the number of fertilized eggs that successfully transition (recruit) to the next life stage divide into two groups: (1) those that affect the eggs during descent through the water column and (2) those that affect the eggs after they arrive at the bottom of the water column. The CEM recognizes these two groups as distinct critical biological processes: egg descent and egg settling/adhesion.

FORAGING

RASU begin foraging as dispersing larvae, once they have assimilated their yolk and become able to swim, and continue through all remaining life stages. They forage for phytoplankton, microinvertebrates, smaller macroinvertebrates (e.g., insect larvae), and detritus along the benthos and on the leaf surfaces of submerged vegetation; and for zooplankton and phytoplankton in the water column, with food item sizes and other dietary preferences varying among the life stages (e.g., depending on larval versus mature mouth position, mouth size, and presumably agility) (see also Langhorst and Marsh 1986; Mueller 2006; Marsh 1987). Zooplankton can make a significant contribution to the diet (Mueller 2006). Diet may also vary between lentic and lotic environments (Reclamation 2008), and hatchery-reared RASU may develop distinct feeding habits prior to repatriation.

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 flow velocities and turbulence in excess of tolerable ranges; burial by a rapid influx of sediment; stranding by a sudden drop in water level; inundation by water levels too deep for embryos to mature; wounding and buffeting from unsuccessful predator attacks; damage during scientific sampling; 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 (Mueller 2006). Non-lethal mechanical stress may leave affected individuals vulnerable to infections and mortality from other causes (see also Brandenburg et al. 2002; Mueller et al. 2003a; Mueller 2006; Hunt 2008; Hunt et al. 2012; Mueller et al. 2008; Reclamation 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 is the case with all animals. Every animal species evolves strategies that permit its persistence despite predation, including specific behaviors, body features, or reproductive strategies that allow it to avoid, escape, defend against, or counterbalance its losses from predation.

RASU face predation from both aquatic and avian species. As discussed further in chapter 6, each RASU life stage experiences predation from a distinct spectrum of these species (and sometimes different life stages among these species) with potentially different foraging behaviors (Bozek et al. 1984; Langhorst and Marsh 1986; Horn et al. 1994; 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; Karam and Marsh 2010; Albrecht et al. 2010b; Bestgen et al. 2011, 2012).

The spectrum of native predators in the historic, unregulated river 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. 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 that 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. 2012). Larger RASU use cover for protection and may also bury themselves in fine substrates (Mueller 2006; Valdez et al. 2012). 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. For example, Kesner et al. (2012) found that individuals >450 mm TL experience much lower rates of mortality than do smaller individuals, although the study did not specifically identify differences in predation rates as the cause of this difference in survivorship. Finally, the characteristic deep-bodied, humpbacked RASU body form may also have evolved as an outcome of predatory pressure (Hambright 1994; Portz and Tyus 2004; Nowlin et al. 2006).

However, these evolved 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, as indicated for example by their differential consumption of RASU and other native fishes compared to their consumption of other non-natives (Pilger et al. 2008; Yard et al. 2011).

Furthermore, hatchery-reared subadults may experience uniquely higher rates of predation due to their lack of experience with predators and due to patterns of surfacing behavior developed at their rearing facilities. This has led to the hypothesis that pre-conditioning might help RASU better avoid predators (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). 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 the 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 capturing RASU directly from the shallows of a spawning site.

RESTING

RASU, during every mobile life stage, need to rest to conserve energy. They may have specific preferences for the habitat conditions they seek in resting locations that afford them protection from predators and thermal, chemical, or mechanical stress, and these preferences may differ among life stages and by season (see also Mueller et al. 2000; Lee et al. 2006; Mueller 2006; Hedrick et al. 2009; Bestgen et al. 2011, 2012). The ability of RASU to find suitable resting sites presumably increases as their range of mobility increases with size and age. 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 sites within these ranges as recorded for adults (Minckley et al. 1991; Reclamation 2008), 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).

RIPENING

“Ripening” is associated with a single RASU life stage, spawning adults, 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 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 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 a single – although large – suite 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 scales that encompass entire lakes and, where present, flowing river and tributary waters 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” (as reported in 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 (Minckley et al. 1991; Modde and Irving 1998; USFWS 1998, 2002a; Mueller 2006; Reclamation 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, personal communications concerning Imperial Ponds, September 2013). Whether pheromones are also involved in triggering spawning is not known.

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; Reclamation 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 Imperial Ponds (LCR MSCP biologists, personal communications, September 2013). The understanding of substrate selection for spawning is complicated by a lack of quantitative information on substrates at spawning sites (e.g., the use of qualitative descriptions such as “cobble” and “gravel” [see review by Valdez et al. 2012]) and by a lack of substrate data comparing sites selected versus ignored for spawning.

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, using “eye flashes” to signal their presence 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 Reclamation (2008) 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. 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. Juveniles and older RASU swim over increasingly large distances within and sometimes 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 may be solitary or in "schools." Schooling – aggregation not associated with spawning – first appears among dispersing larvae and has been reported for all subsequent age classes (USFWS 2001; Snyder and Muth 2004; Mueller 2006). Schooling may explain the uneven distributions of juveniles/subadults encountered by LCR MSCP biologists during riverine and backwater sampling (LCR MSCP biologists, personal communications, August–September 2013). There are anecdotal reports of schooling among subadult and/or adult RASU in the LCR (e.g., presentations and discussion observed by the lead author of this document at the 2013 Colorado River Aquatic Biology annual meeting) (Laughlin, Nevada, January 9–10, 2013). These reports precipitated energetic discussions around whether these are actual schooling behaviors or merely aggregations of repatriated RASU, persisting for days or weeks (or months) following release, perpetuating a pattern of behavior learned in the hatchery environment. Alternatively, given reports of schooling across all age classes along the river over many years, such non-spawning 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 subadults may lack stamina for long-distance movement initially following release and lack strength for avoiding 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). The potential benefits of conditioning swimming abilities among reared RASU prior to release are the subject of ongoing research (http://www.lcrmscp.gov/fish/fish_res_mon.html). 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 due to 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; Reclamation 2008; 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, reducing fitness and increasing vulnerability to other hazards. However, Wesp and Gibb (2003) did not see evidence of adverse temperature effects on predator avoidance behaviors among RASU larvae in laboratory experiments. RASU repatriated subadults may be more vulnerable to thermal stress initially than their wild-born cousins due to a lack of conditioning (see also Mueller and Foster 1999). However, 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. This can pose a challenge, however, when RASU seek cooler water during summer months, as such cooler water may also have lower concentrations of DO (Mueller 2006).

Chapter 4 – Habitat Elements

Habitat elements consist of specific habitat conditions that ensure, allow, or interfere with critical biological activities and processes.

This chapter identifies 16 habitat elements that affect 1 or more critical biological activities or processes across the 8 RASU life stages. Some of these habitat elements differ in their details among life stages. For example, different RASU life stages experience different taxa, sizes, and densities of predators – the subject of "predator activity" – depending on the RASU life stage. However, using the same labels for the same *kinds* of habitat elements across all life stages makes comparison and integration of the CEMs for the individual life stages across the entire life cycle less difficult. Table 3 lists the 16 habitat elements and the critical activities and processes that they *directly* affect across all RASU life stages.

Table 3.—Habitat elements directly affecting critical activities and processes

Critical activity or process ➔ **⬇ Habitat element**	**Chemical stress**	**Disease**	**Drifting**	**Egg descent**	**Egg settling/adhesion**	**Foraging**	**Mechanical stress**	**Predation**	**Resting**	**Ripening**	**Staging and spawning**	**Swimming**	**Thermal stress**
Competitor activity								X				X	
Depth				X			X			X	X		
Flow/turbulence			X	X	X		X		X	X	X	X	
Genetic diversity		X											
Infectious agents		X											
Macrohabitat geometry			X									X	
Mesohabitat geometry/cover			X			X		X	X		X	X	
Plankton-benthos-particulate organic matter						X							
Predator activity								X				X	
Pre-release conditioning	X	X				X		X				X	X
Scientific study				X	X		X						
Substrate texture/dynamics					X		X		X		X		
Transport/release							X						
Turbidity						X		X	X		X	X	
Water chemistry	X								X	X	X		
Water temperature	X								X	X	X	X	X

The diagrams and other references to habitat elements elsewhere in this document identify the habitat elements by a one- or two-word short name. However, each short name in fact refers to a longer, full name such as “abundance and distribution of XXX.” The paragraphs below document the full name for each habitat element and provide a full definition. The elements identified across the eight life stages appear here in alphabetical order.

The basic sources of the information used to identify the habitat elements are Minckley et al. (1991), (USFWS 1998, 2002a), (Reclamation 2004, 2008), Mueller (2006), Albrecht et al. (2010a), Zelasko et al. (2009), and Valdez et al. (2011, 2012). The identification also integrates information from both older and more recent works as well as the expert knowledge of LCR MSCP fish biologists.

Valdez et al. (2012) in particular provides a thorough review of the literature and expert knowledge to catalog the abiotic (physical and chemical) characteristics of settings in which RASU occur during different life stages – specifically during spawning, larval drift, larval maturation, and as subadults and adults. The review also summarizes possible biological and ecological reasons for these associations, although this is not its primary emphasis. The present CEM does not repeat the detailed tabulations provided by Valdez et al. (2012), but rather refers the reader to the appropriate sections of Valdez et al. (2012) when appropriate. As with all tabulations of habitat associations, inferences that particular habitat characteristics are critical to a species or life stage require evidence and CEMs for why each association matters to species viability (Rosenfeld 2003; Rosenfeld and Hatfield 2006). Table 4 provides a key for locating the information in their report that corresponds to each habitat element in the RASU conceptual ecological model as follows:

Table 4.—Habitat characterization in Valdez et al. (2012) and in the RASU conceptual ecological model

Habitat characteristic in Valdez et al. (2012)	Habitat element in RASU CEM
Mesohabitat	Mesohabitat geometry/cover
Microhabitat: temperature	Water temperature
Microhabitat: depth	Depth
Microhabitat: velocity	Flow/turbulence
Microhabitat: substrate	Substrate texture/dynamics

COMPETITOR ACTIVITY

Full name: **The types, abundance, and distribution of competitors and their patterns of activity.** RASU potentially face a wide array of competitors at every life stage, some native but mostly non-native. This element refers to a set of closely related variables that affect the likelihood that different species will affect RASU activities by competing for food or habitat space. The variables include the species and sizes of the aquatic fauna that compete with RASU for dietary items or habitat features, such as cover during different RASU life stages, among the mesohabitats where those RASU life stages occur; the density and spatial distribution of these competitors among these mesohabitats; and whether competitor activity may vary in relation to other factors (e.g., time of day, water temperature, flow or turbulence, turbidity, etc.).

DEPTH

Full name: **The abundance and distribution of habitat with a suitable range of depth.** This element refers to the depth of water covering the habitat sites potentially used by individuals in each specific life stage and the way that depth may vary over time. "Depth" for gametes and fertilized eggs in open water, and for embryos and larvae on/in the substrate (life stages 1 and 2), refers to conditions only at the spawning sites themselves. Depth may directly affect habitat suitability, or it may do so indirectly by its effects on other habitat elements such as water temperature or chemistry, flow velocities, or benthic biological community composition. Depending on timing, variation in depth may be a cueing factor 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). Valdez et al. (2012) provide a review of depths of occurrence/activity of RASU during different life stages. Water depths depend almost entirely on operational decisions at the dams above, and within the LCR, and/or at intakes and pumps used to control pond levels (see chapter 5).

FLOW, TURBULENCE

Full name: **The abundance and distribution of habitat with suitable ranges of flow velocity and turbulence**. This element refers to the range of water flow velocities and turbulence encountered by individuals of each life stage. Flow and velocity affect numerous critical RASU activities and processes during all life stages. Velocity fields may be large (e.g., spanning an entire interreservoir reach), intermediate (e.g., thermal currents in reservoirs), or small (e.g., concentrated at a dam [turbine] or 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 propulsion system [jets or propellers]). Valdez et al. (2012) provide a detailed review of flow velocity ranges in areas of RASU activity during different life stages. Flow/turbulence at all scales along the LCR depend on water storage-delivery management, which includes all dam and pond operations. At intermediate spatial scales, it also depends on tributary inflow and on channel/reservoir geometry as represented in the model by two other habitat elements: macrohabitat geometry and mesohabitat geometry/cover. At fine spatial scales, flow/turbulence also depend on motorboat activity and the effects of mesohabitat geometry/cover. Weather also affects flow/turbulence through the effects of storms on wave formation – a factor outside the scope of this CEM.

GENETIC DIVERSITY

Full name: **The genetic diversity of RASU individuals.** This element refers to the genetic homogeneity versus heterogeneity of the population during each life stage. 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 (USFWS 2002a; Minckley et al. 2003; Hurt and Hedrick 2004; Dowling et al. 2005, 2011, 2012; Reclamation 2008; Wilson 2011, 2012).

INFECTIOUS AGENTS

Full name: **The types, abundance, and distribution of infectious agents.** This element refers to the spectrum of viruses, bacteria, fungi, and parasites – including *Lerneae* spp. and *Myxobolus* spp. – present and capable of infecting RASU in the open environment of the LCR (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 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.

MACROHABITAT GEOMETRY

Full name: **The types, abundance, and distribution of aquatic macrohabitats.** This element refers to the large-scale (i.e., 1–100 km scale) shape of the river channel, backwaters and other off-channel wetted areas, and the connected flood plain as well as the distribution of specific aquatic macrohabitat types. Examples of macrohabitat types 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 also constitute macrohabitats for purposes of this model. Macrohabitats define the overall flow path(s) for water and sediment moving through the system and establish the template for the formation of mesohabitats. Macrohabitat geometry historically was shaped by main stem and tributary riverflows and also by their sediment transport, interacting with flood plain vegetation and geology. Presently, the historic geometry remains only in a few places where the channel is confined by bedrock and at tributary confluences (although the latter are often submerged by reservoirs). Otherwise, today, macrohabitat geometry depends on main stem water storage-delivery management, tributary inflow, and channel and shoreline management. Valdez et al. (2012) provide a detailed review of macrohabitat types and conditions in areas of RASU activity during different life stages.

MESOHABITAT GEOMETRY/COVER

Full name: **The types, abundance, and distribution of suitable aquatic mesohabitats and suitable cover provided by these habitats.** This element refers to the finer-scale (i.e., site scale) shape of aquatic habitat along the river channel, off-channel wetted areas, and the connected flood plain as well as the distribution of the resulting specific aquatic mesohabitat types. Mesohabitats are portions of macrohabitats that vary in depth, flow velocity and turbulence, substrate, and vegetation. Examples include littoral and deltaic shallows, snags, pools, islands, point-bars, etc. Mesohabitats may include features such as emergent vegetation, snags, overhangs, and hollows that can provide cover for individuals of different life stages (Mueller 2006). Fish behavior often varies strongly with mesohabitat setting (Parasiewicz et al. 2008). RASU exhibit strong fidelity to individual or limited sets of spawning sites (Tyus and Karp 1990; Modde and Irving 1998; USFWS 1998; Mueller et al. 2000; Reclamation 2008; Wydoski et al. 2010; Wydoski and Lantow 2012) and to overwintering sites (Mueller et al. 2000). These sites presumably constitute locations specifically selected among the mesohabitats available for some suite of characteristics. Mesohabitat geometry, including provision of cover for RASU, historically was shaped by the same factors that shaped macrohabitat geometry but at a finer spatial scale (i.e., by main stem and tributary riverflows and their loads of sediment and snags interacting with flood plain vegetation and geology). Mesohabitat geometry 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 geometry depends on main stem water storage-delivery management, tributary inflow, channel and shoreline management, and the effects of macrohabitat geometry. Remnants of individual historic mesohabitat sites remain, 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; Reclamation 2008; Schooley et al. 2008; Albrecht et al. 2010a; Patterson et al. 2012; Valdez et al. 2012). Valdez et al. (2012) provide a detailed review of mesohabitat geomorphics associated with RASU activity during different life stages.

PLANKTON-BENTHOS-PARTICULATE ORGANIC MATTER

Full name: **The types, abundance, distribution, and composition of planktonic and benthic organisms and particulate organic matter.** This element refers to the taxonomic and body size composition of the planktonic and benthic assemblages of biofilms, algae, and micro and macroinvertebrates that individual RASU can encounter during each life stage as well as the density and spatial distribution of these assemblages among mesohabitats. RASU feed on planktonic and benthic organisms, but dietary preferences for different sizes and types of planktonic and benthic organisms differ among the different RASU life stages. This element also refers to the organic detritus – particulate organic matter, or “POM,” on which RASU also may feed during some life stages. The assemblage of benthic organisms may include some, such as crayfish and certain kinds of insect larvae, that prey on larval and early juvenile RASU (Horn et al. 1994; Mueller et al. 2006) and may also include filter-feeding species such as the introduced quagga and zebra mussel that compete with RASU for plankton and floating detritus.

Historically, the abundance, distribution, and types of plankton, benthos, and POM in the river and its backwaters depended on natural inputs of nutrients supporting primary productivity in the river and its wetlands, constrained by turbidity (depth of light penetration), and inputs of POM from upstream and from the main stem and tributary flood plain woodlands and wetlands entrained during flood events. Today, the main stem no longer interacts with a natural suite of flood plain woodlands and wetlands; natural inputs of POM, therefore, are likely much reduced. Further, primary productivity is likely affected by alterations to water chemistry by, for example, hypolimnetic discharge from dams as well as wastewater and other contaminant inputs; the effects of introduced filter feeders, introduced plankton and algae, and other fauna that may compete with RASU for food items or prey on them; the effects of non-RASU fishery management on the abundance of competitors for RASU food items and predators on RASU; and the interactions of numerous other habitat elements, especially turbidity.

PREDATOR ACTIVITY

Full name: **The types, abundance, and distribution of predators and their patterns of activity.** RASU face numerous predators at every life stage, some native but mostly non-native. This element refers to a set of closely related variables that affect the likelihood that different kinds of predators will encounter and successfully prey on RASU in each life stage: the species and sizes of the aquatic and avian (e.g., osprey, kingfisher, cormorant, pelican) fauna that prey on RASU during different life stages; the density and spatial distribution of these fauna among (or flying over) these mesohabitats; and whether predator activity may vary in relation to other factors (e.g., time of day, water temperature, flow or turbulence, turbidity, etc.).[3] Predator activity affecting the different RASU life stages otherwise depends on nuisance species introductions and management, non-RASU fishery management, and the effects of numerous other habitat elements including water temperature, turbidity, mesohabitat geometry/cover, and the composition of the benthic biological community.

PRE-RELEASE CONDITIONING

Full name: **The types and extent of pre-release conditioning of reared RASU physiology and behavior.** 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. A growing literature base indicates 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; Ward and Hilwig 2004; Lee et al. 2006; Mueller 2006; Mueller et al. 2007; Schooley et al. 2008; Reclamation 2008; Kegerries and Albrecht 2009; Avery et al. 2011; Senger and Sjöberg 2011; Bestgen et al.

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[3] The factors that shape the abundance and distribution of avian predators on RASU lie outside the scope of this model For example, the conceptual model could recognize water storage-delivery management, Tributary Inflow, and Management of Channel, Lake, Pond Geometry as affecting the availability of habitat and other foods for birds that prey on RASU. Avian predation may vary by season, too (Campbell et al. 2007). However, expanding the model to include factors shaping avian predator activity would result in a large expansion of the scope of the model and still not adequately address all critical factors affecting the densities and activity patterns of the avian predators.

2011, 2012; Olson et al. 2012). Further investigations are underway. Pre-release conditioning depends on the policies and practices of RASU rearing in controlled environments, which the CEM does not address.

SCIENTIFIC STUDY

Full name: **The types, frequencies, and duration of scientific monitoring, capture, and handling.** This element refers to the possibility of capture, examination, tagging, and removal of RASU during scientific studies. 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 vary 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. As noted in the discussion of critical activities and processes, above, the relative degree of solitary versus aggregated movement reciprocally may shape the effectiveness of different detection and capture methods and their associated sampling designs. The types and methods of scientific study of RASU carried out along the LCR depend on LCR MSCP policies and the practices of numerous lake and river monitoring programs, which the CEM does not address.

SUBSTRATE TEXTURE/DYNAMICS

Full name: **The abundance and distribution of substrates with suitable texture, stability, and other features.** This element refers to the particle size distribution of benthic sediment within mesohabitats; to substrate dynamics such as the frequency of shifting, scour, and burial; and to other potentially important features of the substrate. These features may affect substrate suitability for RASU spawning and embryo development and for use as resting sites by free-swimming individuals as well as affect the benthos assemblage. 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. However, the literature does not indicate what particular features make these sites attractive compared to other sites with similar substrates (compare Minckley et al. 1991; Modde and Irving 1998; USFWS 1998, 2002a; Mueller 2006; Reclamation 2008; Schooley et al. 2008; Albrecht et al. 2010a, 2010b; Bestgen et al. 2011, 2012; Patterson et al. 2012; Valdez et al. 2012). Part of the problem may be that substrate descriptions use qualitative terms such as “cobble” and “pebble” rather than providing quantitative metrics of particle size distributions (Valdez et al. 2012). The abundance and distribution of substrates along the LCR today depend on main stem water storage-delivery management, tributary inflow, and mesohabitat geometry/cover, 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.

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 (Hancock et al. 2005; Boulton et al. 2010), as it does in other alluvial river settings, or affect substrate suitability as resting or spawning habitat, as has been observed for salmonids (Geist et al. 2008; Kondolf et al. 2008; Tonina and Buffington 2009). However, no specific studies of such interactions along the LCR appear to exist. At the same time, the literature on RASU along the LCR recognizes a strong fidelity to spawning sites, but does not identify the specific attributes that make these gravel-and-cobble sites attractive compared to other sites where similar substrates occur (see above). It might therefore be useful to determine whether hyporheic discharge plays any role in RASU spawning site selection. The literature on RASU habitat requirements (e.g., Valdez et al. 2012) does not appear to address this topic.

TRANSPORT/RELEASE

Full name: **The methods of transport and release of reared RASU for repatriation.** This element refers to the process of transporting and releasing reared RASU for repatriation. Stress during transport/release can affect survival among the freshly released individuals (Hawkins 2008; Schooley et al. 2008; Sykes 2013). Further investigations of this topic are underway (http://www.lcrmscp.gov/fish/fish_res_mon.html).

TURBIDITY

Full name: **The abundance and distribution of suitable ranges of turbidity.** This element refers to the turbidity at sites potentially used by individuals in each specific life stage, including the way that turbidity may vary over time. “Turbidity” for gametes and fertilized eggs in open water and for embryos and larvae on/in the substrate (life stages 1 and 2) refers to conditions only at the spawning sites themselves. This element directly affects several critical RASU behaviors such as foraging, navigating, and predator avoidance (Minckley et al. 1991; USFWS 1998, 2002a; Johnson and Hines 1999; Reclamation 2008; Valdez et al. 2012). It also affects planktonic and benthic (periphyton) productivity (see the “Plankton-Benthos-Particulate Organic Matter” section above) as well as competitor and predator behavior through its effects on light penetration and sighting distances. Historically, turbidity levels and their variation over time and space depended on main stem and tributary flows, channel and backwater geometry, and sediment loads. The Colorado River, before regulation, was highly turbid, especially along its main channel and during flow pulses, with lower turbidity along channel margins and in off-channel settings. Turbidity levels 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 and both macro and mesohabitat geometry – with added effects from tributary inflow, channel and shoreline management (Reclamation 2004), nuisance species introduction and management, and (in a feedback relationship) planktonic and benthic (periphyton) productivity. Valdez et al. (2012) qualitatively summarize the ways in which turbidity affects RASU behavior, and/or affects predation on RASU, under the general heading of “cover,” but note that the scientific literature includes only sparse data on RASU cover associations, including turbidity.

The effects of nuisance species on turbidity arise because these species include additions to the planktonic and benthic invertebrate communities such as algae that may create blooms and quagga and zebra mussels that filter out large amounts of plankton and POM. Introduced benthic feeders such as carp also can cause significant disturbance of benthic sediment, generating at least local turbidity. Conversely, Osterling et al. (2007) found that sediment turbidity produced by mayfly larval bioturbation inhibited quagga mussel colonization.

WATER CHEMISTRY

Full name: **The abundance and distribution of suitable ranges of water chemistry.** This element refers to the water chemistry at sites potentially used by individuals in each specific life stage, including the way that water chemistry may vary over time. It includes parameters such as DO, pH, salinity, naturally occurring dissolved ions, and contaminants such as added nitrate, perchlorate, selenium, and artificial organic compounds (Reclamation 2004, 2005, 2010, 2011b, 2011c; Turner et al. 2011; Stolberg 2009, 2012). RASU during different life stages are vulnerable to alterations to water chemistry either directly or through the accumulation of contaminants in invertebrates on which RASU feed (Hamilton et al. 2005a; Stolberg 2009, 2012). Alterations to water chemistry along the LCR, specifically nutrient enrichment, also affect planktonic and benthic primary productivity, which in turn affect turbidity, although productivity may be more phosphorus limited than nitrogen limited (Turner et al. 2011). Contaminants in the LCR arrive from an array of point and non-point sources (see below). Main stem water storage-delivery management also affects water chemistry through its effects on reservoir operations and releases (see below). Numerous habitat elements affect water chemistry, particularly depth and temperature and their variation.

WATER TEMPERATURE

Full name: **The abundance and distribution of suitable ranges of water temperatures.** This element refers to the water temperature at the sites potentially used by individuals in each specific life stage and the way temperature varies over time. "Water temperature" for gametes and fertilized eggs in open water and for embryos and larvae on/in the substrate (life stages 1 and 2) refers to conditions only at the spawning sites themselves. Water temperature may affect RASU habitat suitability directly, or it may act indirectly through its 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. Water temperature along the river and its lakes depends strongly on operational decisions at the dams above, and within the LCR, which affect the temperature of dam releases and also affect water depths (Clarkson and Childs 2000), which in turn affect thermal gradients in the reservoirs. Similarly, groundwater pumped into refuge ponds can also alter water temperatures within these isolated waters. Valdez et al. (2012) review the effects of water temperature on different RASU life stages and catalog the ranges of temperatures recorded in areas of RASU activity during different life stages along with the evidence for how temperature affects activity and development.

Chapter 5 – Controlling Factors

Controlling factors consist of environmental conditions and dynamics – both natural and anthropogenic – that determine the abundance, spatial and temporal distribution, and quality of the conditions that comprise the habitat template. A hierarchy of such factors exists, with long-term dynamics of climate and geology at the top. However, this CEM focuses on seven immediate controlling factors that are within the scope of potential human manipulation. The seven controlling factors identified in this CEM do not constitute individual variables; rather, each identifies a category of variables (including human activities) that share specific features that make it useful to treat them together. Table 5 lists the seven controlling factors and the habitat elements they *directly* affect.

Table 5.—Habitat elements directly affected by controlling factors

Controlling factor ➔ **⬇ Habitat element**	**Management of channel, lake, pond geometry**	**Motorboat activity**	**Non-RASU fishery management**	**Nuisance species introduction and management**	**Tributary inflow**	**Wastewater and other contaminant inflow**	**Water storage-delivery management**
Competitor activity			X	X			
Depth	X						X
Flow/turbulence		X			X	X	X
Genetic diversity	*(n/a)*						
Infectious agents			X	X		X	
Macrohabitat geometry	X				X		X
Mesohabitat geometry/cover	X			X	X		
Plankton-benthos-POM			X	X	X	X	
Predator activity			X	X			
Pre-release conditioning	*(n/a)*						
Scientific study	*(n/a)*						
Substrate texture/dynamics		X		X	X		X
Transport/release	*(n/a)*						
Turbidity	X			X	X	X	
Water chemistry					X	X	X
Water temperature					X	X	X

Four habitat elements are not directly affected by any of the seven controlling factors. The model recognizes that three of these – pre-release conditioning, scientific study, and transport/release – are controlled by decisions within the LCR MSCP HCP and its partner institutions. The model does not treat these decisions as a separate controlling factor. In turn, the model recognizes that genetic diversity is controlled by another habitat element, scientific study.

MANAGEMENT OF CHANNEL, LAKE, POND GEOMETRY

This factor addresses the activities of Reclamation, USFWS , and the States and Tribes in managing the geometry of the river channel, river impoundments, off-channel habitats, and off-channel impoundments. It covers activities such as dredging; shoreline armoring; construction and maintenance of river levees and training structures; construction and maintenance of connected and isolated backwater environments, including wildlife refuges; and other modifications in areas of intense development (Reclamation 2004). These activities thus strongly shape macro and mesohabitat geometry and moderately shape depth profiles throughout the system. However, areas of active dredging along the channel, and dredging/shaping of refuge ponds, are spatially limited and only moderately frequent (LCR MSCP biologists, personal communications, April–September 2013). Channel, shoreline, and pond management activities such as dredging and bank maintenance also can disturb sediment in ways that potentially can produce localized turbidity that disperses with distance from the location of the activity. The HCP specifically recognizes this as one of the ways in which Federal actions may routinely affect RASU (Reclamation 2004). However, the effects will be localized and brief due to the limited flow velocities present in the regulated LCR and refuges.

MOTORBOAT ACTIVITY

This factor addresses motorboat activity, which can cause boat wakes and propeller turbulence that damage habitat or disturb egg clusters, or can harm individual fish (larvae to larger individuals) entrained in the vortex created by a spinning propeller or water jet. Boating regulations and signage enforce no-wake zones along some reaches and in river-connected refuges along the LCR. Turbulence from intensive boating activity in areas of shallow depths, and boat grounding 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 FISHERY MANAGEMENT

This factor addresses the active management of non-RASU fisheries along the LCR that could affect RASU or their habitat. Effects may include the introduction of infectious agents, changing or maintaining a spectrum of predators on RASU, changing the spectrum of species that compete with RASU for food or habitat, and altering physical habitat. Infectious (including parasitic) organisms likely introduced with non-native sport fishes that are known to or potentially could affect RASU include *Lerneae* spp. and *Myxobolus* spp. (Valdez 1990; Clarkson et al. 1997; Robinson et al. 1998; Choudhury 2004; Mueller 2006; Ward et al. 2007).

The States bordering the LCR recognize and oversee sport fisheries for introduced fishes along the river, its reservoirs, and its tributaries. The fishes recognized by these States as non-native sport fishes include intentionally introduced and/or stocked species and accidental introductions. The States and recreational fishers have also introduced forage species to support the sport fisheries. These forage species may be caught as sport fish and may also be nuisance species. Arizona lists the official sport fishes for the State (http://www.azgfd.gov/h_f/sport_fish.shtml) and State records for any caught along the LCR (http://www.azgfd.gov/h_f/state_records.shtml). The potential for conflicts between sport fishery management and the conservation of native fishes along the Colorado River is a longstanding concern (Minckley et al. 2003; Clarkson et al. 2005).

Table 6 lists non-native sport species introduced into the LCR (for introduced forage and other non-native, non-game fishes, see the "Nuisance Species Introductions and Management" section below). One column indicates whether one or more life stages of the species are known to prey on ("***P***") one or more RASU life stages (Bozek et al. 1984; Minckley et al. 1991; USFWS 1998, 2002a; Portz and Tyus 2004; Mueller and Burke 2005; Mueller 2005, 2006; Mueller et al. 2007; Carpenter and Mueller 2008; Pilger et al. 2008; Schooley et al. 2008; Reclamation 2008; Albrecht et al. 2010a; Karam and Marsh 2010; Yard et al. 2011; Farrington et al. 2013). Two additional columns indicate whether juveniles ("***J***") or adults ("***A***") of the species potentially could compete with ("***-C***") one or more life stages for food items such as zooplankton, smaller benthic macroinvertebrates, or POM. The "***J-C***" and "***A-C***" column entries rest on information in FishBase, a global database on fish ecology (www.fishbase.org). Numerous studies identify competition as a potential factor affecting RASU survivorship 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).

Table 6.—Introduced sport fish in the LCR; possible predators on/competitors with RASU

Introduced sport species	***P***	***J-C***	***A-C***
Bass, largemouth (*Micropterus salmoides*)	X	X	
Bass, smallmouth (*Micropterus dolomieu*)		X	
Bass, striped (*Morone saxatilis*)	X	X	
Bass, white (*Morone chrysops*) (aka sand bass)		X	
Bluegill (*Lepomis macrochirus*)	X	X	X
Bullhead, black (*Ameiurus melas*)		X	X
Bullhead, yellow (*Ameiurus natalis*)	X	X	X
Carp (*Cyprinus carpio*)	X	X	X
Carp, grass (*Ctenopharyngodon idella*) (aka White Amur)		X	X
Catfish, channel (*Ictalurus punctatus*)	X	X	X
Catfish, flathead (*Pylodictis olivaris*)	X	X	X
Crappie, black (*Pomoxis nigromaculatus*)		X	
Crappie, white (*Pomoxis annularis*)		X	
Sunfish, green (*Lepomis cyanellus*)	X	X	
Sunfish, redear (*Lepomis microlophus*)		X	
Sunfish, warmouth (*Lepomis gulosus*) (aka warmouth bass)		X	
Tilapia (*Oreochromis*, *Sarotherodon*, or *Tilapia* spp.)		X	X
Trout, brook (*Salvelinus fontinalis*)		X	
Trout, brown (*Salmo trutta*)		X	
Trout, cutthroat (*Oncorhynchus clarkii*)		X	
Trout, rainbow (*Oncorhynchus mykiss*)	X	X	
Walleye (*Sander vitreus*)		X	

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 by the LCR MSCP HCP (Reclamation 2004) – bonytail (*Gila elegans*), humpback chub (*Gila cypha*), and flannelmouth sucker (*Catostomus latipinnis*) – and one, roundtail chub (*Gila robusta*), is managed as a non-threatened sport fish.

The Colorado pikeminnow (*Ptychocheilus lucius*) is managed as an endangered species in the UCRB but not along the LCR. It was almost certainly a native predator on RASU; in fact, historically, it was the only major predatory fish in the Colorado River (Minckley 1973; http://www.fws.gov/southwest/SJRIP/GB_FS.cfm; USFWS 2002b; Portz and Tyus 2004; Franssen et al. 2007; Dale Ryden, USFWS, personal communication, November 2013). The species lacks teeth in its jaws, but possesses pharyngeal teeth on its gills in the back of its throat, with which it grasps and holds its prey. Pikeminnow become exclusively piscivorous after they reach 200 mm TL, and their selection of prey is strongly gape limited (Vanicek and Kramer 1969; Portz and Tyus 2004). As a result, they consume primarily small-bodied, soft-rayed, cylindrical prey lacking a dorsal keel, including bluehead sucker, carp, fathead minnow, flannelmouth sucker, red shiner, redside shiner, roundtail chub, sand shiner, speckled dace, and white sucker (Vanicek and Kramer 1969; USFWS 2002b; Dale Ryden, USFWS, personal communication, November 2013). Ryden (Dale Ryden, USFWS, personal communication, November 2013) and Franssen et al. (2007) estimate that pikeminnow prefer deep-bodied prey no more than 33–37 percent their own body length.

Smaller RASU meet the requirements for being potential pikeminnow prey. The North American Native Fishes Association specifically warns that captive young pikeminnow will eat *smaller* RASU placed in the tanks with them (http://www.nanfa.org/captivecare/ptychocheilus.shtml). However, RASU develop a characteristic adult bony keel as they grow (Mueller 2006). This, along with increasing RASU size as adults, discourages predation of larger RASU by pikeminnow (Portz and Tyus 2004; Franssen et al. 2007; Dale Ryden, USFWS, personal communication, November 2013). Pikeminnow today are rare along the LCR. However, pikeminnow predation may have shaped the evolution of RASU body form and behaviors, which in turn affect RASU vulnerability to the predators in the system today (see chapters 1 and 3).

NUISANCE SPECIES INTRODUCTIONS AND MANAGEMENT

This factor addresses animals and plants introduced into LCR waters and wetlands *but not officially managed by the states for recreation or as bait or forage for a sport fishery* that affect RASU survival or reproduction. The introduction may have been intentional or not. The potential list of species in this group includes microbes (e.g., viruses or invasive plankton). The nuisance species may 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.

The non-native reed, *Phragmites australis*, for example, alters shoreline and wetland cover; the non-native golden alga (*Prymnesium parvum*) produces a toxin harmful to RASU and many other fishes (Brooks et al. 2011); and non-native quagga (*Dreissena rostriformis bugensis*) and zebra (*Dreissena polymorpha*) mussels filter out large quantities of plankton and blanket benthic habitat. Quagga and zebra mussel filtering activities potentially can increase water clarity, potentially allowing more growth of emergent macrophytes across a given shallow-water setting, as suggested by LCR MSCP biologists (personal communications, September 2013). Rogalski and Skelly (2012) also report a possible positive relationship between *Phragmites* expansion and non-native American bullfrog (*Rana catesbeiana*) productivity. State agencies and private parties introduced some of the nuisance species as bait or forage for sport fisheries, including threadfin shad (*Dorosoma petenense*), red shiner (*Notropis lutrensis*), western mosquitofish (*Gambusia affinis*), fathead minnow (*Pimephales promelas*), and at least two species of crayfish (*Orconetes virilis* and *Procambarus clarkii*). Several fish species are considered both as forage species and as sport fish themselves: bluegill (*Lepomis macrochirus*), carp (*Cyprinus carpio*), rainbow trout (*Oncorhynchus mykiss*), and green sunfish (*Lepomis cyanellus*). Most of these introduced forage and bait species are known to prey on RASU, as are the two introduced crayfishes and tadpoles of the American bullfrog (Minckley et al. 1991; Mueller et al. 2003b, 2005; Mueller and Burke 2005; Mueller 2006; Mueller et al. 2006; Carpenter and Mueller 2008; Reclamation 2008; Farrington et al. 2013).

State and Federal actions to control nuisance species (e.g., *Tamarix*, *Phragmites*, 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 a toxic algal bloom (Brooks et al. 2011; Roelke et al. 2011).

TRIBUTARY INFLOW

The vast majority of the water flowing through the LCR originates upstream in the UCRB. However, the LCR also receives water from its own natural tributaries, including the Virgin, Muddy, Bill Williams, and Gila Rivers. The first two flow into Lake Mead, the Bill Williams into Lake Havasu, and the Gila River into the Colorado at Yuma, Arizona. All four tributaries are themselves highly regulated, but nevertheless contribute both water and sediment to their respective confluence reaches. Lake Mead also receives water from Las Vegas Wash, consisting of wastewater and stormwater from the Las Vegas, Nevada, metropolitan area. The inflow from Las Vegas Wash is included under a separate controlling factor, “Wastewater and Other Contaminant Inflow,” below.

Tributary inflow confluences create distinctive zones of flow variation, turbidity, water chemistry and temperature, and geomorphology, constituting 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, in the present regulated condition, tributaries are probably the largest external sources of sediment and their confluences among the most geologically active sites along the river. Tributary inflows may also include suspended POM. For these reasons, RASU may interact with or use tributary confluences as distinct habitat settings. However, these confluence zones are small relative to the extent of the LCR overall.

WASTEWATER AND OTHER CONTAMINANT INFLOW

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 municipal wastewater systems, most notably from Las Vegas via Las Vegas Wash. The LCR also receives diffuse wastewater input, for example, from the septic systems of Lake Havasu City. Finally, non-point source pollution, including that from irrigation return flows and storm runoff from individual sites of chemical contamination, bring additional contaminants into the river (Seiler et al. 2003; Reclamation 2004; Hamilton et al. 2005a, 2005b; Sanchez et al. 2005; Reclamation 2005; Acharya and Adhikari 2010a, 2010b; Reclamation 2010; Adhikari et al. 2011; Turner et al. 2011; Reclamation 2011b, 2011c; Stolberg 2009, 2012).

Wastewater point-source inflow confluences also create distinctive zones of flow variation, turbidity, water temperature, and geomorphology, constituting macrohabitats with distinct assemblages of mesohabitat types. They may also include suspended POM. For these reasons, RASU may interact with or use wastewater confluences as distinct habitat settings as appears to be the case with the Las Vegas Wash delta in Lake Mead (Albrecht et al. 2010a, 2010b).

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 carry pathogens directly into the LCR, and regulated wastewater treatment facilities may sometimes release pathogens due to limits to the operational capabilities of these facilities (including any associated treatment wetlands). Recreational users of the LCR waters and shores presumably also leave wastes that possibly also could contain pathogens able to affect RASU.

WATER STORAGE-DELIVERY MANAGEMENT

The LCR 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, and municipal users as well as for hydropower generation. In addition, the dams along and above the LCR trap essentially all of the sediment that would have flowed past their locations prior to their construction. This combination of flow regulation, impoundments, and sediment trapping has created a river in which water management is the overwhelmingly dominant force affecting hydraulic and hydrogeomorphic dynamics (Reclamation 2004). This CEM also encompasses the wildlife refuges and other protected areas along the LCR managed as RASU habitat under the auspices of the LCR MSCP HCP. Water depths and flows in these areas depend on the regulated conditions along the river and reservoirs and/or on site-level management decisions, including management of gates and surface and groundwater pumping to deliver water.

Dam releases and water diversions create intense velocity fields immediately around their intakes, and dams have downstream tailwater effects. In addition, dam releases and water diversions control the amount of water flowing along the LCR and the amount stored in its reservoirs, thus strongly determining velocity fields within the lakes and along the flowing reaches (Reclamation 2004). At hydrologically disconnected ponds, surface and groundwater pumping similarly exert overwhelming control over flow/turbulence.

Dam releases are often from a single thermal layer of the upstream reservoir, either the epilimnion or the hypolimnion, each of which has a unique chemistry and thermal range that in turn affects water chemistry and temperature for some distance below each dam. For example, hypolimnetic water typically is cold, has little or no DO, and contains metal ions that are soluble in such anoxic conditions but are insoluble in fully oxygenated water where they are oxidized (Reclamation 2004). Groundwater pumped into hydrologically disconnected ponds similarly arrives with a distinctive water chemistry that shapes the overall chemistry of the affected pond.

Chapter 6 – Conceptual Ecological Model by Life Stage

This chapter contains eight sections, each presenting the conceptual ecological model for a single RASU life stage. The text and diagrams identify the critical biological activities and processes for each life stage, the habitat elements that support or limit the success of these critical activities and processes, the controlling factors that determine the abundance and quality of these habitat elements, and the causal links among them. The model sections specifically refer to the river and lakes of the LCR and to wildlife refuges and other protected areas managed as RASU habitat. It does not include facilities managed exclusively for rearing RASU larvae into subadults, but does include protected areas into which RASU subadults are repatriated as part of the augmentation program (Reclamation 2006). The model thus addresses this landscape as a whole rather than any single reach or managed area.

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 A for further details):

- **Character and direction** categorizes a causal relationship as positive, negative, involving a threshold response, or complex. Positive means that an increase (or decrease) in the causal agent results in an increase (or decrease) in the affected element, and negative means that an increase (or decrease) in the agent results in a decrease (or increase) in the affected element. Thus, positive or negative here do *not* mean that a relationship is beneficial or detrimental. The terms only provide information analogous to the sign of a correlation coefficient. Threshold means that a change in the causal agent must cross some value before we see an effect. Complex means that there is more going on than a simple positive, negative, or threshold effect.

- **Magnitude** refers to "…the degree to which a linkage controls the outcome relative to other drivers. While the models are designed to encompass critical drivers, linkages, and outcomes, this concept recognizes that some are more important than others in determining how the system works" (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.

- **Predictability** refers to the consistency with which the causal agent shapes the affected condition. The more variable the relationship, or the more the relationship depends on the interactions and effects of other factors, the less predictable the relationship (DiGennaro et al. 2012).

- **Scientific 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.

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

The diagrams for the life stages use a common set of conventions for identifying the controlling factors, habitat elements, critical biological activities and processes, and life stage success as well as for displaying information about the causal links. Figure 2 illustrates these conventions. Each life stage is illustrated with a CEM diagram, showing all controlling factors, habitat elements, critical biological activities and processes, and causal links identified during the assessment. This “basic” diagram for each life stage does not provide information on the character and direction, magnitude, predictability, or scientific understanding of each link.

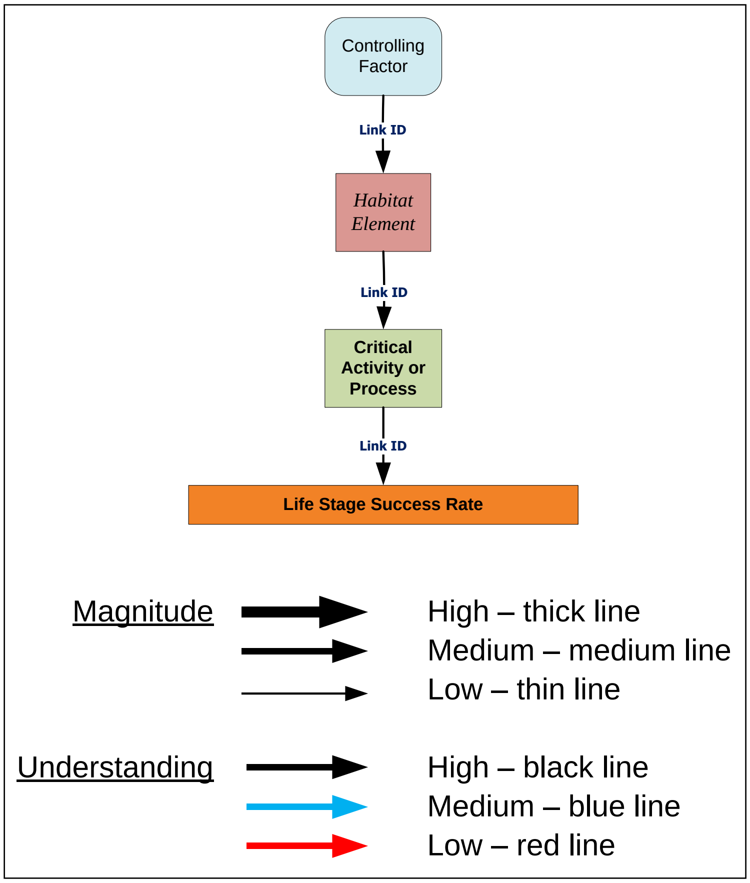

Figure 2.—Diagram conventions for LCR MSCP conceptual ecological models.

A separate spreadsheet records the assessment of the character and direction, magnitude, predictability, and scientific understanding for each causal link along with the underlying rationale and citations. However, displaying the information on all four properties at the same time producesin extremely confusing CEM diagrams. For this reason, each life stage is illustrated with a second CEM diagram, **displaying information only on the magnitude and scientific understanding of each causal link, and only for links with high or medium ratings for magnitude**.

The discussion of each life stage includes an analysis of the information contained in the spreadsheet. The analyses highlight causal chains that strongly affect survivorship, identify important causal relationships with different levels of predictability, and identify important causal relationships with high scientific uncertainty. The latter constitutes topics of potential importance for adaptive management investigation.

The causal relationships among controlling factors and habitat elements are essentially identical across all eight life stages. For this reason, the discussion of controlling factor-habitat element linkages across all eight life stages appears in a subsequent chapter.

RASU LIFE STAGE 1 – GAMETES AND FERTILIZED EGGS IN OPEN WATER

As described in chapter 2, spawning RASU males and females release gametes into the open water above sites selected for spawning, and fertilization takes place in the open water (Minckley and Gustafson 1982; Bozek et al. 1984; Langhorst and Marsh 1986; Snyder and Muth 2004). The spawning activity itself may help prepare the selected sites to receive and protect the eggs by agitating the surface of the benthic substrate, thereby removing fine sediment and/or excavating nest-like depressions (Bozek et al. 1984; Snyder and Muth 2004; Mueller 2006). 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. Spawning RASU “finning” during the spawning act not only may remove fine sediment and excavate depressions in the substrate, but also may drive the eggs into the substrate, eliminating the “descent” step altogether (Mueller 2006). Success for the gametes consists of their combining to produce fertilized eggs, and success for the fertilized eggs consists of their surviving in the open water to adhere to or become embedded in the substrate and begin embryological development.

The CEM (figures 3 and 4) recognizes six critical biological activities and processes for this life stage, and they are presented here in alphabetical order:

1. *Chemical stress*: RASU gametes and eggs during descent and settling/adhesion are vulnerable to exposure to harmful dissolved contaminants (Hamilton et al. 2005a; Stolberg 2009, 2012).

2. *Egg descent*: This is the first of the two processes that make up the life stage itself that must take place for successful transition to the subsequent, embryonic life stage. As noted above, "finning" activity of spawning adults may drive the eggs into the substrate, eliminating the "descent" step altogether (Mueller 2006).

3. *Egg settling/adhesion*: This is the second of the two processes that make up the life stage itself, as described above, that must take place for successful transition to the subsequent, embryonic life stage.

4. *Mechanical stress*: RASU gametes and eggs during descent and settling/adhesion are vulnerable to stress – including outright physical destruction – due to substrate disturbance, entrainment in excessive flow velocities and turbulence, and wounding from unsuccessful predator attacks as documented for the immediately subsequent, embryonic life stage (Bozek et al. 1984; Minckley et al. 1991; Valdez et al. 2012).

5. *Predation*: Several species may or are known to prey on RASU eggs (Bozek et al. 1984; Mueller 2006), including channel catfish, carp, juvenile largemouth bass, bullfrogs and their tadpoles, and red swamp crayfish. RASU and bonytail adults may also prey on RASU eggs as they are known to do on bonytail egg masses (Mueller 2006).

6. *Thermal stress*: RASU gametes and eggs during descent and settling/adhesion are vulnerable to stress due to changes in temperature beyond the range suitable for their successful transition to the substrate, similar to their vulnerability as embryos and larvae (Bozek et al. 1990; Minckley et al. 1991; USFWS 1998; Clarkson and Childs 2000; Ward et al. 2007; Bestgen 2008; Reclamation 2008; Bestgen et al. 2011; Valdez et al. 2012).

The evaluation of causal linkage magnitude (figure 4) indicates that, among the six aforementioned critical biological activities and processes, three have high- or medium-magnitude direct effects on the outcome of this life stage in the present-day system: egg descent, egg settling/adhesion, and predation. This evaluation refers to all reaches of the LCR and in the wildlife refuges and other protected areas along the LCR managed as RASU habitat under the auspices of the LCR MSCP HCP.

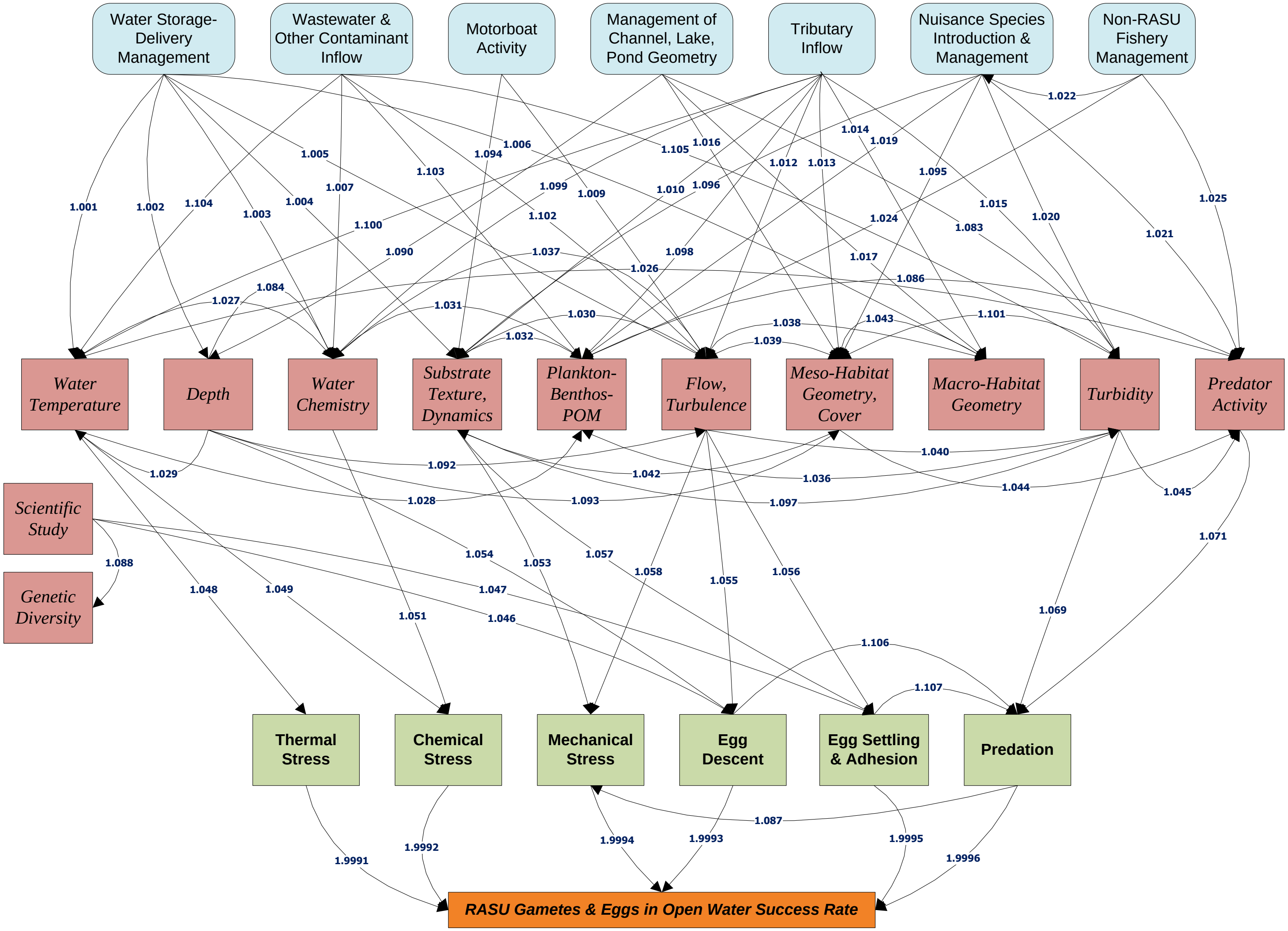

Figure 3.—RASU life stage 1 – gametes and fertilized eggs in open water, basic CEM diagram.

Razorback Sucker (*Xyrauchen texanus*) (RASU)
Basic Conceptual Ecological Model

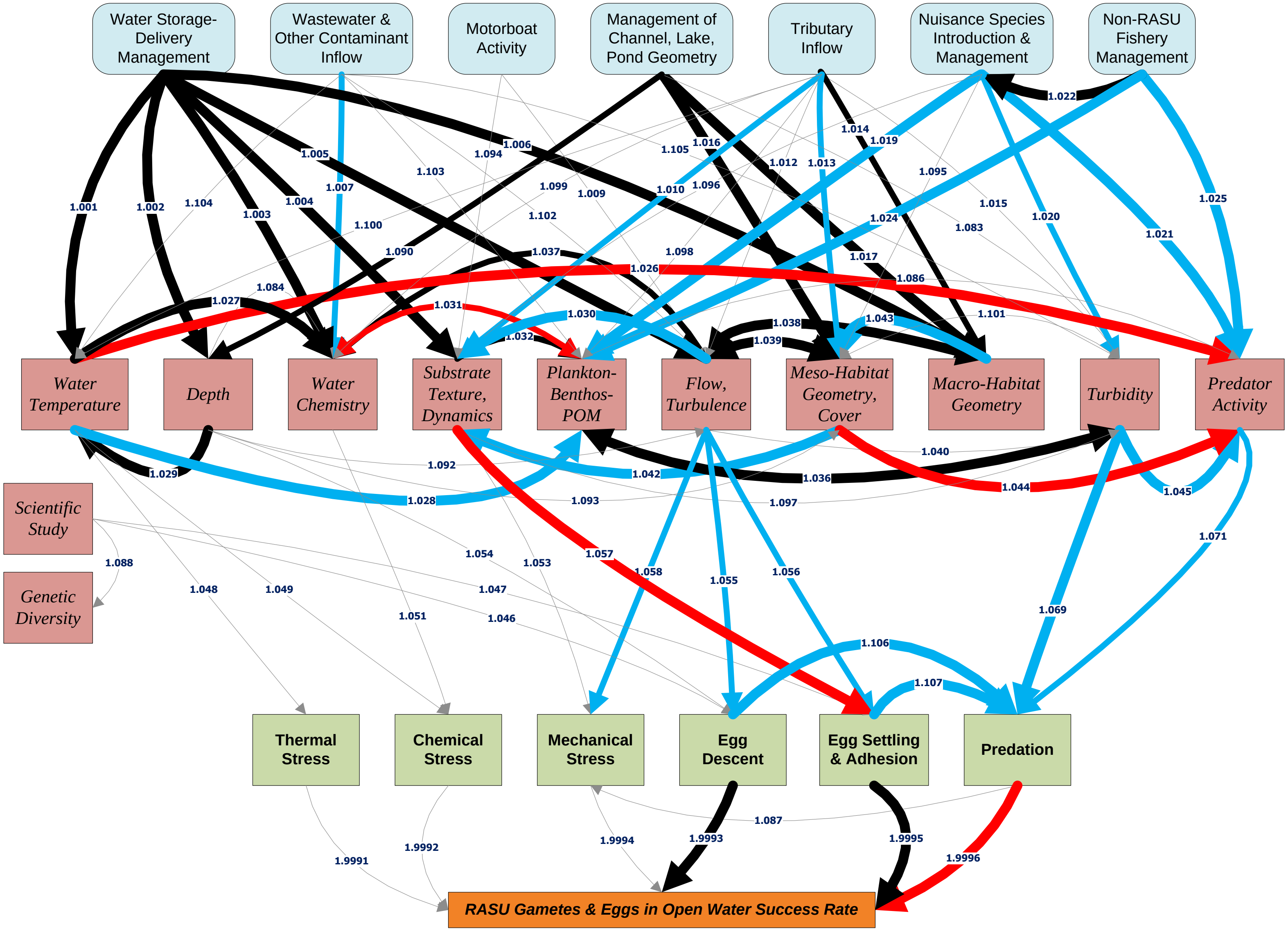

Figure 4.—RASU life stage 1 – gametes and fertilized eggs in open water, high- and medium-magnitude relationships.

The assessment indicates that the direct effects of predation have high predictability (i.e., its effects on the overall success rate for this life stage do not depend on the effects of other factors). In turn, the direct effects of egg descent and egg settling/adhesion on the success of this life stage have only medium predictability. Theoretically, eggs that successfully descend and/or settle/adhere may still suffer damage as a result mechanical, thermal, or chemical stress and therefore not survive for those separate reasons. However, the assessment found no evidence that the other three critical activities and processes are altered in ways that significantly directly affect the overall success rate for the life stage. Thermal stress, chemical stress, and mechanical stress do not appear strongly linked to altered success for the life stage. The possible detrimental effects of pollution on RASU was a concern in the literature a few years ago (Cooke et al. 2005), including the effects of selenium (Hamilton et al. 2005a), and while this remains a concern in the UCRB, studies in the LCR have not raised this concern (Mueller 2006; Reclamation 2008; Stolberg 2009, 2012).

This assessment of the relative impact of different biological activities and processes on the overall success rate for gametes and fertilized eggs in open water comes with an important caveat: these are hypotheses based on the information presented in the literature and provided by LCR MSCP biologists. One of the three direct strong (high-magnitude) linkages between critical biological activities and processes and successful outcomes for gametes and fertilized eggs in the open water receives a rating of low for scientific understanding, indicating that understanding of the relationship is subject to wide disagreement or uncertainty in peer-reviewed studies from within the ecosystem of concern and in scientific reasoning among experts familiar with the ecosystem (see attachment A). Specifically, the literature clearly identifies predation as having an impact on gametes and fertilized eggs in the open water (Bozek et al. 1984; Mueller et al. 2005; Mueller 2006), and as noted in chapter 1, RASU eggs naturally may have had a high rate of mortality due to predation under natural, pre-regulation conditions. However, the literature only identifies the fact that particular species prey on RASU eggs, and it does not indicate what rate of mortality is involved or whether any environmental conditions (e.g., turbidity, substrate conditions) affect this rate.

Additionally, the assessment identifies two critical biological activities and processes as *indirectly* affecting the overall success rate for gametes and fertilized eggs in the open water with high magnitude. Specifically, the assessment indicates that aspects of egg descent and egg settling/adhesion likely strongly affect the rate of predation, which in turn strongly affects the overall success rate for the life stage. As noted above, “finning” activity during spawning may directly embed eggs in the substrate, eliminating any “descent” phase. Both the absence of a descent phase and the embedding of eggs in the substrate will reduce the exposure of eggs to predators. However, it is possible that some predators may feed on RASU eggs by probing in the substrate itself. Further, the topic has not been systematically studied. As a result, these two relationships receive ratings of medium for scientific understanding.

The assessment identifies four habitat elements that directly and significantly (high or medium magnitude) support or limit rates of the three critical biological activities or processes with direct, high-magnitude impacts on gametes and fertilized eggs in the open water, specifically:

- The assessment indicates that the rate of predation strongly depends on (is directly influenced by, at a high magnitude) turbidity and moderately depends on predator activity.

    - The effect of turbidity on predation has low predictability. Little of the literature for the LCR addresses how turbidity affects the hunting behavior of individual non-native predator species that might prey on RASU eggs in the open water. Albrecht et al. (2010b) found stronger selection for, and higher rates of spawning success at, sites in Lake Mead with higher turbidity. However, Mueller (2006) records predation on RASU eggs in the open water by fully developed RASU and bonytail. These native fishes are adapted to turbid water; consequently, the intensity of their feeding on RASU eggs in the open water may not vary with turbidity. The effect of turbidity on predation also receives a medium score for scientific understanding. The knowledge may exist to evaluate how turbidity will affect each introduced predator species and whether each is a potential predator on RASU eggs; however, assembly of this information for the LCR has not progressed significantly since the studies by Mueller and others at Cibola nearly a decade ago (Mueller et al. 2005; Mueller 2006). Further, the literature provides little information on the range of turbidity conditions at spawning sites during egg descent and adhesion (Albrecht et al. 2010b; Valdez et al. 2012).

    - The effect of predator activity on predation has medium predictability and medium scientific understanding. The overall abundance and diversity of predators may not shape the rate of predation on gametes and fertilized eggs in the open water as much as does the simple presence of just one or two generalist predators with an affinity for RASU eggs, and turbidity and the availability of cover for different kinds of predators may also shape these interactions. However, the subject has not been studied systematically.

- The assessment indicates that the success rates for egg descent and egg settling/adhesion moderately depend on the eggs experiencing low flow velocities and turbulence (medium magnitude). RASU appear to select spawning sites in part based on their moderate flow velocities and lack of turbulence (Valdez et al. 2012). In turn, excessive flow velocities or turbulence during spawning could disrupt descent or settling, scattering the eggs. However, this latter relationship has low predictability. RASU may spawn quite close to the substrate, thus minimizing egg exposure to potentially at least moderately unsuitable flow velocities or turbulence. Anecdotally, too, spawning may involve activities that create slight depressions for the eggs or directly force the eggs into the substrate without any "descent" phase (Bozek et al. 1984; Mueller 2006), which also would reduce exposure to moderately unsuitable flow velocities or turbulence during descent.

- Finally, the assessment indicates that successful egg settling/adhesion also strongly depend on the eggs arriving on/in a substrate that provides a suitable range of texture and stability. The literature presents only a few reports (Bozek et al. 1984) of substrate disruption as a factor in embryo development in situ and, by implication, as a factor in egg settling/adhesion. Bozek et al. (1984) indicate that storms can agitate shallow-water sediments in ways that disrupt embryo development, and presumably this would affect settling/adhesion as well. Otherwise, a lack of information on substrate disruption as a factor for this life stage may reflect a pattern of RASU selection of spawning sites (see life stage 8 – spawning adults) that favors more stable geomorphic settings.

  Mueller (2006) notes that "the single commonality [among settings for spawning] appears to be appropriate substrate, a mixture of large gravels and small cobbles... that have been flushed of [fine] sediments." The range of locations that RASU select for spawning along the present-day river and reservoirs includes active deltaic environments and areas where flow conditions produce gravel bars (Mueller et al. 2006; Albrecht et al. 2010a, 2010b; Valdez et al. 2012). Both comprise settings where macrohabitat conditions can produce substrates that are stable except for regular flushing/removal of fines, resulting in a substrate with the right type of interstices for RASU egg embedding. As discussed for spawning adults, the CEM suggests that the pattern of selection of spawning sites may be understood as an adaptation (product of evolutionary selection) both for embryo survival and for the successful dispersal of RASU larvae into habitats suitable for their own survival and maturation. That is, the selected ranges of substrate stability and particle size distribution are important both because they promote embryo survival and because they tend to occur in settings that promote successful larval dispersion. However, these relationships presently are poorly understood. The literature reflects much uncertainty over why spawning RASU prefer some sites over others from the standpoint of substrate texture and stability (Minckley et al. 1991; Modde and Irving 1998; USFWS 1998, 2002a; Mueller 2006; Reclamation 2008; Schooley et al. 2008; Albrecht et al. 2010a, 2010b; Bestgen et al. 2011, 2012; Patterson et al. 2012; Valdez et al. 2012). The literature contains many observations of substrate conditions at spawning sites, but little information on how these conditions differ from those at other sites that RASU do not use for spawning. Observations of RASU spawning on substrates different from what they would have encountered under natural conditions, such as the artificial boat ramp at Imperial Ponds (LCR MSCP biologists, personal communication, September 2013) further challenge the understanding of substrate preferences during spawning. In addition, published descriptions of spawning site substrate provide only qualitative information, using often-subjective terms such as “cobble” and “gravel,” rather than quantitative measurements (see review by Valdez et al. 2012). Consequently, it is not yet possible to frame hypotheses concerning substrate selection for spawning in quantitative terms for testing.

The assessment also identifies several habitat elements that significantly but *indirectly* support or limit the rates of those critical biological activities or processes with high-magnitude impacts on egg descent and settling/adhesion. Specifically, the assessment identifies the following relationships:

- Water temperature and turbidity affect predator activity with high magnitude.

- Mesohabitat geometry/cover affects predator activity with high magnitude because species that prey on RASU eggs may use cover during their foraging.

- Both macro and mesohabitat geometry strongly shape flow/turbulence, and macrohabitat geometry strongly shapes the abundance and spatial distribution of mesohabitat types.

- Turbidity and the composition and abundance of the plankton-benthos-POM assemblage strongly shape each other. Plankton concentrations directly affect light penetration, and the depth of light penetration strongly affects the depth to which phytoplankton and periphyton may grow. Plankton concentrations, in turn, also are shaped by water chemistry (medium magnitude) and water temperature (high magnitude).

- Substrate texture/dynamics moderately shape the composition and abundance of the plankton-benthos-POM assemblage.

- Turbidity and the composition and abundance of the plankton-benthos-POM assemblage strongly shape each other. Plankton concentrations directly affect light penetration, and the depth of light penetration strongly affects the depth to which phytoplankton and periphyton may grow.

- Both flow/turbulence and mesohabitat geometry strongly shape substrate texture/dynamics, and flow/turbulence strongly shapes mesohabitat geometry and the abundance and spatial distribution of mesohabitat types. Flow/turbulence thus shapes substrate texture/dynamics directly as well as indirectly through its influence on mesohabitat conditions.

Among the direct and indirect causal relationships, through which habitat elements support or limit critical activities or processes, the assessment rates roughly half as having low or medium scientific understanding in the literature. For example, hypotheses concerning the influence of mesohabitat geometry/cover on predator activity have not received detailed consideration, let alone formal testing. Hypotheses concerning which species prey on RASU eggs have been subjected to few detailed studies (Mueller et al. 2005).

Finally, the assessment permits an analysis of the cumulative impact of individual habitat elements that directly affect one or more of the critical biological activities or processes that strongly shape the rate of success for this life stage. Across the three critical biological activities and processes for this life stage with the strongest impact on gametes and fertilized eggs in the open water, the following five habitat elements have the highest cumulative magnitudes of impact. Each of these five is strongly influenced (high or medium magnitude) by one or more other habitat elements, and the list below identifies those with the highest impacts on the listed habitat element:

- Flow/turbulence

    - Habitat elements with the strongest influence on this element include macrohabitat geometry, mesohabitat geometry/cover, and depth

- Substrate texture/dynamics

    - Habitat elements with the strongest influence on this element include flow/turbulence and mesohabitat geometry/cover

- Predator activity

    - Habitat elements with the strongest influence on this element include mesohabitat geometry/cover, turbidity, and water temperature.

- Water temperature
    - The habitat element with the strongest influence on this element is depth.
- Turbidity
    - Habitat elements with the strongest influence on this element include plankton-benthos-POM assemblage abundance and composition, flow/turbulence, and substrate texture/dynamics.

RASU LIFE STAGE 2 – EMBRYOS AND LARVAE ON/IN SUBSTRATE

Numerous studies (Minckley and Gustafson 1982; Bozek et al. 1984, 1990; Langhorst and Marsh 1986; Minckley et al. 1991; Snyder and Muth 2004; Ward et al. 2007; Reclamation 2008) describe the stages of RASU embryo development. Embryos typically require approximately 6–7 days to hatch, and swim-up develops approximately 4–7 days later. Success during this life stage – successful transition (recruitment) to the next stage – involves embryo and protolarval survival and maturation. Individuals have no ability to move voluntarily to avoid threats or to forage. The CEM (figures 5 and 6) recognizes five critical biological activities and processes for this life stage, and they are presented here in alphabetical order:

1. *Chemical stress*: RASU embryos and protolarvae are vulnerable to stress due to an insufficient supply of DO, insufficient removal of wastes, and exposure to harmful dissolved contaminants, possibly including selenium (Hamilton et al. 2005a; Stolberg 2009, 2012).

2. *Disease*: RASU embryos and protolarvae are vulnerable to stress and mortality due to microbial infection, including infection by fungi (Ward and Finch 2009).

3. *Mechanical stress*: RASU embryos and protolarvae are vulnerable to stress – including outright physical destruction – due to scour or burial of the spawning site substrate or by deep submergence or exposure to the air due to a change in water surface elevation (Bozek et al. 1984; Minckley et al. 1991; Kretschmann and Leslie 2006; Reclamation 2008).

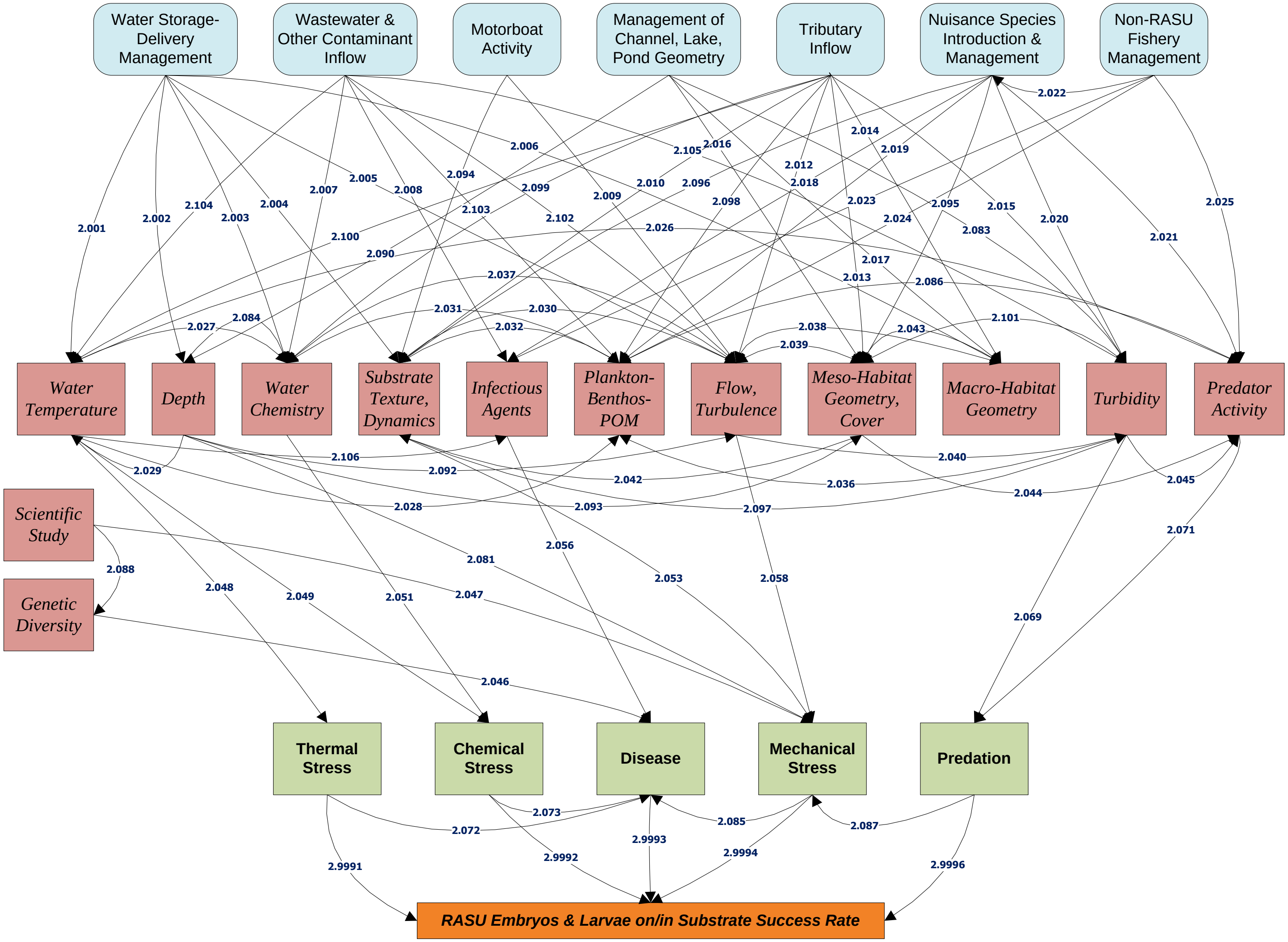

Figure 5.—RASU life stage 2 – embryos and larvae on/in the substrate, basic CEM diagram.

Razorback Sucker (*Xyrauchen texanus*) (RASU)
Basic Conceptual Ecological Model

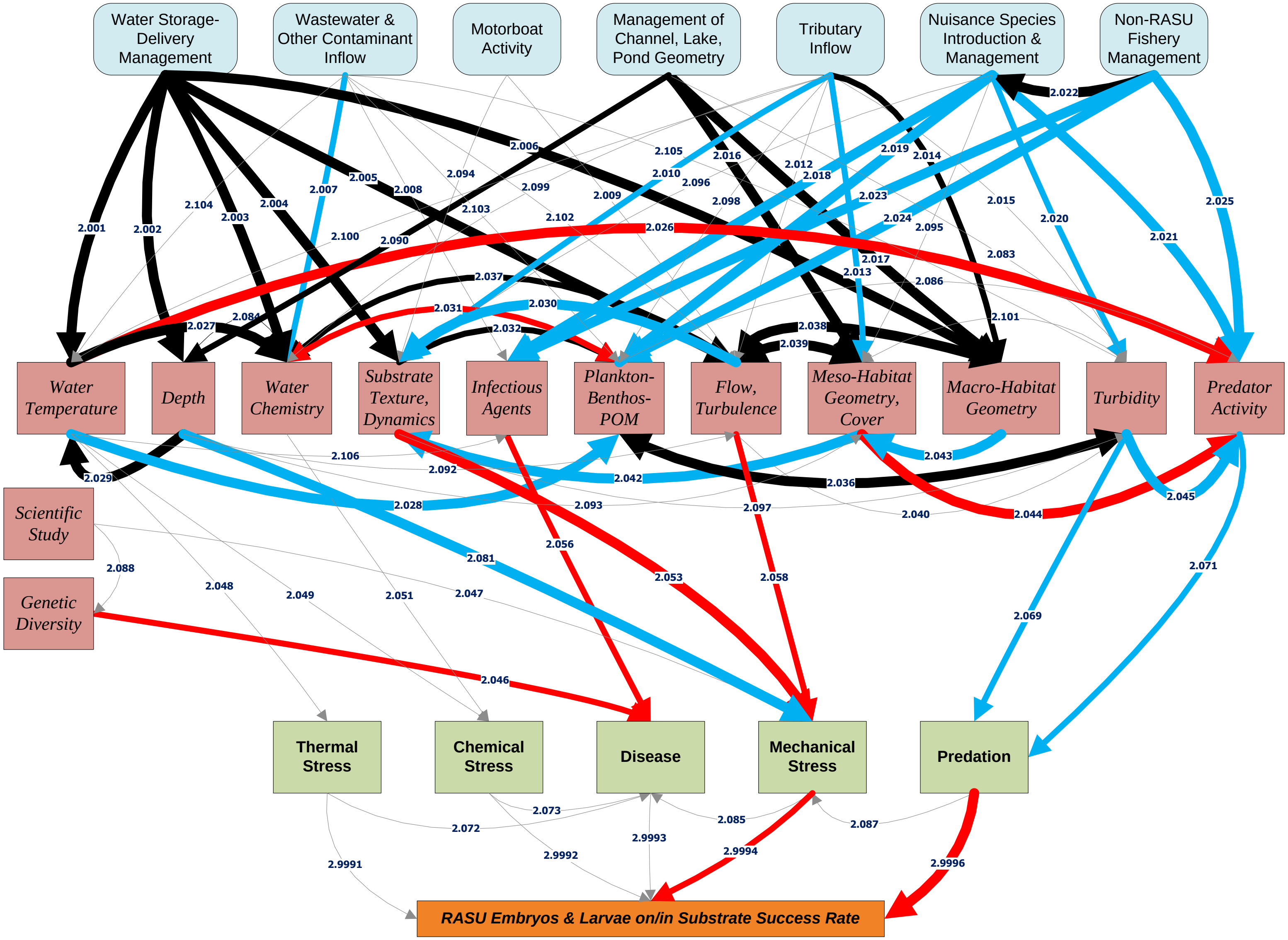

Figure 6.—RASU life stage 2 – embryos and larvae on/in the substrate, high- and medium-magnitude relationships.

4. *Predation*: RASU embryos and protolarvae are vulnerable to predation. The small size of the embryos and protolarvae and their lack of mobility may make them prey to a distinct spectrum of predator species or life stages, including adult RASU (Bozek et al. 1984; Langhorst and Marsh 1986; Minckley et al. 1991; Horn et al. 1994; USFWS 1998, 2002a; Christopherson et al. 2004; Dowling et al. 2005; Mueller et al. 2003b, 2005, 2006; Mueller 2006; Bestgen 2008; Carpenter and Mueller 2008; Reclamation 2008; Albrecht et al. 2010a; Bestgen et al. 2011, 2012). Specifically, Bozek et al. (1984) and Mueller (2006) identify channel catfish, carp, juvenile largemouth bass, bullfrogs and their tadpoles, and red swamp crayfish as well as RASU and bonytail adults as predators on RASU eggs.

5. *Thermal stress*: RASU embryos and protolarvae are vulnerable to stress due to changes in temperature beyond the range suitable for their maturation (Bozek et al. 1990; Minckley et al. 1991; Clarkson and Childs 2000; Mueller et al. 2005; Bestgen 2008; Reclamation 2008; Bestgen et al. 2011; Valdez et al. 2012).

The evaluation of causal linkage magnitude (see figure 6) indicates that, among the five aforementioned critical biological activities and processes, two have high- or medium-magnitude direct effects on the outcome of this life stage in the present-day system: predation and mechanical stress. The assessment did not identify any critical biological activities and processes as *indirectly* affecting embryo and protolarval development with either high or medium magnitude. This evaluation collectively addresses all reaches of the LCR and the wildlife refuges and other protected areas along the LCR managed as RASU habitat under the auspices of the LCR MSCP HCP.

The assessment indicates that the direct effects of predation have high predictability (i.e., its effects on embryo and protolarval development do not depend on the effects of other factors). However, this relationship could be affected by habitat conditions that provide different predators with more or less cover within the vicinity (within their foraging radius) of spawning sites. In turn, the assessment rates the predictability of mechanical stress as low. The literature presents only a few reports (Bozek et al. 1984) of substrate disruption as a factor in embryo development in situ. Bozek et al. (1984) indicate that storms can agitate shallow-water sediments in ways that disrupt embryo development. Otherwise, a lack of information on substrate disruption as a factor for this life stage may reflect a pattern of RASU selection of spawning sites (see discussions below and for life stages 1 and 8) that favors more stable geomorphic settings. Substrate disruption could strongly affect embryo and protolarval development when it occurs, but the circumstances in which it will occur, especially in the modern highly regulated system, are unpredictable. It should also be noted that the possible detrimental effects of chemical stress on RASU from pollution was a concern in the literature a few years ago (Cooke et al. 2005), including concerns for the effects of selenium (Hamilton et al. 2005a). While this remains a concern in the UCRB, studies over the past decade in the LCR have not raised this concern (Mueller 2006; Reclamation 2008; Stolberg 2009, 2012).

This assessment of the relative impact of different biological activities and processes on embryo and protolarval development comes with an important caveat: these are hypotheses based on the information provided in the literature and by LCR MSCP biologists. The impacts of both predation and mechanical stress on embryo and protolarval development receive low scores for scientific understanding, indicating that understanding of the relationship is subject to wide disagreement or uncertainty in peer-reviewed studies from within the ecosystem of concern and in scientific reasoning among experts familiar with the ecosystem (see attachment A). The literature clearly identifies predation as a cause of embryo mortality (Bozek et al. 1984; Mueller et al. 2005; Mueller 2006), and as noted in chapter 1, RASU eggs naturally may have had a high rate of mortality due to predation under natural, pre-regulation conditions. However, the literature only identifies the fact that particular species prey on RASU eggs. It does not indicate what rate of mortality is involved or whether any environmental conditions (e.g., turbidity, substrate conditions) affect this rate. Similarly, the factors that produce a rating of low predictability for the effects of mechanical stress on embryo and protolarval development, noted above, also result in a low rating for understanding of this relationship.

The assessment identifies five habitat elements that directly and significantly (high or medium magnitude) support or limit rates of predation and mechanical stress affecting embryo and protolarval development. Specifically, the assessment identifies the following relationships, with varying levels of predictability:

- The assessment indicates that the rate of predation moderately depends on (is directly influenced by, at a medium magnitude) turbidity and predator activity.
    - The effect of turbidity on predation has low predictability and a rating of medium for scientific understanding. The list of potential predators on RASU eggs in the LCR and its refuges has not been systematically updated since the studies by Mueller and others nearly a decade ago (Mueller et al. 2005; Mueller 2006). The literature for the LCR and its refuges also does not address how turbidity affects the hunting behavior of individual non-native predator species that might prey on RASU eggs; however, the literature does record predation on RASU eggs by fully developed RASU and bonytail (Mueller 2006). Since these native fishes are adapted to turbid water, the intensity of their feeding on RASU eggs in the open water may not vary with turbidity. As Mueller (2006) notes, predation by native fishes on RASU eggs may be an adaptation to the otherwise low incidence of other food during the spawning season.

  - The effects of predator activity on predation have medium predictability. The overall abundance and diversity of predators may not shape the rate of predation on gametes and fertilized eggs in the open water as much as does the simple presence of just one or two generalist predators with an affinity for RASU eggs, and turbidity and the availability of cover for different kinds of predators may also shape the interactions.

- The assessment indicates that the incidence of mechanical stress depends strongly (high magnitude) on depth and substrate texture/dynamics as well as moderately on flow/turbulence.

  - The effects of depth on mechanical stress arise because rapid changes in water surface elevation – and therefore in depth – can occur along the main stem LCR as a result of water storage and delivery operations. In turn, such rapid changes can result in embryos and larvae on/in the substrate becoming trapped in rapidly dewatered backwaters as described by Bozek et al. (1984) and suggested by Kretschmann and Leslie (2006). No matter how brief, any exposure of eggs to the open air would be harmful to embryo development. The same concerns may not apply to isolated refuges where water levels are controlled for refuge purposes. The relationship between depth and mechanical stress has low predictability but high scientific understanding. It has low predictability because it depends on the coincidence of several factors related to dam and/or refuge operations and the presence of embryos and larvae on/in the substrate in habitat settings where they might become stranded or excessively inundated. It has high scientific understanding because the likely impacts of exposure on developing embryos are well understood even though its incidence has not been studied systematically since the observations by Bozek et al. (1984).

  - The effects of substrate texture/dynamics on mechanical stress arise because any disruption of the substrate during embryo or protolarval development could disrupt that development. Bozek et al. (1984) documents substrate disruption as a factor in embryo development, indicating that storms can agitate shallow-water sediments in ways that disrupt embryo development. However, this relationship has low predictability and low scientific understanding. There is a general lack of information on substrate disruption as a factor for this life stage, but this lack may reflect a pattern of RASU selection of spawning sites (see “Spawning Adults” in chapter 2) that favors more stable geomorphic settings.

As discussed for gametes and eggs, above, Mueller (2006) notes that "the single commonality [among settings for spawning] appears to be appropriate substrate, a mixture of large gravels and small cobble... that have been flushed of [fine] sediments." The range of spawning locations along the river and reservoirs includes active deltaic environments and areas where flow conditions produce gravel bars (Mueller et al. 2006; Albrecht et al. 2010a, 2010b; Valdez et al. 2012). Both comprise settings where macrohabitat conditions can produce substrates that are stable except for regular flushing/removal of fines, resulting in a substrate with the right type of interstices for RASU embryo development. As discussed for spawning adults, the CEM suggests that the pattern of selection of spawning sites may be understood as an adaptation (product of evolutionary selection) both for embryo survival and for the successful dispersal of RASU larvae into habitats suitable for their own survival and maturation. That is, the selected ranges of substrate stability and particle size distribution are important both because they promote embryo survival and because they tend to occur in settings that promote successful larval dispersion. However, these relationships presently are poorly understood. The literature reflects much uncertainty over why spawning RASU prefer some sites over others from the standpoint of substrate texture and stability (Minckley et al. 1991; Modde and Irving 1998; USFWS 1998, 2002a; Mueller 2006; Reclamation 2008; Schooley et al. 2008; Albrecht et al. 2010a, 2010b; Bestgen et al. 2011, 2012; Patterson et al. 2012; Valdez et al. 2012). The literature contains many observations of substrate conditions at spawning sites, but little information on how these conditions differ from those at other sites that RASU do not use for spawning. Observations of RASU spawning on substrates different from what they would have encountered under natural conditions, such as the artificial boat ramp at Imperial Ponds (LCR MSCP biologists, personal communications, September 2013) further challenge the understanding of substrate preferences during spawning. In addition, published descriptions of spawning site substrate provide only qualitative information, using often-subjective terms such as "cobble" and "gravel," rather than quantitative measurements (see review by Valdez et al. 2012). Consequently, it is not yet possible to frame hypotheses concerning substrate selection for spawning in quantitative terms for testing.

- The effects of flow/turbulence on mechanical stress for developing embryos and protolarvae arise because disturbances by elevated flows or turbulence potentially could disrupt embryo development (Bozek et al. 1984). However, as with the relationship of substrate texture/dynamics to mechanical stress, this relationship has low predictability and low scientific understanding. As noted above

> and for spawning adults, the literature reflects much uncertainty concerning why RASU may prefer some sites over others for spawning from the standpoint of flows and turbulence (Minckley et al. 1991; Modde and Irving 1998; USFWS 1998, 2002a; Mueller 2006; Reclamation 2008; Schooley et al. 2008; Albrecht et al. 2010a, 2010b; Bestgen et al. 2011, 2012; Patterson et al. 2012; Valdez et al. 2012). The literature contains many observations of flow conditions at spawning sites, but this information is more widely available for the UCRB than for the LCR, and no systematic information exists for the LCR on how observed conditions of flow/turbulence at spawning sites might differ from conditions at other sites that are not used for spawning (Valdez et al. 2012). However, the hypothesis proposed above, concerning substrate texture/dynamics also applies to flow/turbulence for life stages 1, 2, and 8 (gametes and fertilized eggs in open water, embryos and larvae on/in the substrate, and spawning adults). This hypothesis proposes that the characteristics of spawning sites may be understood as an adaptation (product of evolutionary selection) for spawning on sites that most reliably allow for embryo survival and the successful dispersal of RASU larvae into habitats suitable for their own survival and maturation, with suitable flow velocities and turbulence as critical elements of the optimal habitat.

The assessment also identifies several habitat elements that significantly but *indirectly* support or limit the rates of those critical biological activities or processes with high-magnitude impacts on embryo and protolarval survival. Specifically, the assessment identifies the following relationships:

- Water temperature and turbidity affect predator activity with high magnitude.

- Mesohabitat geometry/cover affects predator activity with high magnitude because species that prey on RASU eggs and protolarvae may use cover during their foraging.

- Both macro and mesohabitat geometry strongly shape flow/turbulence, and macrohabitat geometry strongly shapes the abundance and spatial distribution of mesohabitat types.

- Turbidity and the composition and abundance of the plankton-benthos-POM assemblage strongly shape each other. Plankton concentrations directly affect light penetration, and the depth of light penetration strongly affects the depth to which phytoplankton and periphyton may grow. Plankton concentrations, in turn, also are shaped by water chemistry (medium magnitude) and water temperature (high magnitude).

- Substrate texture/dynamics moderately shapes the composition and abundance of the plankton-benthos-POM assemblage.

- Both flow/turbulence and mesohabitat geometry strongly shape substrate texture/dynamics, and flow/turbulence strongly shapes mesohabitat geometry and the abundance and spatial distribution of mesohabitat types. Flow/turbulence thus shapes substrate texture/dynamics directly as well as indirectly through its influence on mesohabitat conditions.

Among the direct and indirect causal relationships, through which habitat elements support or limit critical activities or processes, the assessment rates more than half as having low or medium scientific understanding in the literature. For example, hypotheses concerning the influence of mesohabitat geometry/cover on predator activity have not received detailed consideration, let alone formal testing. Hypotheses concerning which species prey on RASU eggs and protolarvae have been subjected to few detailed studies (Mueller et al. 2005).

Finally, the assessment permits an analysis of the cumulative impact of individual habitat elements that affect one or more critical biological activities or processes for this life stage. Across the three critical biological activities and processes for this life stage with the strongest impact on embryo and protolarval development, the following five habitat elements have the highest cumulative magnitudes of impact. Each of these six is strongly influenced (high or medium magnitude) by one or more other habitat elements, and the list below identifies those with the highest impacts on the listed habitat element:

- Depth

    - No other habitat element strongly influences this element.

- Flow/turbulence

    - Habitat elements with the strongest influence on this element include macrohabitat geometry, mesohabitat geometry/cover, and depth.

- Predator activity

    - Habitat elements with the strongest influence on this element include mesohabitat geometry/cover, turbidity, and water temperature.

- Substrate texture/dynamics

    - Habitat elements with the strongest influence on this element include flow/turbulence and mesohabitat geometry/cover.

- Turbidity
    - Habitat elements with the strongest influence on this element include plankton-benthos-POM assemblage abundance and composition, flow/turbulence, and substrate texture/dynamics.

RASU LIFE STAGE 3 – DISPERSING LARVAE

Minckley et al. (1991), Wydoski and Wick (1998), Modde et al. (2001), Reclamation (2008) and recent studies such as Hedrick et al. (2009), Albrecht et al. (2010a, 2010b), Bestgen et al. (2011, 2012), and Valdez et al. (2012) provide information on RASU larval dispersal. Some of their findings pertain specifically to the UCRB where flow variability and greater geomorphic complexity (including active flood plains) present a different suite of conditions from those present along the LCR. However, the UCRB literature provides information on the range of evolved behaviors and habitat requirements for this life stage applicable to the LCR.

Within a short time after they emerge, RASU larvae become capable of moving both up and down in the water column and of actively foraging. At this point, they disperse from the spawning sites, mostly carried by currents but also moving vertically and horizontally along and in/out of the drift pathway. When not moving, they may shelter in areas of vegetative cover or in interstitial spaces in substrate gravels (Valdez et al. 2012). They may control their drift by moving into flow currents preferentially at night and during times of higher flow velocities (Modde and Irving 1998; Tyus et al. 2000). They may move as solitary individuals or in groups, the latter indicated by their uneven distribution encountered during sampling and capture (LCR MSCP biologists, personal communications, August 27, 2013). Success during this life stage – successful transition to the next stage – involves larval survival and maturation during the process of dispersal, ending with arrival in a setting appropriate for further development, sometimes termed “nursery” habitat (Valdez et al. 2012). These nursery settings consist of locations with low flow velocities and shallow depths such as off-channel and flood plain wetlands (UCRB) and shoreline shallows and backwaters (LCR). The dispersing larvae actively interact with their environment – navigating, avoiding threats, and foraging. They are also subject to capture by scientists for removal to hatcheries for the RASU LCR augmentation program (Reclamation 2006; Dowling et al. 2011).

The CEM for this life stage (figures 7 and 8) recognizes nine critical biological activities and processes for this life stage, and they are presented here in alphabetical order:

Razorback Sucker (*Xyrauchen texanus*) (RASU)
Basic Conceptual Ecological Model

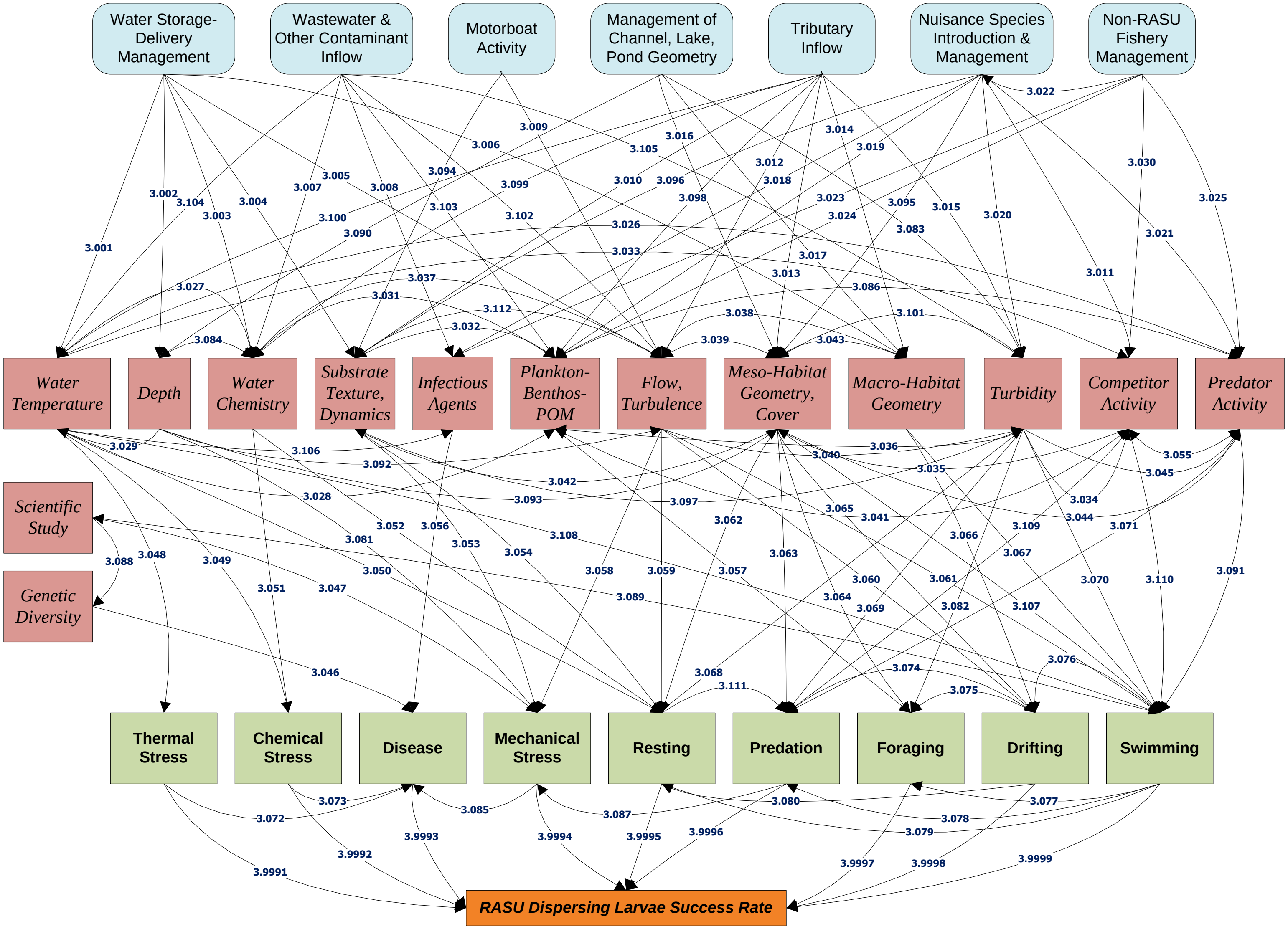

Figure 7.—RASU life stage 3 – dispersing larvae, basic CEM diagram.

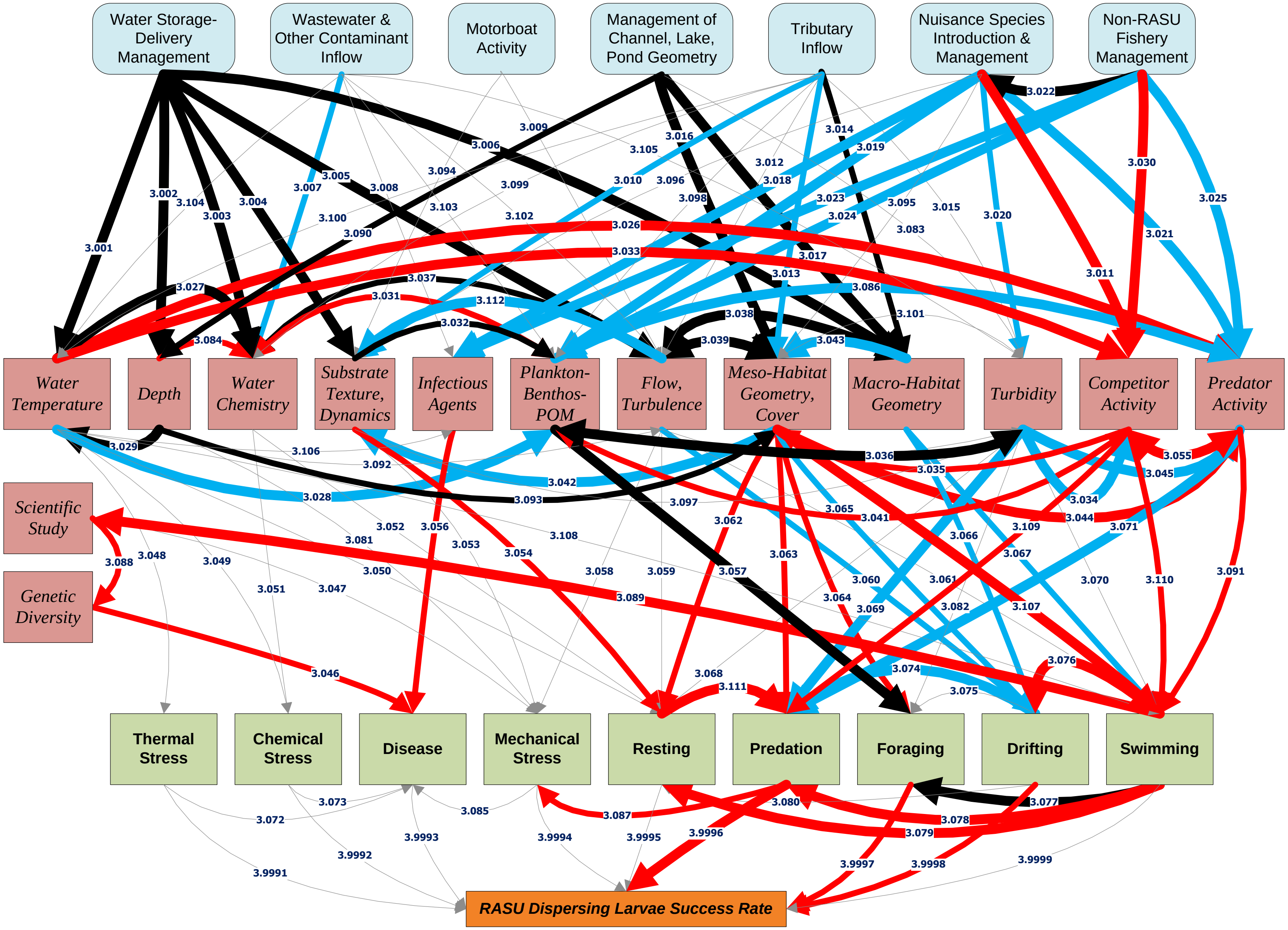

Figure 8.—RASU life stage 3 – dispersing larvae, high- and medium-magnitude relationships.

1 *Chemical stress*: RASU dispersing larvae are vulnerable to stress due to an insufficient supply of DO and exposure to harmful dissolved contaminants (Stolberg 2009, 2012).

2. *Disease*: RASU dispersing larvae are vulnerable to stress and mortality due to microbial infection (USFWS 2002a; Mueller 2006; Ward and Finch 2009).

3. *Drifting*: RASU dispersing larvae move primarily passively by the force of water currents, although they may try to control the timing of drift by swimming in/out of currents (see also Modde and Irving 1998; Tyus et al. 2000). The preference for night drifting may be an adaptation for avoiding predation (see also Johnson et al. 1993; Horn et al. 1994; Johnson and Hines 1999; USFWS 1998).

4. *Foraging*: RASU dispersing larvae forage mostly on detritus and plankton, including increasingly selecting for zooplankton, for which the RASU larvae presumably would require some minimal agility (Langhorst and Marsh 1986; Minckley et al. 1991; USFWS 1998, 2002a; Mueller 2006; Reclamation 2008). Several studies in the UCRB suggest that low foraging success (starvation) may affect survivorship among dispersing larvae due to the low productivity of the river during the spring, cold-water dispersal period (Wydoski and Wick 1998; Farrington et al. 2013). However, larval survivorship in the warmer LCR may not be food-limited (Papoulias and Minckley 1992).

5. *Mechanical stress*: RASU dispersing larvae are vulnerable to stress – including outright physical destruction – due to habitat scour, burial, or exposure to the open air; entrainment in propeller wash and dam intakes; wounding and stress from unsuccessful predator attacks; and handling during encounters with scientific sampling (Minckley et al. 1991; Brandenburg et al. 2002; Kretschmann and Leslie 2006; Mueller 2006; Reclamation 2008; Bestgen et al. 2012).

6. *Predation*: Direct predation on dispersing larvae is difficult to observe outside of controlled settings. The small size of the larvae and their limited mobility make them prey to a distinct spectrum of predator species or life stages, but larval behaviors such as active avoidance/escape movement, preference for movement at night (see above), and use of cover may help them avoid predation (Bozek et al. 1984; Langhorst and Marsh 1986; Minckley et al. 1991; Johnson et al. 1993; Horn et al. 1994; USFWS 1998, 2002a; Wesp and Gibb 2003; Christopherson et al. 2004; Dowling et al. 2005; Mueller et al. 2003b, 2005, 2006; Mueller and Burke 2005; Mueller 2006; Bestgen 2008; Carpenter and Mueller 2008; Reclamation 2008; Albrecht et al. 2010a, 2010b; Bestgen et al. 2011, 2012; Valdez et al. 2012; Farrington et al. 2013). Areas of greater

turbidity may also support lower rates of predation (Johnson and Hines 1999; Albrecht et al. 2010b). Predation rates may be higher among larvae with greater drift distances and/or drift pathways with less cover available (Albrecht et al. 2010a, 2010b). Lenon et al. (2002) also found that, by consuming crayfish, adult bonytail help reduce predation by crayfish on RASU larvae.

7. *Resting*: Dispersing larvae rest in shallow, low-velocity habitat (Minckley et al. 1991; Mueller et al. 2000; Mueller 2006; Reclamation 2008; Hedrick et al. 2009; Bestgen et al. 2011, 2012). They prefer resting sites with vegetative cover and/or interstitial spaces in gravels for concealment (Valdez et al. 2012) and may prefer sites with elevated turbidity when available (see also Johnson and Hines 1999; Albrecht et al. 2010b).

8. *Swimming*: RASU larvae exhibit a range of swimming behaviors to avoid predators. Johnson et al. (1993) and Wesp and Gibb (2003) report that these behaviors are comparable to those of young of other species that evolved in predator-rich environments. RASU dispersing larvae navigate into, out of, and within drift currents and avoid threats by swimming, although their small size presumably limits their ability to maneuver and the swimming speeds and distances they can achieve (see “Resting” in chapter 3). Swimming may be solitary or in aggregations, and the relative time spent dispersed (solitary swimming) or aggregated (schooling) may affect other activities and processes such as foraging and their vulnerability to predation and scientific handling. Reciprocally, the relative incidence of solitary versus aggregated movement may affect the effectiveness of different detection and capture methods and survey designs.

9. *Thermal stress*: RASU dispersing larvae are vulnerable to stress due to changes in temperature beyond the optimal range for their maturation and engagement in many behaviors (Bozek et al. 1990; Minckley et al. 1991; USFWS 1998; Clarkson and Childs 2000; Mueller et al. 2005; Bestgen 2008; Reclamation 2008; Bestgen et al. 2011; Valdez et al. 2012).

The evaluation of causal linkage magnitudes (see figure 8) indicates that, among the aforementioned nine critical biological activities and processes, three have high- or medium-magnitude direct effects on the outcome of this life stage in the present-day system: predation (high magnitude), foraging, and drifting (the latter two with medium magnitude). This assessment refers to overall, average survivorship across all reaches of the LCR and all wildlife refuges and other protected areas along the LCR managed as RASU habitat under the auspices of the LCR MSCP HCP. The assessment also indicates that swimming behaviors strongly affect life stage survivorship indirectly through their effects on predation, foraging, and drifting. In particular, the assessment indicates that aggregation behavior (an aspect of swimming) may help RASU larvae collectively avoid predators and locate food concentrations. Further, the assessment indicates that drifting dynamics (duration and distance along drift pathways during which the larvae are exposed) and resting behaviors (ability of larvae to find suitable resting habitat) also strongly influence predation rates.

The assessment indicates that the effects of predation, foraging, and drifting on overall survivorship all warrant high ratings for predictability (i.e., their effects on overall survivorship do not depend on the effects of other contingent factors). However, the assessment also indicates that the effects of swimming on predation have only low predictability because the relationship is highly contingent on the habitat setting. In confined habitats, such as in dense emergent vegetation and other settings with plentiful cover, the larvae likely can better avoid or escape at least some predation. But in open, clear water, in daylight, RASU have fewer options for escaping predators other than agile swimming, and aggregation under such circumstances may increase rather than decrease the ease with which predators may detect them. Additionally, the assessment indicates that the influence of resting behaviors on predation may have only medium predictability because resting site selection may not necessarily be a dominant factor in predator avoidance, although this has not been formally studied.

This assessment of the relative impact of different biological activities and processes on survivorship among dispersing larvae also comes with an important caveat: these are hypotheses based on the information provided in the literature and by LCR MSCP biologists. All except two of the causal linkages highlighted in the preceding paragraph receive low scores for scientific understanding, indicating that the understanding of the relationship is subject to wide disagreement or uncertainty in peer-reviewed studies from within the ecosystem of concern and in scientific reasoning among experts familiar with the ecosystem (see attachment A). The literature suggests that predation on dispersing larvae and unsuccessful foraging (starvation) may be responsible for high rates of mortality (Minckley et al. 1991; Wydoski and Wick 1998; USFWS 2002a; Reclamation 2008; Farrington et al. 2013). The literature also suggests that a lack of appropriately proximate resting habitat with appropriate levels of vegetative cover along drift pathways may expose the larvae to higher rates of attrition than would naturally occur (Albrecht et al. 2010a, 2010b; Mueller 2006). However, none of these hypotheses has received formal testing, and problems with food availability may be greater in the UCRB than along the LCR (Papoulias and Minckley 1992). On the other hand, these hypotheses are supported by specific observations, such as the absence of larvae greater than 12 mm TL in riverine and reservoir environments, and evidence for successful recruitment in Lake Mead and some refuge ponds where the availability of suitable – and suitably proximate – resting habitat appears to reduce vulnerability to predation.

The assessment identifies several habitat elements, in turn, that strongly and directly support or limit: (1) predation, drifting, and foraging, the three critical biological activities or processes with high- or medium-magnitude impacts on survivorship for this life stage or (2) resting and swimming behaviors, the two critical activities or processes that strongly *indirectly* influence survivorship for this life stage through their effects on other critical activities or processes. Specifically, the assessment identifies the following relationships, all but three of which are rated as having high predictability:

- The condition of mesohabitat geometry/cover has a high-magnitude influence on swimming behavior. The literature suggests that the spatial distribution of mesohabitat types and the density of vegetative cover among these types will affect the distances over which dispersing RASU larvae must swim in and out of drift pathways during dispersal, the amount of open-water across which they will be exposed during movement in/out of drift pathways, and the density of cover within which they must swim. The latter variables may also affect the likelihood that the larvae will aggregate as they move, including while they drift.

- Habitat elements with medium-magnitude influences on swimming behaviors also include predator activity and competitor activity (stimuli for avoidance behaviors) as well as macrohabitat geometry (shaping the spatial distribution of mesohabitats).

- No habitat element has a high-magnitude influence on present drifting behavior, but habitat elements with medium-magnitude influence include macrohabitat geometry, mesohabitat geometry/cover, and flow/turbulence, which all shape drift distances. These habitat elements affect the distances that dispersing RASU larvae will drift and the duration of their drift during dispersal, the amount of open-water across which they will be exposed during drift, and the density of cover along the drift pathways in/out of which they can swim.

- The abundance and composition of plankton, benthos, and POM exerts a strong (high-magnitude) influence on foraging success as the primary determinant of food availability. Mesohabitat geometry/cover exerts a medium-magnitude influence on foraging success since the availability of food items may vary with mesohabitat type and since foraging success may involve the use of cover.

- Two habitat elements exert strong (high-magnitude) influence on predation rates: predator activity (the abundance, composition, and activity levels of the assemblage of predators surrounding the dispersing larvae); and turbidity (shaping the effectiveness of sight-feeding predators). Two other habitat elements exert medium-magnitude influence on predation rates: competitor activity (providing potential alternative food sources for species that would otherwise prey on RASU larvae) and mesohabitat geometry/cover (shaping the availability of cover for both the predators and the RASU larvae). The assessment indicates that the interaction between competitor activity and predator activity has only medium predictability because the interactions depend on which competitor and predator species are present, which in turn depends on several aspects of habitat.

- Two habitat elements exert medium-magnitude influence on resting behavior: mesohabitat geometry/cover and substrate texture/dynamics. Both relationships recognize the importance of cover and substrate stability and texture in providing suitable resting conditions for the dispersing larvae. The assessment rates both relationships as having only medium predictability because their magnitudes depend on other factors (e.g., flow) and the interactions of mesohabitat geometry/cover and substrate texture/dynamics with each other.

The assessment also identifies several habitat elements that significantly but *indirectly* support or limit the rates of those critical biological activities or processes with high-magnitude impacts on survivorship for this life stage. Specifically, the assessment identifies the following relationships:

- Predator activity is strongly influenced (high-magnitude relationship) by competitor activity (species that compete with RASU larvae may also prey on them and vice versa), turbidity, mesohabitat geometry/cover (shaping the abundance and composition of the predator community in general), water temperature, and the composition of the benthic macroinvertebrate community (benthos) since several benthic macroinvertebrates may prey on RASU larvae.

- Turbidity and water temperature also shape competitor activity

- Mesohabitat geometry is strongly (high-magnitude relationship) influenced by macrohabitat geometry, which determines the abundance and spatial distribution of the former.

- Flow/turbulence at different spatial scales strongly shapes mesohabitat geometry, the abundance and spatial distribution of mesohabitat types, and macrohabitat geometry. These, in turn, also reciprocally shape flow/turbulence.

- Turbidity and the composition and abundance of the plankton-benthos-POM assemblage strongly shape each other. Plankton concentrations directly affect light penetration, and the depth of light penetration strongly affects the depth to which phytoplankton and periphyton may grow.

Plankton concentrations, in turn, also are shaped by water chemistry and substrate texture/dynamics (medium magnitude) and water temperature (high magnitude).

- Competitor activity also exerts a medium-magnitude influence on mesohabitat geometry/cover (competition with RASU larvae for habitat features). Competitor activity also moderately shapes the composition and abundance of the plankton-benthos-POM assemblage, and reciprocally, the composition and abundance of the plankton-benthos-POM assemblage strongly shapes competitor activity. The medium rating of magnitude for this latter feedback relationship reflects the lack of evidence in the literature with which to assess the intensity of the relationship.

- Both flow/turbulence and mesohabitat geometry strongly shape substrate texture/dynamics. Flow/turbulence thus shapes substrate texture/dynamics directly as well as indirectly through its influence on mesohabitat conditions (see above).

Among the direct and indirect causal relationships, through which habitat elements support or limit critical activities or processes, the assessment rates roughly half as having low scientific understanding in the literature. For example, hypotheses concerning the influence of mesohabitat geometry/cover on predator activity or actual predation rates; swimming, resting, or drifting behaviors; or foraging rates have not received detailed consideration, let alone formal testing. Hypotheses concerning which species prey on or compete with RASU larvae, and how the ecology (e.g., habitat preferences) of these species interacts with the ecology of RASU larvae, similarly have not been subjected to detailed discussion or analysis.

Finally, the assessment permits an analysis of the cumulative magnitude of impact of individual habitat elements that directly affect one or more of the critical biological activities or processes that most strongly shape survivorship for this life stage. Each of the habitat elements with large cumulative impacts on critical activities or processes for this life stage is strongly influenced (high or medium magnitude) by one or more other habitat elements, and the list below identifies those with the highest impacts on the listed habitat element:

- Competitor activity
    - Habitat elements with high- or medium-magnitude influence on this element include predator activity, turbidity, water temperature, and plankton-benthos-POM assemblage abundance and composition.

- Flow/turbulence
    - Habitat elements with the strongest influence on this element include macrohabitat geometry and mesohabitat geometry/cover.
- Macrohabitat geometry
    - The habitat element with high- or medium-magnitude influence on this element is flow/turbulence.
- Mesohabitat geometry/cover
    - The habitat element with high- or medium-magnitude influence on this element is macrohabitat geometry.
- Plankton-benthos-POM
    - Habitat elements with high- or medium-magnitude influence on this element include competitor activity, predator activity, substrate texture/dynamics, turbidity, water chemistry, and water temperature.
- Predator activity
    - Habitat elements with high- or medium-magnitude influence on this element include water temperature, competitor activity, plankton-benthos-POM assemblage abundance and composition, mesohabitat geometry/cover, and turbidity.
- Substrate texture/dynamics
    - Habitat elements with the strongest influence on this element include flow/turbulence and mesohabitat geometry/cover.
- Turbidity
    - The habitat element with high- or medium-magnitude influence on this element is plankton-benthos-POM assemblage abundance and composition.
- Water temperature
    - The habitat element with high- or medium-magnitude influence on this element is depth.

The list of habitat elements with the cumulative highest direct influence on critical biological activities and processes for this life stage includes two (water temperature and flow/turbulence) that do not strongly directly influence the three critical biological activities or processes with the strongest impact on RASU dispersing larval survivorship. However, these two habitat elements have low-magnitude direct effects on many of the other five critical biological activities and processes for this life stage, and the ranking here reflects this broader cumulative impact.

RASU LIFE STAGE 4 – RESETTLED LARVAE

Minckley et al. (1991), Wydoski and Wick (1998), Modde et al. (2001), Mueller (2006), and Reclamation (2008) summarize the scientific understanding of resettled larvae based on the literature to 2008. Albrecht et al. (2010a, 2010b), Bestgen et al. (2011, 2012), Valdez et al. (2012), and Farrington et al. (2013) provide additional information from both the LCR and UCRB. Some of their findings pertain specifically to the UCRB, where flow variability and greater geomorphic complexity (including active flood plains) present a different suite of conditions from those present along the LCR. However, the UCRB literature provides information on the range of evolved behaviors and habitat requirements for this life stage applicable to the LCR and its refuges.

Larvae that reach suitable habitat for continuing survival and maturation following dispersal (also termed “nursery” habitat; see life stage 3) continue to grow in size and mature in their foraging and other behaviors. It takes approximately 1 to 3 months for resettled larvae to develop into juveniles (see below). As larvae, their mouth remains in the terminal position, consistent with sight feeding in a forward direction. They use cover both to avoid predators and to prey on other organisms. They may swim among habitats, although the scale (distances) of movement is not well understood, and they may move passively with currents (drift). The literature does not indicate the extent to which they move and rest as solitary individuals or congregate in groups (schools). Success during this life stage – successful transition to the next stage – again involves organism survival and maturation.

The CEM (figures 9 and 10) recognizes the same nine critical biological activities and processes for this life stage as recognized for the preceding life stage, dispersing larvae, and they are presented here in alphabetical order. Although the CEM identifies the same activities and processes for resettled larvae as for the dispersing larvae, the dynamics differ because of increased RASU size, maturing behaviors, and less drifting.

Razorback Sucker (*Xyrauchen texanus*) (RASU)
Basic Conceptual Ecological Model

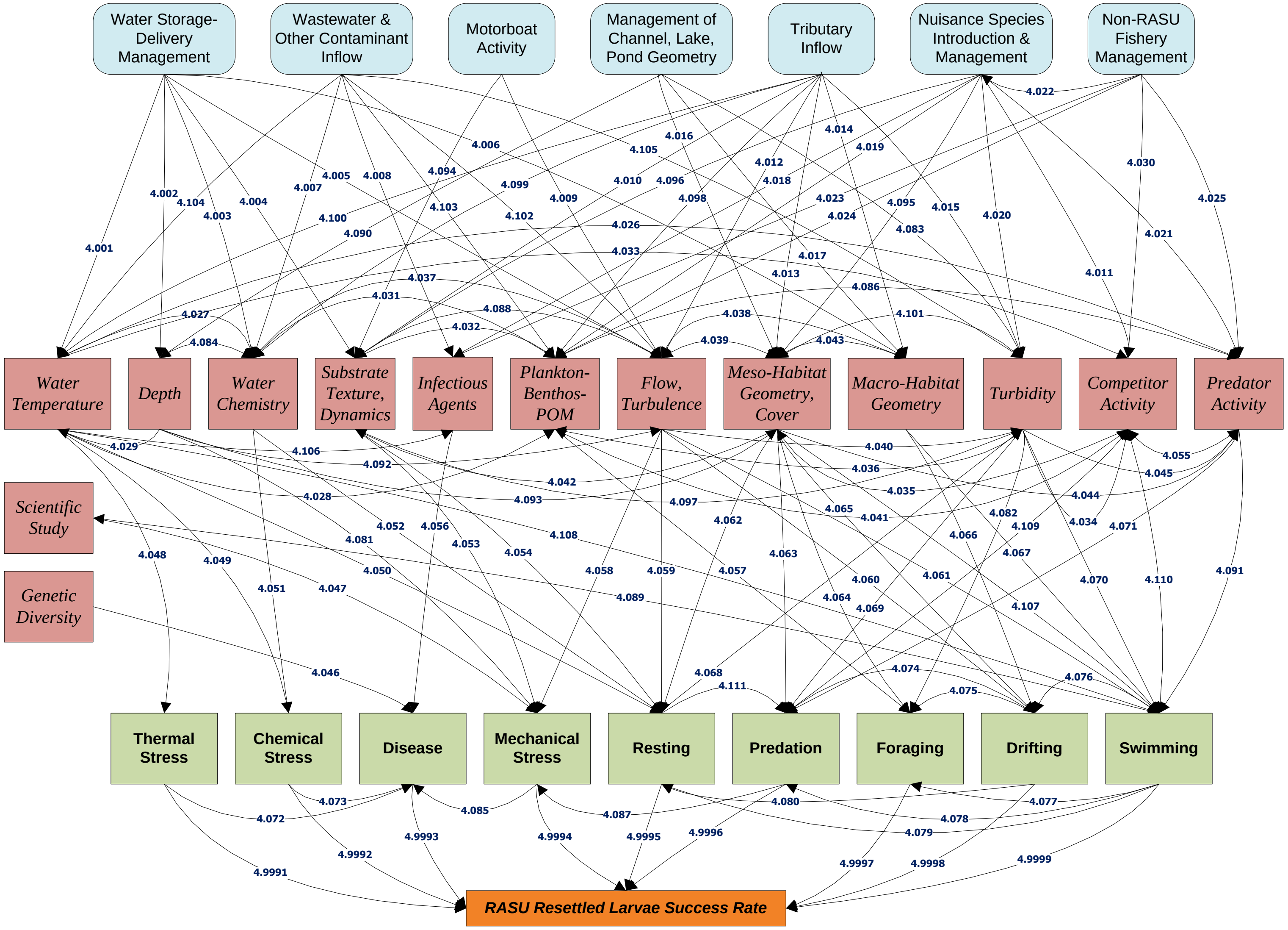

Figure 9.—RASU life stage 4 – resettled larvae, basic CEM diagram.

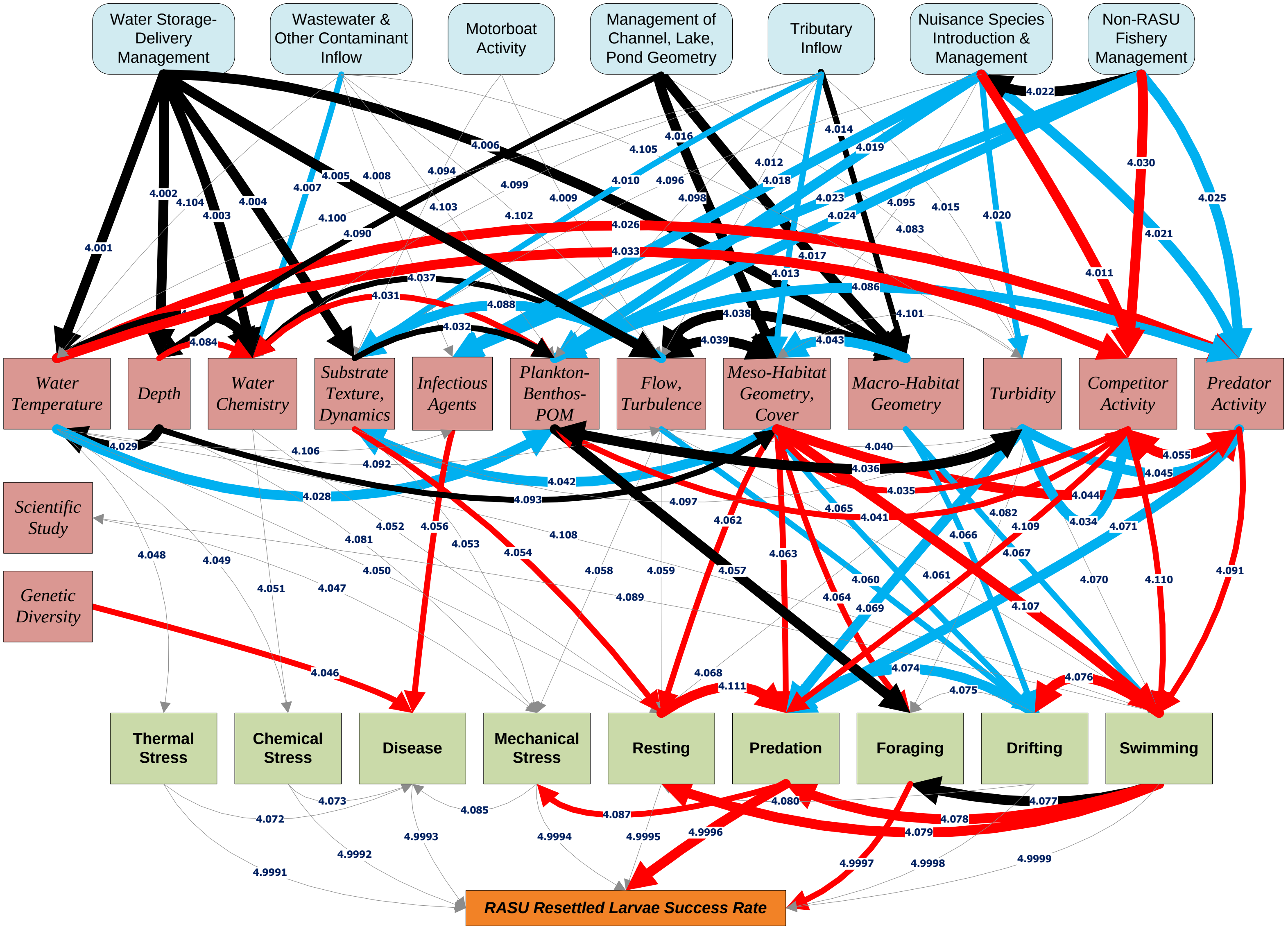

Figure 10.—RASU life stage 4 – resettled larvae, high- and medium-magnitude relationships.

1. *Chemical stress*: RASU resettled larvae are vulnerable to stress due to an insufficient supply of DO and exposure to harmful dissolved matter including contaminants (Stolberg 2009, 2012).

2. *Disease*: RASU resettled larvae are vulnerable to stress and mortality due to microbial infection (USFWS 2002a; Mueller 2006; Ward et al. 2007; Ward and Finch 2009).

3. *Drifting*: RASU resettled larvae move passively by the force of water currents, but this mode of movement presumably is less important than swimming (Modde and Irving 1998; Tyus et al. 2000). Resettled larvae mostly remain in a limited area (e.g., a single backwater) rather than moving more widely (Valdez et al. 2012). As noted for the previous life stage, a preference for night drifting may help RASU larvae avoid predation (see also Johnson et al. 1993; Horn et al. 1994; Johnson and Hines 1999; USFWS 1998).

4. *Foraging*: RASU resettled larvae prefer to feed on plankton, including increasingly larger zooplankton for which agility presumably would be required during foraging (Langhorst and Marsh 1986; USFWS 1998, 2002a; Mueller 2006; Marsh 1987). Several studies in the UCRB suggest that low foraging success (starvation) may affect survivorship among resettled larvae due to the low productivity of the river during the Spring, cold-water dispersal period (Wydoski and Wick 1998; Farrington et al. 2013). However, larval survivorship in the warmer LCR may not be food-limited (Papoulias and Minckley 1992).

5. *Mechanical stress*: RASU resettled larvae are vulnerable to stress due to habitat scour, burial, or exposure to the open air; entrainment in propeller wash and dam intakes; wounding and stress from unsuccessful predator attacks; and handling during encounters with scientific sampling (Minckley et al. 1991; Brandenburg et al. 2002; Kretschmann and Leslie 2006; Mueller 2006; Reclamation 2008; Bestgen et al. 2012).

6. *Predation*: RASU resettled larvae are vulnerable to predation. Again, direct predation on resettled larvae is difficult to observe outside of controlled settings. However, the evidence from controlled settings contributes to our understanding of predation on resettled larvae in the LCR and its off-channel habitats. The increasing but still small size of the larvae and their habitat preferences presumably make them prey to a distinct spectrum of predator species or life stages, but behaviors such as active avoidance/escape movement, preference for movement at night (see above), and their ability to find cover may help them avoid predation (Bozek et al. 1984; Langhorst and Marsh 1986; Minckley et al. 1991; Horn et al. 1994; USFWS 1998, 2002a; Johnson and Hines 1999; Gibb et al. 2006; Christopherson et al. 2004; Dowling et al. 2005; Mueller et al.

2003b, 2005, 2006; Mueller and Burke 2005; Mueller 2006; Bestgen 2008; Carpenter and Mueller 2008; Reclamation 2008; Albrecht et al. 2010a, 2010b; Bestgen et al. 2011, 2012; Farrington et al. 2013). Areas of higher levels of turbidity may also provide settings with lower rates of predation (Johnson and Hines 1999; Albrecht et al. 2010b). The presence of adult bonytail may help reduce predation of RASU larvae by crayfish because bonytail prey on crayfish (Lenon et al. 2002).

7. *Resting*: RASU resettled larvae need to rest to conserve energy, as is the case with every mobile life stage. The ability of the larvae to find suitable resting sites depends on the interaction of a large number of factors (Minckley et al. 1991; Mueller et al. 2000; Mueller 2006; Reclamation 2008; Hedrick et al. 2009; Bestgen et al. 2011, 2012). Vegetative cover and/or interstitial spaces in gravels may be particularly important for concealment (Valdez et al. 2012) as may turbidity (see also Johnson and Hines 1999; Albrecht et al. 2010b).

8. *Swimming*: As noted above, RASU larvae exhibit a range of swimming behaviors to avoid predators. Johnson et al. (1993) and Wesp and Gibb (2003) report that these behaviors are comparable to those of young of other fish species that evolved in predator-rich environments. RASU resettled larvae are able to move over large areas, including navigating within drift currents and avoiding threats, by swimming. Compared to younger larvae, their increasing but still small size presumably limits their ability to maneuver and limits the swimming speeds and distances they can achieve (see “Resting” in chapter 3). Swimming may be solitary or in “schools,” and the relative time spent dispersed (solitary swimming) or aggregated (schooling) may affect other activities and processes such as foraging and (vulnerability to) predation and scientific handling. Reciprocally, the relative degree of solitary versus aggregated movement may affect the effectiveness of different detection and capture methods and their associated survey designs.

9. *Thermal stress*: RASU resettled larvae are vulnerable to stress due to changes in temperature beyond a range suitable for their maturation and engagement in many behaviors (Bozek et al. 1990; Minckley et al. 1991; USFWS 1998; Clarkson and Childs 2000; Mueller et al. 2005; Bestgen 2008; Reclamation 2008; Bestgen et al. 2011; Valdez et al. 2012).

The evaluation of causal linkage magnitudes (see figure 10) indicates that, among the nine aforementioned critical biological activities and processes, only two have high- or medium-magnitude direct effects on the outcome of this life stage in the present-day system: predation (high magnitude) and foraging (medium magnitude). As noted in chapter 1, this assessment refers to overall, average survivorship across all reaches of the LCR and all wildlife refuges and other protected areas along the LCR managed as RASU habitat under the auspices of the LCR MSCP HCP.

The assessment indicates that drifting does not strongly directly affect overall survivorship among resettled larvae, in contrast to the preceding life stage. Drifting is simply a less important means of movement among resettled larvae. The assessment also indicates that swimming behaviors strongly *indirectly* affect life stage survivorship through their effects on predation, foraging, and drifting. Aggregation behavior (an aspect of swimming) in particular may help the larvae collectively avoid predators and locate food concentrations. Both drifting and resting dynamics also strongly affect predation and therefore indirectly affect life-stage survivorship. Drifting dynamics shape the duration and distance along drift pathways during which the larvae may be exposed to predators, and the ability of larvae to find resting habitat with suitable cover and substrate (and possibly also turbidity) also strongly influences predation rates. In turn, swimming behaviors strongly shape both drifting and resting success.

The effects of predation and foraging on overall survivorship both receive high scores for predictability (i.e., their effects on overall survivorship do not depend on the effects of other contingent factors). The effects of drifting on predation, and swimming on foraging, also have high predictability. However, the assessment also indicates that the effects of swimming on predation have only low predictability because the relationship is highly contingent on the habitat setting. In confined habitats, such as in dense emergent vegetation and in settings with plentiful cover, the larvae likely can swim away from and escape at least some predation. But in clear, open water, in daylight, there is probably little that RASU larvae can do to escape predators, and aggregation under such circumstances may increase rather than decrease the ease with which predators may detect them. Additionally, the assessment indicates that the influence of resting behaviors on predation may have only medium predictability because resting site selection may not necessarily be a dominant factor in predator avoidance – although, as noted for dispersing larvae, this has not been formally studied.

These findings come with an important caveat, as noted for other life stages: these are hypotheses based on the information provided in the literature and by LCR MSCP biologists. All except two of the causal linkages highlighted in the preceding paragraph receive low scores for scientific understanding, indicating that understanding of the relationship is subject to wide disagreement or uncertainty in peer-reviewed studies from within the ecosystem of concern and in scientific reasoning among experts familiar with the ecosystem (see attachment A). The literature suggests that predation on resettled larvae and unsuccessful foraging (starvation) may be responsible for high rates of mortality (Minckley et al. 1991; Wydoski and Wick 1998; USFWS 2002a; Reclamation 2008; Farrington et al. 2013). The literature also suggests that a lack of appropriate resting habitat (e.g., with suitable cover, substrate, or turbidity) may expose RASU resettled larvae to higher rates of attrition than would naturally occur (Albrecht et al. 2010a, 2010b; Mueller 2006). However, none of these hypotheses concerning predation, food availability, or habitat has received formal testing, and problems with food availability may be greater in the UCRB than along the LCR (Papoulias and Minckley 1992). On the other hand, these hypotheses are supported by specific observations, such as the absence of larvae greater than 12 mm TL in riverine and reservoir environments, and evidence for successful recruitment in Lake Mead and some refuge ponds where the availability of suitable – and suitably proximate – resting habitat appears to reduce vulnerability to predation.

The assessment identifies several habitat elements, in turn, that directly and significantly support or limit the rates of: (1) predation and foraging, the two critical biological activities or processes with high- or medium-magnitude direct impacts on survivorship for this life stage or (2) resting, drifting, and swimming behaviors, which have strong indirect effects on survivorship. Specifically, the assessment identifies the following relationships, all but three of which have high scores for predictability:

- The condition of mesohabitat geometry/cover has a high-magnitude influence on swimming behavior. The literature suggests that the spatial distribution of mesohabitat types and the density of vegetative cover among these types will affect the distances over which resettled RASU larvae must swim, the amount of open-water across that they will be exposed to during movement, and the density of cover within which they must swim. The latter variables may also affect the likelihood that the larvae will aggregate as they move.

- Habitat elements with medium-magnitude influences on swimming behaviors also include predator activity and competitor activity (stimuli for avoidance behaviors) as well as macrohabitat geometry/cover (shaping the spatial distribution of mesohabitats).

- No habitat element has a high-magnitude influence on the present rates of drifting, but habitat elements with medium-magnitude influence include macrohabitat geometry, mesohabitat geometry/cover, and flow/turbulence. These elements affect the distances that dispersing RASU larvae may drift and the duration of their drift during dispersal, the amount of open-water across which they will be exposed to during drift, and the density of cover along the drift pathways in/out of which they can swim.

- The abundance and composition of plankton, benthos, and POM exerts a strong (high-magnitude) influence on foraging success as the primary determinant of food availability. Mesohabitat geometry/cover exerts a medium-magnitude influence on foraging success since the availability of food items may vary with mesohabitat type and since foraging success may involve the use of cover.

- Two habitat elements exert a strong (high-magnitude) influence on predation rates: predator activity (the abundance, composition, and activity levels of the suite of predators surrounding the dispersing larvae), and turbidity (shaping the effectiveness of sight-feeding predators). Two other habitat elements exert medium-magnitude influence on predation rates: competitor activity (providing potential alternative food sources for species that would otherwise prey on RASU larvae) and mesohabitat geometry/cover (shaping availability of cover for both the predators and the RASU larvae). The assessment indicates that the interaction between competitor activity and predator activity has only medium predictability because the interactions depend on which competitor and predator species are present, which in turn depends on several aspects of habitat.

- Two habitat elements exert medium-magnitude influence on resting: mesohabitat geometry/cover and substrate texture/dynamics. Both relationships recognize the importance of cover and substrate stability and texture in providing suitable resting conditions for RASU larvae. Both relationships are assigned ratings of medium for predictability because their magnitude depends on other factors (e.g., flow) and the interactions of mesohabitat geometry/cover and substrate texture/dynamics with each other.

The assessment also identifies several habitat elements that significantly but *indirectly* support or limit the rates of those critical biological activities or processes with high-magnitude impacts on survivorship for this life stage. Specifically, the assessment identifies the following relationships:

- Competitor activity also exerts a medium-magnitude influence on mesohabitat geometry/cover (competition with RASU larvae for habitat features). Competitor activity also moderately shapes the composition and abundance of the plankton-benthos-POM assemblage, and reciprocally, the composition and abundance of the plankton-benthos-POM assemblage strongly shapes competitor activity. The rating of medium for magnitude for this latter feedback relationship reflects the lack of evidence in the literature with which to assess the intensity of the relationship.

- Flow/turbulence at different spatial scales strongly shapes mesohabitat geometry, the abundance and spatial distribution of mesohabitat types, and macrohabitat geometry. These, in turn, also reciprocally shape flow/turbulence.

- Flow/turbulence and mesohabitat geometry both strongly shape substrate texture/dynamics. Flow/turbulence thus shapes substrate texture/dynamics directly as well as indirectly through its influence on mesohabitat conditions (see above).

- Mesohabitat geometry is strongly (high-magnitude relationship) influenced by macrohabitat geometry, which determines the abundance and spatial distribution of the former. Mesohabitat geometry/cover, in turn, strongly shapes substrate texture/dynamics.

- Predator activity is strongly influenced (high-magnitude relationship) by competitor activity (species that compete with RASU larvae may also prey on them and vice versa), turbidity, mesohabitat geometry/cover (shaping the abundance and composition of the predator community in general), water temperature, and the composition of the benthic macroinvertebrate community (benthos) since several benthic macroinvertebrates may prey on RASU larvae.

- Turbidity and the composition and abundance of the plankton-benthos-POM assemblage strongly shape each other. Plankton concentrations directly affect light penetration, and the depth of light penetration strongly affects the depth to which phytoplankton and periphyton may grow. Plankton concentrations, in turn, also are shaped by water chemistry, substrate texture/dynamics (medium magnitude), and water temperature (high magnitude).

- Turbidity and water temperature also shape competitor activity.

Among the direct and indirect causal relationships, through which habitat elements support or limit critical activities or processes for RASU resettled larvae, the assessment identifies half as having low scientific understanding in the literature. For example, hypotheses concerning the influence of mesohabitat geometry/cover on predator activity or actual predation rates; swimming, resting, or drifting behaviors; or foraging rates have not received detailed consideration, let alone formal testing. Hypotheses concerning which species prey on or compete with RASU larvae, and how the ecology (e.g., habitat preferences) of these species interacts with the ecology of RASU larvae, similarly have not been subjected to detailed discussion or analysis.

Finally, the assessment permits an analysis of the cumulative magnitude of impact of individual habitat elements that directly affect one or more of the critical biological activities or processes that most strongly shape survivorship for this life stage. Each of the habitat elements with large cumulative impacts on critical activities or processes for this life stage is strongly influenced (high or medium magnitude) by one or more other habitat elements, and the list below identifies those with the highest impacts on the listed habitat element:

- Competitor activity
    - Habitat elements with high- or medium-magnitude influence on this element include predator activity, turbidity, water temperature, and plankton-benthos-POM assemblage abundance and composition.
- Flow/turbulence
    - Habitat elements with the strongest influence on this element include macrohabitat geometry and mesohabitat geometry/cover.
- Macrohabitat geometry
    - The habitat element with high- or medium-magnitude influence on this element is flow/turbulence.
- Mesohabitat geometry/cover
    - The habitat element with high- or medium-magnitude influence on this element is macrohabitat geometry.
- Plankton-benthos-POM
    - Habitat elements with high- or medium-magnitude influence on this element include competitor activity, predator activity, substrate texture/dynamics, turbidity, water chemistry, and water temperature.
- Predator activity
    - Habitat elements with high- or medium-magnitude influence on this element include water temperature, competitor activity, plankton-benthos-POM assemblage abundance and composition, mesohabitat geometry/cover, and turbidity.
- Substrate texture/dynamics
    - Habitat elements with the strongest influence on this element include flow/turbulence and mesohabitat geometry/cover.
- Turbidity
    - The habitat element with high- or medium-magnitude influence on this element is plankton-benthos-POM assemblage abundance and composition.

- Water temperature
    - The habitat element with high- or medium-magnitude influence on this element is depth.

The list of habitat elements with the cumulative highest direct influence on critical biological activities and processes for this life stage includes two (water temperature and flow/turbulence) that do not strongly directly influence the three critical biological activities or processes with the strongest impact on RASU dispersing larval survivorship. However, these two habitat elements have direct, low-magnitude effects on many of the other five critical biological activities and processes for this life stage, and the ranking here reflects this broader cumulative impact.

RASU LIFE STAGE 5 – JUVENILES/SUBADULTS, WILD BORN

Minckley et al. (1991), Mueller (2006), and Reclamation (2008) summarize the understanding of RASU juveniles/subadult biology and ecology in LCR riverine and backwater environments up to 2008. Albrecht et al. (2010a), Bestgen et al. (2011, 2012), and Valdez et al. (2012) provide additional information from both the LCR and UCRB. It is crucial to note that wild-born juveniles and subadults are no longer detected during fish surveys along the LCR outside of pond refuges and Lake Mead (Albrecht et al. 2010a, 2010b; LCR MSCP biologist personal communications, August 2013).

Larvae mature into juveniles within 30–100 days following hatching, depending on water temperature and food availability (Gustafson 1975; Clarkson and Childs 2000; Bestgen 2008; Valdez et al. 2012), with the transition marked by changes in morphology and in foraging and other behaviors. The critical changes in morphology include a shift in mouth position to a more inferior position, allowing greater access to benthic food resources (Snyder and Muth 2004). The transition occurs when larvae reach approximately 25 mm TL (Snyder and Muth 2004). Following this transition, the young RASU rapidly grow in size for the first 6 years, developing their characteristic bony dorsal keel (around 200 mm TL) and become sexually mature within 2–6 years (Minckley et al. 1991). They use emergent vegetation and other cover to avoid predators, rest, and forage on other organisms. They swim over increasingly large distances within and sometimes among river macrohabitats (e.g., within and between the flowing river segment above Lake Mohave and the Lake itself) (Kesner et al. 2012; Wydoski and Lantow 2012) and may use currents to facilitate this movement. Their vulnerability to involuntary entrainment in large flow events/currents presumably decreases as their size and strength increase. According to Snyder and Muth

(2004), individuals >25 mm TL (which for these authors means mostly juveniles) may "travel in large schools in warm shallows along shore." LCR MSCP biologist field observations in fact suggest that schooling may occur throughout this life stage, as evidenced by uneven distributions of juveniles/subadults encountered historically during riverine and backwater sampling and more recently in pond settings alone (LCR MSCP biologists, personal communications, August 2013). Success during this life stage again involves organism survival and maturation.

The CEM (figures 11 and 12) recognizes eight critical biological activities and processes for this life stage, and they are presented here in alphabetical order:

1. *Chemical stress*: RASU wild-born juveniles/subadults are vulnerable to stress due to an insufficient supply of DO and exposure to harmful dissolved matter, including contaminants, possibly including selenium (Hamilton et al. 2005b). However, they have an increasingly greater ability (compared to previous life stages) to avoid or escape settings in which they may sense unsuitable conditions – at least where circumstances (lack of confinement, small areas of unsuitability) allow such avoidance or escape.

2. *Disease*: RASU wild-born juveniles/subadults are vulnerable to stress and mortality due to infection, including that from parasites (Valdez 1990; Clarkson et al. 1997; Robinson et al. 1998; USFWS 1998, 2002a; Choudhury 2004; Mueller 2006; Marsh 1987; Ward et al. 2007; Ward and Finch 2009).

3. *Foraging*: RASU wild-born juveniles/subadults increasingly feed on benthos and can target increasingly large invertebrates for which agility presumably would be required during foraging (Langhorst and Marsh 1986; Marsh 1987; USFWS 1998, 2002a; Mueller 2006). The relative importance of zooplankton may vary depending on food availability in more lentic versus more lotic environments (Reclamation 2008).

4. *Mechanical stress*: RASU wild-born juveniles/subadults are vulnerable to physical stress – including outright physical destruction – due to habitat scour, burial, or exposure to the open air; entrainment in propeller wash and dam intakes; wounding during unsuccessful predator attacks; and handling during encounters with scientific sampling (Minckley et al. 1991; Brandenburg et al. 2002; Mueller 2006; Hunt 2008, 2012; Mueller et al. 2008; Reclamation 2008; Bestgen et al. 2012). However, compared to earlier mobile life stages, they have a greater ability – increasing as they grow – to avoid or escape potentially mechanically stressful conditions simply by swimming away – at least where circumstances (lack of confinement, small areas of unsuitability) allow such avoidance or escape.

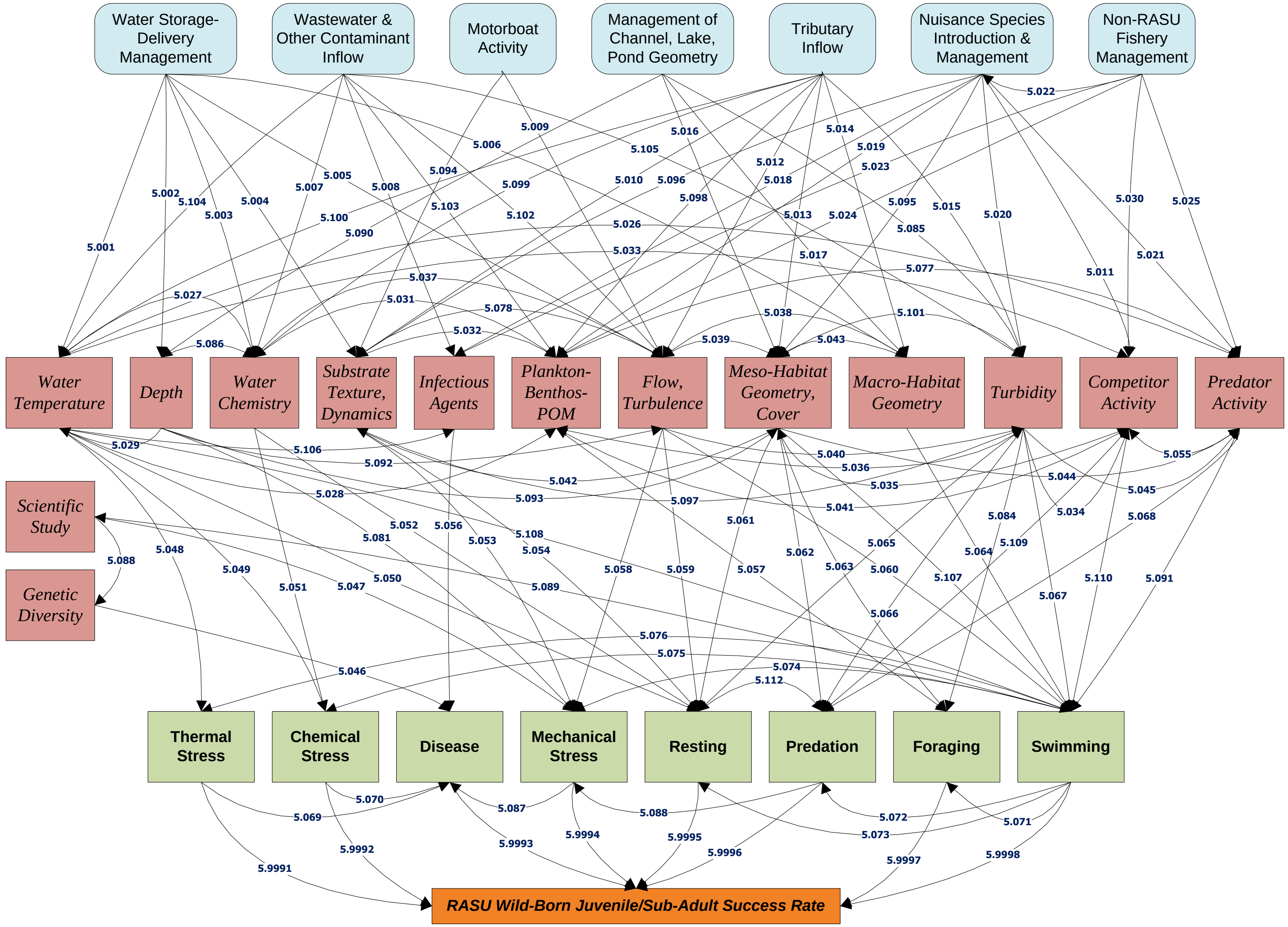

Figure 11.—RASU life stage 5 – wild-born juveniles and subadults, basic CEM diagram.

Razorback Sucker (*Xyrauchen texanus*) (RASU)
Basic Conceptual Ecological Model

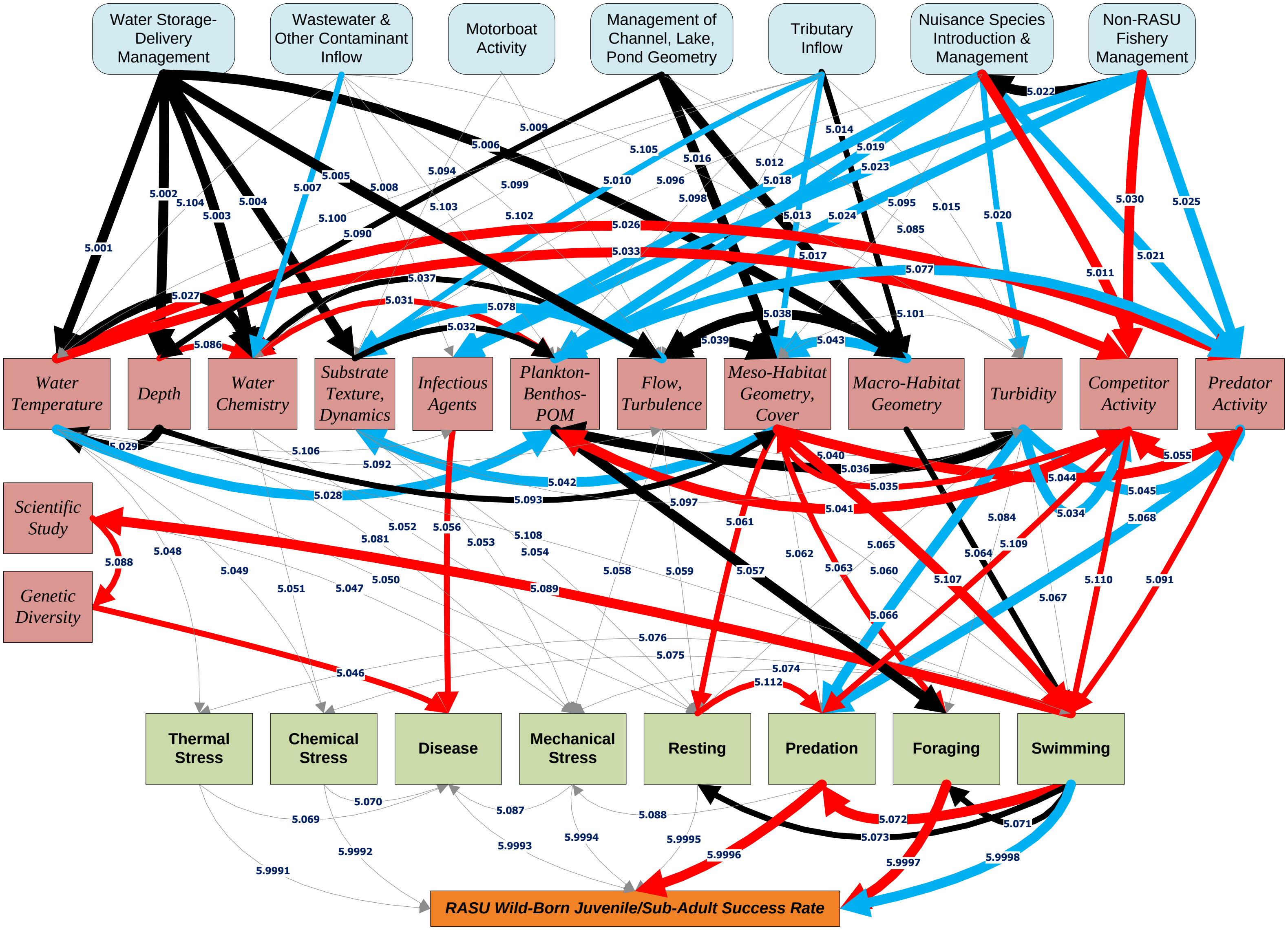

Figure 12.—RASU life stage 5 – wild-born juveniles and subadults, high- and medium-magnitude relationships.

5. *Predation*: RASU wild-born juveniles/subadults are vulnerable to predation. As they grow, their increasing size presumably makes them prey to a shifting spectrum of predator species or life stages (Bozek et al. 1984; Langhorst and Marsh 1986; Minckley et al. 1991; USFWS 1998, 2002a; Bonar et al. 2002; USFWS 2002b; Portz and Tyus 2004; Dowling et al. 2005; Mueller et al. 2005; Mueller 2006; Schooley et al. 2008; Reclamation 2008; Albrecht et al. 2010a; Bestgen et al. 2011, 2012; Karam and Marsh 2010). For example, Kesner et al. (2012) found that individuals >450 mm TL experience much higher rates of survival than do smaller individuals, although the study did not specifically identify shifts in predation rates as the cause of this shift in survivorship. As noted in chapter 5, the Colorado pikeminnow may have been the dominant predator on RASU in the LCR prior to the introduction of numerous non-native predators and the decline of the pikeminnow. However, as noted earlier, pikeminnow predation on RASU is gape limited, with pikeminnow ignoring RASU larger than approximately 33–37 percent of the length of the predator once RASU develop their characteristic dorsal keel at approximately 200 mm TL. The decline in the pikeminnow in the Colorado River and the arrival of other predators with different feeding behaviors, morphology, and gape limitations would have changed the predatory pressures on juvenile and subadult RASU. The increasing range of RASU movement among macrohabitats, the distances they travel among mesohabitats with cover, and the decline in overall turbidity along the LCR conceivably also may affect their vulnerability to predation.

6. *Resting*: RASU wild-born juveniles/subadults need to rest to conserve energy and avoid predators. Throughout this life stage, they 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 begin to exhibit some seasonal variation in their selection of macro and mesohabitats as resting sites within these ranges, as recorded for adults, with an overall preference for shallow-water, low-velocity settings (Minckley et al. 1991; Reclamation 2008; Valdez et al. 2012). Their ability to find resting sites depends on the interaction of a large number of factors affecting habitat availability, including turbidity and the availability of cover (Minckley et al. 1991; Mueller et al. 2000; Mueller 2006; Reclamation 2008; Hedrick et al. 2009; Bestgen et al. 2011, 2012).

7. *Swimming*: RASU wild-born juveniles/subadults are able to move over large areas, including navigating within drift currents and avoiding threats, by swimming. However, their agility and the speeds and distances they can achieve presumably vary with individual size, strength, and stamina (see “Resting” in chapter 3). Swimming may be solitary or in “schools” (see chapter 3), and the relative time spent dispersed (solitary

swimming) or aggregated (schooling) may affect other activities and processes such as foraging and (vulnerability to) predation, scientific handling, and other causes of stress.

8. *Thermal stress*: RASU wild-born juveniles/subadults are vulnerable to stress due to changes in temperature beyond the range suitable for their maturation and engagement in many behaviors (Bozek et al. 1990; Minckley et al. 1991; USFWS 1998; Mueller et al. 2005; Mueller 2006; Reclamation 2008; Bestgen et al. 2011; Valdez et al. 2012). However, compared to earlier mobile life stages, they have a great ability to avoid potentially mechanically stressful conditions simply by swimming away – at least where circumstances (lack of confinement, small areas of unsuitability) allow such avoidance or escape.

The evaluation of causal linkage magnitude (see figure 12) indicates that, among the eight aforementioned critical biological activities and processes, only three have high-magnitude direct effects on the outcome of this life stage in the present-day system (and none with medium-magnitude direct effects): predation, foraging, and swimming. As noted in chapter 1, this assessment refers to overall, average survivorship across all reaches of the LCR and all wildlife refuges and other protected areas along the LCR managed as RASU habitat under the auspices of the LCR MSCP HCP.

The assessment also indicates that two critical biological activities and processes *indirectly* affect survivorship with high or medium magnitude. Specifically, swimming behaviors strongly indirectly affect life stage survivorship through their effects on predation (high magnitude) and on foraging and resting (medium magnitude). Swimming agility and strength, and potential behaviors such as aggregation, help RASU avoid and escape predators. Swimming agility and strength also support foraging success and allow RASU to locate and move to/from resting locations. Resting behaviors, in turn, include finding suitable cover and other habitat features that help RASU avoid predation (medium-magnitude indirect influence on survivorship).

The assessment indicates that the effects of predation, foraging, and swimming on overall survivorship among wild-born juvenile and subadult RASU all warrant high scores for predictability (i.e., their effects on overall survivorship do not depend on the effects of other contingent factors). However, the assessment also indicates that the effects of swimming on foraging and resting have only low predictability. Differences in swimming ability and strength among RASU juveniles and subadults probably have little effect on foraging success because individual predators of different sizes will select size-appropriate prey, and the relationship between swimming and resting is highly contingent on the habitat setting. In confined habitats, such as in dense emergent vegetation and in settings with plentiful cover, RASU of this life stage likely can find suitable cover for resting, but in clear, open water, in daylight, there is probably little that the RASU of this life stage can do to hide from predators. Consequently, the assessment rates the effects of swimming and resting on predation as having only medium predictability. In clear, open water, in daylight, aggregation may increase the ease with which predators may detect RASU, but also help the RASU collectively detect predators, spread the alarm, and escape being attacked.

The assessment found no evidence that several other critical activities and processes are altered in ways that significantly affect survivorship during this life stage. Thermal stress, chemical stress, disease, and mechanical stress do not appear strongly linked to altered survivorship. However, the effects of such stressors could be invisible in the data because they would simply increase the vulnerability of RASU to mortality from other factors such as predation or poor foraging success. Data on external markers of stress (e.g., external deformities, eroded fins, lesions, and tumors – *aka* DELT anomalies) (Sanders et al. 1999) might provide a means for assessing rates of sublethal stress.

As noted for previous life stages, this assessment of the relative impact of different biological activities and processes on survivorship comes with an important caveat: these are hypotheses based on the information provided in the literature and by LCR MSCP biologists. Two of the three direct linkages and two of the four indirect linkages between critical biological activities and processes and survivorship receive low scores for scientific understanding, indicating that understanding of the relationship is subject to wide disagreement or uncertainty in peer-reviewed studies from within the ecosystem of concern and in scientific reasoning among experts familiar with the ecosystem (see attachment A). The literature suggests that predation on wild-born juveniles and subadults, and unsuccessful foraging, both shaped by the availability and proximity of habitat, may be responsible for high rates of mortality in many settings (Minckley et al. 1991; Mueller 2006; Reclamation 2008; Albrecht et al. 2010a, 2010b). However, these hypotheses have not received any formal testing. They are supported by evidence for successful survivorship in Lake Mead and some refuge ponds where the availability of suitable – and suitably proximate – resting habitat along with suitable densities of food appears to reduce vulnerability to predation and increase foraging success.

The assessment identifies several habitat elements that directly and significantly (high or medium magnitude) support or limit rates of the three critical biological activities or processes with direct, high-magnitude impacts on survivorship for this life stage. Specifically, the assessment identifies the following relationships with varying levels of predictability:

- The assessment indicates that the rate of predation is directly influenced by turbidity and predator activity at a high magnitude, and by competitor activity at a medium magnitude. The effect of turbidity on predation has high predictability through its effect on sight-feeding behavior among predators and sight-based avoidance behaviors among RASU. The effect of predator activity on predation has medium predictability due to the intervening effects of habitat conditions such as turbidity and cover. The effect of competitor activity on predation has low predictability because the intensity of this relationship depends on what predators and competitors are present and the degree to which the other species present offer attractive alternatives to RASU wild-born juveniles and subadults as prey.

- The assessment indicates that the rate of foraging success strongly depends on the composition and abundance of the plankton-benthos-POM assemblage and moderately depends on the abundance and distribution of mesohabitats with suitable geometry/cover. The relationship between the composition and abundance of the plankton-benthos-POM assemblage and foraging success has high predictability. The only factor that might make it less predictable might be the taxonomic composition of the plankton, benthos, and POM if some non-native species were to increase at the expense of preferred food items. The relationship between mesohabitat conditions and foraging has an unknown level of predictability due to a lack of data on habitat usage (average and seasonal) for this life stage in the LCR and its refuges, a consequence of the general lack of recruitment to or detection of this life stage in the system in recent decades.

- The assessment indicates that the effectiveness of swimming behaviors strongly depends on the abundance and proximity of mesohabitats with suitable geometry/cover and moderately depends on the spatial distribution of macrohabitat types, predator activity, and competitor activity. The relationship between mesohabitat conditions and swimming has an unknown level of predictability due to a lack of data on habitat usage (average and seasonal) for this life stage. The effects of macrohabitat distribution have high predictability because the distribution of macrohabitat features along the LCR and in its refuges is essentially fixed and unvarying. The effects of predator and competitor activity have unknown levels of predictability due to a lack of studies of how RASU behave in response to the presence of predators or competitors.

The assessment also identifies the possibility that swimming behaviors could strongly affect scientific study. Specifically, the relative degree of solitary versus aggregated activity could affect the effectiveness of different detection and capture methods and their associated survey designs for estimating reach population sizes and distribution. This relationship has an unknown level of predictability. It has not been studied for the RASU, although the principles are well known in sampling design. There is also no systematic evidence concerning the frequency and magnitude of non-spawning aggregation (“schooling”) and whether it is a part of the RASU natural behavioral repertoire. Nevertheless, if wild-born juvenile/subadult swimming patterns result in spatially uneven fish distributions, and fish surveys do not take this into account, this could result in inaccurate estimates of population numbers and health.

The assessment also identifies several habitat elements that significantly but *indirectly* support or limit the rates of those critical biological activities or processes with high-magnitude impacts on survivorship for this life stage. Specifically, the assessment identifies the following relationships:

- Water temperature affects predator activity and competitor activity (high magnitude) and the composition and abundance of the plankton-benthos-POM assemblage (medium magnitude).
- Competitor activity and predator activity affect each other with high magnitude. Predators on RASU may also prey on species that compete with RASU for food or habitat, and species that compete with RASU may also prey on them.
- Turbidity affects both predator activity and competitor activity with high magnitude.
- Mesohabitat geometry/cover affects predator activity with high magnitude because predators may use cover during their foraging, and RASU may use cover to avoid predators.
- Competitor activity affects mesohabitat availability (medium magnitude) when other species compete with RASU not just for food but also for habitat space.
- Macrohabitat geometry strongly shapes the abundance and spatial distribution of mesohabitat types.
- The composition and abundance of the plankton-benthos-POM assemblage strongly affects predator activity.
- Competitor activity strongly shapes the composition and abundance of the plankton-benthos-POM assemblage, and reciprocally, the composition and abundance of the plankton-benthos-POM assemblage also strongly shapes competitor activity.
- Turbidity and the composition and abundance of the plankton-benthos-POM assemblage strongly shape each other. Plankton concentrations directly affect light penetration, and the depth of light penetration strongly affects the depth to which phytoplankton and periphyton may grow.

- Water chemistry and the composition and abundance of the plankton-benthos-POM assemblage reciprocally affect each other with medium magnitude. Water constituents may support or limit phytoplankton growth, golden alga blooms release toxins, and the invasive quagga and zebra mussels can directly affect DO concentrations.

- Substrate texture/dynamics moderately shape the composition and abundance of the plankton-benthos-POM assemblage.

- Mesohabitat geometry strongly shapes substrate texture/dynamics, and flow/turbulence strongly shapes mesohabitat geometry and the abundance and spatial distribution of mesohabitat types.

Among the direct and indirect causal relationships, through which habitat elements support or limit critical activities or processes, the assessment again rates roughly half as having low scientific understanding in the literature. For example, as noted for earlier life stages, hypotheses concerning the influence of mesohabitat geometry/cover on predator activity or actual predation rates; swimming, resting, or drifting behaviors; or foraging rates have not received detailed consideration, let alone formal testing. Hypotheses concerning which species prey on or compete with RASU juveniles or subadults, and how the ecology (e.g., habitat preferences) of these species interacts with the ecology of RASU juveniles or subadults, similarly have received only limited discussion and analysis.

Finally, the assessment permits an analysis of the cumulative magnitude of impact of individual habitat elements that affect one or more of the four critical biological activities or processes that most strongly shape survivorship for this life stage. The following habitat elements have the highest cumulative magnitudes of impact. Each of these eight habitat elements is strongly influenced (high or medium magnitude) by one or more other habitat elements, and the list below identifies those with the highest impacts on the listed habitat element:

- Competitor activity

    - Habitat elements with the strongest influence on this element include predator activity, turbidity, and water temperature.

- Flow/turbulence

    - Habitat elements with the strongest influence on this element include macrohabitat geometry and mesohabitat geometry/cover.

- Macrohabitat geometry
    - The habitat element with high- or medium-magnitude influence on this element is flow/turbulence.
- Mesohabitat geometry/cover
    - The habitat element with the strongest influence on this element is macrohabitat geometry.
- Plankton-benthos-POM
    - Habitat elements with high- or medium-magnitude influence on this element include competitor activity, predator activity, substrate texture/dynamics, turbidity, water chemistry, and water temperature.
- Predator activity (tied with turbidity and flow/turbulence)
    - Habitat elements with the strongest influence on this element include water temperature, competitor activity, mesohabitat geometry/cover, and turbidity.
- Turbidity (tied with predator activity and flow/turbulence)
    - The habitat element with the strongest influence on this element is plankton-benthos-POM assemblage abundance and composition.
- Water temperature
    - The habitat element with strongest influence on this element is depth.

The list of habitat elements with the cumulative highest direct influence on critical biological activities and processes for this life stage includes two (water temperature and flow/turbulence) that do not strongly influence the three critical biological activities or processes with the strongest impact on RASU wild-born juvenile and subadult survivorship. However, these two habitat elements have direct, low-magnitude effects on many of the other five critical biological activities and processes for this life stage, and the ranking here reflects this broader cumulative impact.

RASU LIFE STAGE 6 – SUBADULTS, REPATRIATED

The CEM for this life stage is identical to that for wild-born subadults in most respects. However, it differs by recognizing: (1) the effects of handling during transport/release, (2) the need for released individuals to assimilate physiologically to their new riverine or backwater habitat, and (3) the need for released individuals to adapt behaviorally to their new riverine or backwater habitat, as shaped in part by pre-release conditioning or its absence. Reared RASU are released after reaching a minimum size of 300 mm TL. After adjusting to their new habitat – during which time they may become food for numerous predators – surviving repatriated RASU are thought to behave and mature similarly to wild-born subadults as described for the "juveniles/subadults, wild born" life stage, above. However, their survivorship may differ from that of their wild-born cousins for some time after their release due to their initial lack of acclimation to and experience in "wild" riverine and backwater environments.

The CEM (figures 13 and 14) recognizes the same eight critical biological activities and processes for this life stage as for the juvenile/subadult, wild born life stage, and they are presented here in alphabetical order:

1. *Chemical stress*: RASU repatriated subadults presumably are vulnerable in the same manner as wild-born subadults to stress due to an insufficient supply of DO and exposure to harmful dissolved matter including contaminants, possibly including selenium (Hamilton et al. 2005b). However, they have an increasingly greater ability (compared to previous life stages) to remove themselves from settings in which they may sense unsuitable conditions – at least where circumstances (lack of confinement, small areas of unsuitability) allow such avoidance or escape.

2. *Disease*: RASU repatriated subadults are vulnerable to stress and mortality due to microbial infection (USFWS 1998, 2002a; Mueller 2006; Marsh 1987; Ward et al. 2007; Ward and Finch 2009). Their new environment may expose the repatriated RASU to different suites of infectious organisms than they faced in their rearing environments.

3. *Foraging*: RASU repatriated subadults feed on a combination of benthos and zooplankton, with the composition of their diet varying apparently in relation to availability in lentic versus lotic environments (Reclamation 2008) and possibly as a consequence of feeding habits developed during rearing. As with wild-born subadults of comparable size, they can target increasingly large invertebrates with agility and force (Marsh 1987; USFWS 1998, 2002a; Mueller 2006).

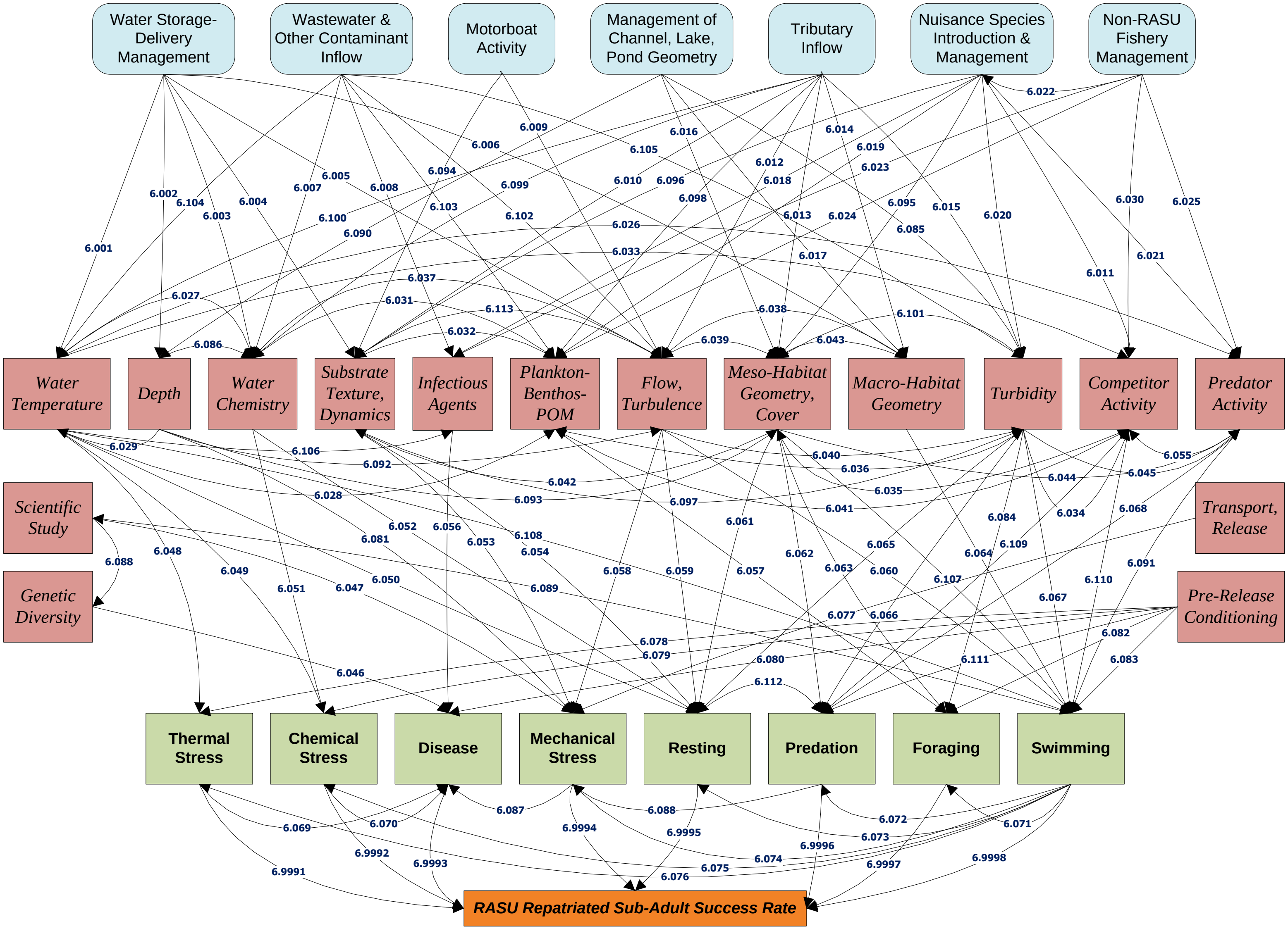

Figure 13.—RASU life stage 6 – repatriated subadults, basic CEM diagram.

Razorback Sucker (*Xyrauchen texanus*) (RASU)
Basic Conceptual Ecological Model

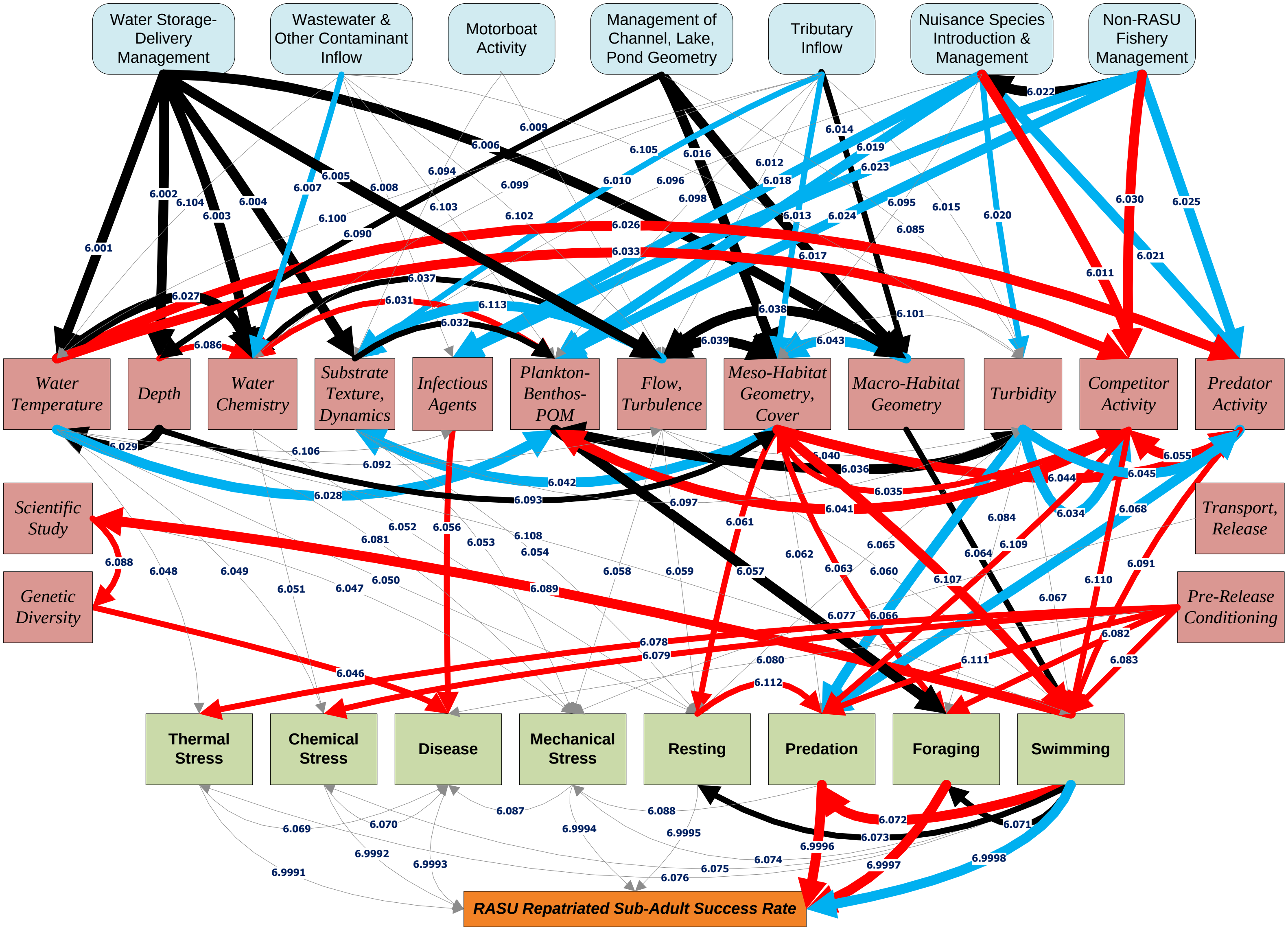

Figure 14.—RASU life stage 6 – repatriated subadults, high- and medium-magnitude relationships.

4. *Mechanical stress*: RASU repatriated subadults are vulnerable to physical stress – including outright physical destruction – due to habitat scour, burial, or exposure to the open air; entrainment in propeller wash and dam intakes; wounding and stress from unsuccessful predator attacks; handling during encounters with scientific sampling; and during transport/release from rearing facilities (Minckley et al. 1991; Mueller and Foster 1999; Mueller et al. 2003a; Mueller 2006; Hunt 2008; Hunt et al. 2012; Mueller et al. 2008; Reclamation 2008; Bestgen et al. 2012). However, they are able to avoid potentially mechanically stressful conditions simply by swimming away – at least where circumstances (lack of confinement, small areas of unsuitability) allow such avoidance or escape.

5. *Predation*: RASU repatriated subadults are vulnerable to predation, as are individuals at every life stage. However, hatchery reared fish may be more vulnerable due to their lack of experience with predators at their rearing facilities and their patterns of surfacing behavior developed at their rearing facilities (Schooley et al. 2008). As they grow, their increasing size presumably makes them prey to a shifting spectrum of predator species or life stages (Bozek et al. 1984; Langhorst and Marsh 1986; Minckley et al. 1991; USFWS 1998, 2002a; Bonar et al. 2002; Portz and Tyus 2004; Dowling et al. 2005; Mueller et al. 2005; Mueller 2006; Schooley et al. 2008; Reclamation 2008; Albrecht et al. 2010a; Bestgen et al. 2011, 2012; Karam and Marsh 2010). As noted in chapter 5 and for wild-born juvenile and subadult RASU, the Colorado pikeminnow may have been the dominant predator on RASU in the Colorado River prior to the introduction of numerous non-native predators and the decline of the pikeminnow. However, as noted earlier, pikeminnow predation on RASU is gape limited, with pikeminnow ignoring RASU larger than approximately 33–37 percent of the length of the predator once RASU develop their characteristic dorsal keel at approximately 200 mm TL. The decline in the pikeminnow in the Colorado River and the arrival of other predators with different feeding behaviors, morphology, and gape limitations would have changed the predatory pressures on juvenile and subadult RASU. The range of movement of repatriated subadults among macrohabitats, the distances they travel among mesohabitats with cover, and the decline in overall turbidity along the LCR conceivably also may affect their vulnerability to predation. For example, as discussed in chapter 2, studies of survivorship among repatriated subadults indicate that individuals >300 mm TL experience less predation than do smaller individuals. The identification of this threshold of diminished vulnerability led to the decision to begin repatriating RASU only when they reached this size (Reclamation 2008). However, Kesner et al. (2012) found that survival of repatriated RASU in Lake Mohave improved significantly for fish with TL >450 mm at release compared to fish with TL only >300 mm. They suggest that the difference reflects an effect of size on vulnerability to predation. Mueller et al. (2007), Schooley et al.

(2008), and others identify the lack of conditioning of repatriated RASU to the presence of predators as a crucial reason for their high rates of mortality due to predation. Lack of strong swimming ability among repatriated RASU may also affect their ability to avoid predators (Mueller and Foster 1999; Mueller et al. 2003a; Ward and Hilwig 2004; Mueller et al. 2007; Kegerries and Albrecht 2009; Avery et al. 2011; Senger and Sjöberg 2011).

6. *Resting*: RASU repatriated subadults need to rest to conserve energy and avoid predators. As noted above, they move widely within and sometimes among connected riverine and lacustrine macrohabitats, with a strong preference for shallow-water, low-velocity settings (Bradford and Gurtin 2000; Mueller et al. 2000; Gurtin et al. 2003; Wydoski et al. 2010; Kesner et al. 2012; Valdez et al. 2012; Wydoski and Lantow 2012). They also may begin to exhibit some seasonal variation in their selection of macro and mesohabitats as resting sites within these ranges as recorded for adults (Minckley et al. 1991; Bradford and Gurtin 2000; Gurtin et al. 2003; Reclamation 2008; Valdez et al. 2012). Their ability to find resting sites depends on the interaction of a large number of factors, including turbidity, the availability of cover, and, initially, their lack of familiarity with their new environment (Minckley et al. 1991; Mueller et al. 2000; USFWS 2002a; Lee et al. 2006; Mueller 2006; Reclamation 2008; Bestgen et al. 2011, 2012).

7. *Swimming*: RASU repatriated subadults theoretically are able to swim large distances, including navigating within drift currents and avoiding threats. However, their stamina for such long-distance movement may be less initially following release than later (Mueller and Foster 1999; Ward and Hilwig 2004; Mueller et al. 2007; Kegerries and Albrecht 2009; Avery et al. 2011; Senger and Sjöberg 2011). Swimming may be solitary or in “schools” (see chapter 3), and the relative time spent dispersed (solitary swimming) or aggregated (schooling) may affect other activities and processes such as foraging and their vulnerability to predation, scientific handling, and other causes of stress. The effect of schooling on predation among repatriated RASU subadults may be exacerbated by surfacing behaviors developed at their rearing facilities, which may make the reared RASU more vulnerable to avian predators (Schooley et al. 2008).

8. *Thermal stress*: RASU repatriated subadults are vulnerable to stress due to changes in temperature beyond the range suitable for their maturation and engagement in many behaviors and may be more vulnerable initially than their wild-born cousins due to a lack of conditioning (Minckley et al. 1991; USFWS 1998; Mueller et al. 2005; Mueller 2006; Schooley et al. 2008; Reclamation 2008; Bestgen et al. 2011; Valdez et al. 2012). However, compared to earlier mobile life stages, they have a great ability

> to avoid potentially mechanically stressful conditions simply by swimming away – at least where circumstances (lack of confinement, small areas of unsuitability) allow such avoidance or escape.

The critical biological activities and processes that most strongly directly or indirectly influence survivorship among RASU repatriated subadults (see figure 14) are the same as those identified for RASU wild-born juveniles and subadults (life stage 5) discussed above. The levels of predictability and understanding identified for these relationships are also the same. The habitat elements that most strongly directly or indirectly influence survivorship among RASU repatriated subadults – and the levels of predictability and understanding identified for these relationships – are also the same as those identified for RASU wild-born juveniles and subadults, discussed above, *with one significant exception*.

The assessment identifies pre-release conditioning as exerting potentially medium-magnitude influence on predation, foraging, and swimming, with low scientific understanding and, consequently, unknown predictability. As noted in chapter 4, a growing literature base indicates that patterns of pre-release conditioning may shape survival among repatriated RASU (as among stocked fishes in general (Olson et al. 2012). The potential effects relate to six factors: (1) the familiarity of hatchery RASU with the presence and behaviors of predators, (2) the ability of aggregated RASU to alarm each other when alerted to the presence of a predator, (3) the ability of RASU to recognize and forage for the range of food items they would encounter outside the hatchery, (4) the strength of RASU to swim against a range of flow velocities, (5) the effects of aggregated surface feeding on vulnerability to avian predation, and (6) the effects of aggregation on predator detection and avoidance by entire schools of fish (Minckley et al. 1991; Mueller and Foster 1999; Mueller et al. 2000; USFWS 2002a; Mueller et al. 2003a; Ward and Hilwig 2004; Lee et al. 2006; Mueller 2006; Campbell et al. 2007; Mueller et al. 2007; Schooley et al. 2008; Reclamation 2008; Kegerries and Albrecht 2009; Avery et al. 2011; Senger and Sjöberg 2011; Bestgen et al. 2011, 2012). Additional investigations are underway (http://www.lcrmscp.gov/fish/fish_res_mon.html). The growing literature thus identifies – and the ongoing studies recognize – an important suite of hypotheses for testing. The potential impacts of pre-release conditioning on predation, foraging, and swimming all receive medium ratings for magnitude. This rating results from consistent ratings of "unknown" for link intensity, while link spatial and temporal magnitudes both receive high ratings. The literature is not sufficient to support a rating of how much impact pre-release conditioning has or could have on survivorship through its effects on predation, foraging, and swimming.

Finally, the assessment permits an analysis of the cumulative magnitude of impact of individual habitat elements that affect one or more of the four critical biological activities or processes that most strongly shape survivorship for this life stage. The following nine habitat elements have the highest cumulative magnitudes of impact. Eight of these nine are strongly influenced (high or medium magnitude) by one or more other habitat elements, and the list below identifies those with the highest impacts on the listed habitat element:

- Competitor activity
    - Habitat elements with the strongest influence on this element include predator activity, turbidity, and water temperature.
- Flow/turbulence
    - Habitat elements with the strongest influence on this element include macrohabitat geometry and mesohabitat geometry/cover.
- Macrohabitat geometry
    - The habitat element with high- or medium-magnitude influence on this element is flow/turbulence.
- Mesohabitat geometry/cover
    - The habitat element with the strongest influence on this element is macrohabitat geometry.
- Plankton-benthos-POM
    - Habitat elements with high- or medium-magnitude influence on this element include competitor activity, predator activity, substrate texture/dynamics, turbidity, water chemistry, and water temperature.
- Predator activity
    - Habitat elements with the strongest influence on this element include water temperature, competitor activity, mesohabitat geometry/cover, and turbidity.
- Pre-release conditioning
    - There are no habitat elements with a strong influence on this element.
- Turbidity
    - The habitat element with the strongest influence on this element is plankton-benthos-POM assemblage abundance and composition.

- Water temperature
    - The habitat element with the strongest influence on this element is depth.

The list of habitat elements with the highest cumulative influence on critical biological activities and processes for this life stage includes two (water temperature and flow/turbulence) that do not strongly directly influence the three critical biological activities or processes with the strongest impact on RASU repatriated subadult survivorship. However, these two habitat elements have low-magnitude effects on many of the other five critical biological activities and processes for this life stage, and the ranking here reflects this broader cumulative impact.

RASU LIFE STAGE 7 – ADULTS

Minckley et al. (1991), Mueller (2006), and Reclamation (2008) again summarize the understanding of adult RASU biology and ecology in LCR riverine and backwater environments up to 2008. Albrecht et al. (2010a), Bestgen et al. (2011, 2012), and Valdez et al. (2012) again provide additional information from both the LCR and UCRB. The adult RASU population of the LCR consists of a mix of wild-born and repatriated individuals that have made the transition from subadult status, defined here as reaching sexual maturity (roughly at size ≥400 mm TL). These adults continue to grow in size as they age. They forage heavily on benthos but, particularly in the lacustrine environments of the LCR, continue to feed on zooplankton as well, as summarized by Reclamation (2008). They use cover to avoid predators, rest, and possibly facilitate their preying on other organisms. They swim over large distances within and sometimes among river macrohabitats (e.g., within and between the flowing river segment above Lake Mohave and the Lake itself) (Kesner et al. 2012; Wydoski and Lantow 2012) and may use currents to facilitate this movement; prefer shallow-water, low-velocity mesohabitat settings; may use different macro and mesohabitats during different seasons; and presumably may be carried involuntarily only by the largest/strongest flow events/currents. Males may be territorial under some circumstances (Mueller 2006; Flamarique et al. 2006). Success during this life stage – successfully persisting over many years and periodically becoming ready to spawn – involves organism survival and continuing growth.

The CEM (figures 15 and 16) recognizes the same eight critical biological activities and processes for this life stage as for wild-born subadults, and they are presented here in alphabetical order:

Razorback Sucker (*Xyrauchen texanus*) (RASU)
Basic Conceptual Ecological Model

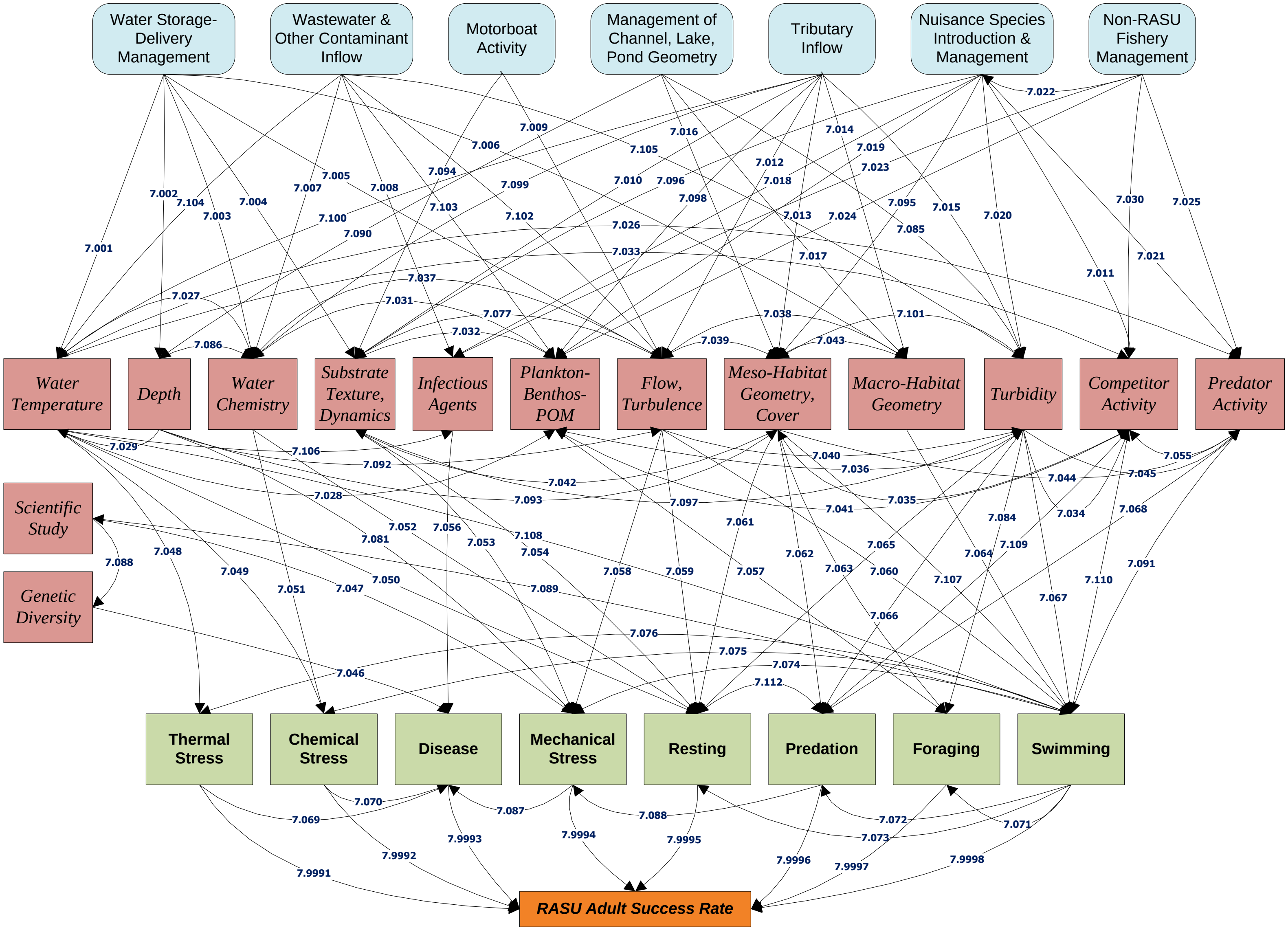

Figure 15.—RASU life stage 7 – adults, basic CEM diagram.

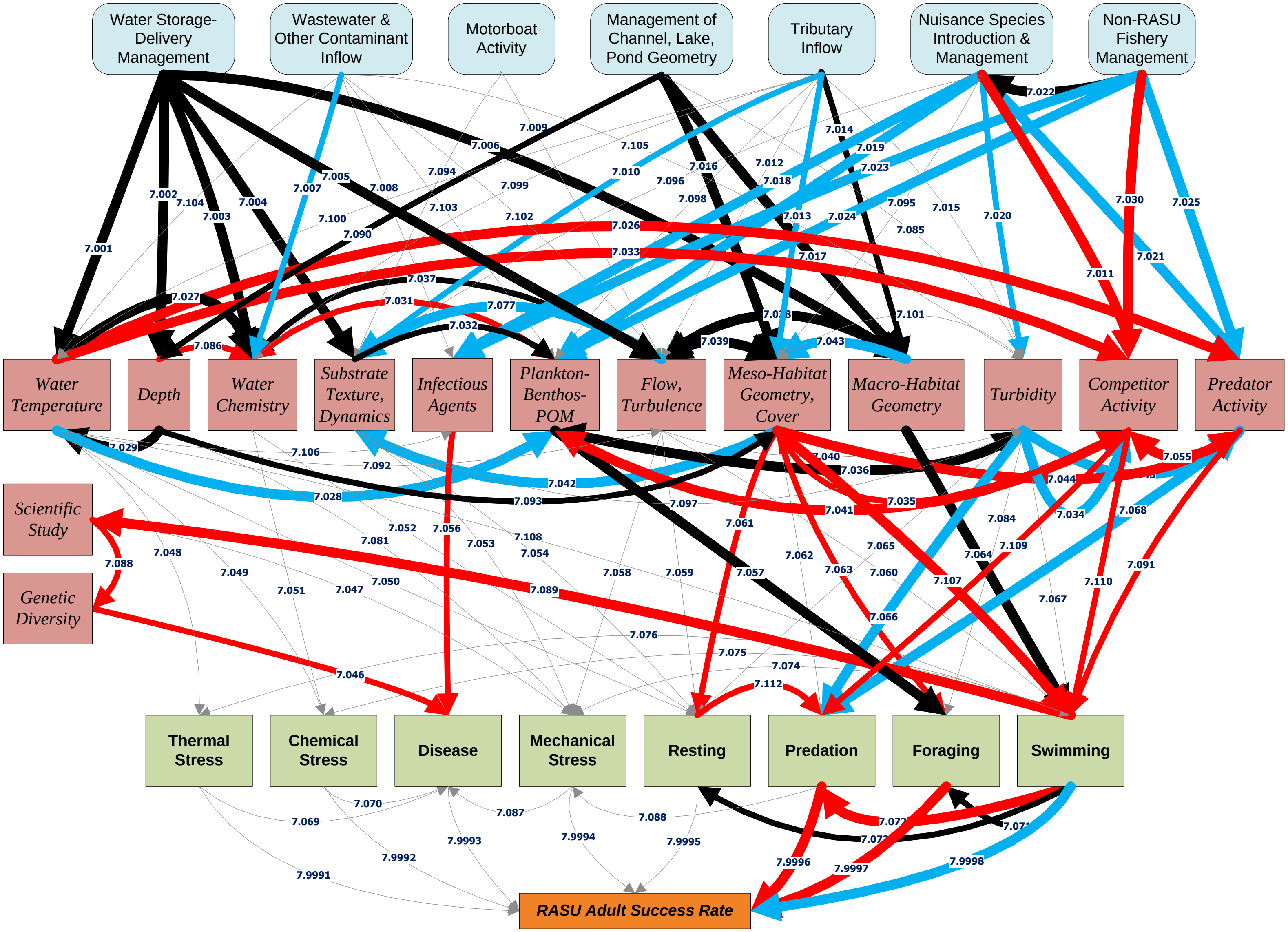

Figure 16.—RASU life stage 7 – adults, high- and medium-magnitude relationships.

1. *Chemical stress*: RASU adults are vulnerable to stress due to an insufficient supply of DO and exposure to harmful dissolved matter including contaminants, possibly including selenium (Hamilton et al. 2005b). However, they can remove themselves from settings in which they may sense unsuitable conditions – at least where circumstances (lack of confinement, small areas of unsuitability) allow such avoidance or escape.

2. *Disease*: RASU adults are vulnerable to stress and mortality due to infection, including that from parasites (Valdez 1990; Clarkson et al. 1997; Robinson et al. 1998; USFWS 1998, 2002a; Choudhury 2004; Mueller 2006; Marsh 1987; Ward et al. 2007; Ward and Finch 2009).

3. *Foraging*: RASU adults feed mostly on benthos and can target increasingly large invertebrates with agility and force due to their larger sizes (Marsh 1987; USFWS 1998, 2002a; Mueller 2006). The relative importance of zooplankton may vary depending on food availability in more lentic versus more lotic environments (Reclamation 2008).

4. *Mechanical stress*: RASU adults are vulnerable to physical stress – including outright physical destruction – due to habitat scour, burial, or exposure to the open air; entrainment in propeller wash and dam intakes; wounding from unsuccessful predator attacks; and handling during encounters with scientific sampling (Minckley et al. 1991; Mueller 2006; Hunt 2008; Hunt et al. 2012; Mueller et al. 2008; Reclamation 2008; Bestgen et al. 2012). However, compared to earlier mobile life stages, they have a great ability to avoid potentially mechanically stressful conditions simply by swimming away – at least where circumstances (lack of confinement, small areas of unsuitability) allow such avoidance or escape.

5. *Predation*: RASU adults are vulnerable to predation. Their large size and their habitat preferences presumably make them prey to a distinct but limited spectrum of large predators (Bozek et al. 1984; Minckley et al. 1991; USFWS 1998, 2002a; Bonar et al. 2002; Dowling et al. 2005; Mueller et al. 2005; Mueller 2006; Schooley et al. 2008; Reclamation 2008; Albrecht et al. 2010a; Bestgen et al. 2011, 2012; Karam and Marsh 2010). Kesner et al. (2012) also note that individuals >450 mm TL experience far higher rates of survival than individuals of any smaller size class and suggest that this shift reflects an effect of size on vulnerability to predation. As noted in chapter 5, the Colorado pikeminnow may have been the dominant predator on RASU in the Colorado River prior to introduction of numerous non-native predators and the decline of the pikeminnow. However, as noted earlier, pikeminnow predation on RASU is gape limited, with pikeminnow ignoring RASU larger than approximately 33–37 percent of the length of the predator once RASU

develop their characteristic dorsal keel at approximately 200 mm TL. As a result, adult RASU would have experienced little or no predation from pikeminnow in the historic/pre-historic Colorado River. The arrival of other large piscivorous fishes with different feeding behaviors, morphology, and gape limitations therefore necessarily has changed the predatory pressures on adult RASU. The increasing range of adult RASU movement among macrohabitats, the distances they travel among mesohabitats with cover, and the decline in overall turbidity along the LCR conceivably also may affect their vulnerability to predation.

6. *Resting*: RASU adults need to rest to conserve energy and avoid predators. As noted above, they move widely within and sometimes among connected riverine, backwater, and lacustrine reaches of the river (Mueller et al. 2000; Wydoski et al. 2010; Kesner et al. 2012; Wydoski and Lantow 2012) and exhibit some seasonal variation in their selection of macro and mesohabitats as resting sites within these ranges, with an overall preference for shallow-water, low-velocity settings (Minckley et al. 1991; Reclamation 2008). Their ability to find resting sites depends on the interaction of a large number of factors, including turbidity and the availability of cover (Minckley et al. 1991; Mueller et al. 2000; Mueller 2006; Reclamation 2008; Bestgen et al. 2011, 2012; Valdez et al. 2012).

7. *Swimming*: RASU adults are able to swim large distances, including navigating within flood currents and avoiding threats (see "Resting" in chapter 3). Swimming may be solitary or in "schools," and the relative time spent dispersed (solitary swimming) or aggregated (schooling) may affect other activities and processes such as foraging and (vulnerability to) predation, scientific handling, and other causes of stress.

8. *Thermal stress*: RASU adults are vulnerable to stress due to changes in temperature beyond the range suitable for their maturation and engagement in many behaviors (Minckley et al. 1991; USFWS 1998; Mueller et al. 2005; Mueller 2006; Reclamation 2008; Bestgen et al. 2011; Valdez et al. 2012). However, compared to earlier mobile life stages, they have a great ability to avoid potentially thermally stressful conditions simply by swimming away – at least where circumstances (lack of confinement, small areas of unsuitability) allow such avoidance or escape.

The critical biological activities and processes that most strongly directly or indirectly influence survivorship among RASU adults (see figure 16) are the same as those identified for RASU wild-born juveniles and subadults (life stage 5), discussed above. The levels of predictability and understanding identified for these relationships are also the same. The habitat elements that most strongly directly or indirectly influence survivorship among RASU adults – and the levels of predictability and understanding identified for these relationships – are nearly the same as those identified for RASU wild-born juveniles and subadults, discussed above. The two life stages differ in body size ranges, presumed strength and agility, food preferences, sexual maturity, and in the body sizes, life stages, and/or taxa of the species that prey on them. However, these differences have no effect on link magnitudes. The two life stages do differ more consequentially in the influence of macrohabitat geometry on swimming. Adult RASU travel over large distances, and the range of their movement thus strongly and predictably depends on the abundance and spatial arrangement of macrohabitat types across the system.

Finally, the assessment permits an analysis of the cumulative magnitude of impact of individual habitat elements that affect one or more of the four critical biological activities or processes that most strongly shape survivorship for this life stage. The following eight habitat elements have the highest cumulative magnitudes of impact. Each of the eight is strongly influenced (high or medium magnitude) by one or more other habitat elements, and the list below identifies those with the highest impacts on the listed habitat element:

- Competitor activity
    - Habitat elements with the strongest influence on this element include predator activity, turbidity, and water temperature.
- Flow/turbulence
    - Habitat elements with the strongest influence on this element include macrohabitat geometry and mesohabitat geometry/cover.
- Macrohabitat geometry
    - The habitat element with high- or medium-magnitude influence on this element is flow/turbulence.
- Mesohabitat geometry/cover
    - The habitat element with the strongest influence on this element is macrohabitat geometry.
- Plankton-benthos-POM
    - Habitat elements with high- or medium-magnitude influence on this element include competitor activity, predator activity, substrate texture/dynamics, turbidity, water chemistry, and water temperature.

- Predator activity
    - Habitat elements with the strongest influence on this element include water temperature, competitor activity, mesohabitat geometry/cover, and turbidity.
- Turbidity
    - The habitat element with the strongest influence on this element is plankton-benthos-POM assemblage abundance and composition.
- Water temperature
    - The habitat element with the strongest influence on this element is depth.

The list of habitat elements with the highest cumulative influence on critical biological activities and processes for this life stage includes two (water temperature and flow/turbulence) that do not strongly influence the three critical biological activities or processes with the strongest impact on RASU adult survivorship. These two habitat elements have low-magnitude effects on many of the other five critical biological activities and processes for this life stage, and the ranking here reflects this broader cumulative impact.

RASU LIFE STAGE 8 – SPAWNING ADULTS

Minckley et al. (1991), Modde and Irving (1998), USFWS (1998, 2002a), Mueller (2006), and Reclamation (2008) summarize the understanding of RASU spawning as of 2008. Schooley et al. (2008), Albrecht et al. (2010a, 2010b, Bestgen et al. (2011, 2012), Valdez et al. (2012), and others provide updates. The cumulative evidence reviewed in these publications indicates that some proportion of the adult population attempts to spawn every year, with males more numerous than females in the spawning aggregations. The spawning process involves three major steps, each with several elements: (1) the development of secondary sexual traits and ripening (development of mature gametes) in both sexes, (2) staging (assembling at/around spawning sites) by males weeks before individual females arrive to spawn, and (3) a series of interactions between males and females at the spawning site, including site preparation and the spawning act itself (Minckley et al. 1991; Modde and Irving 1998; USFWS 1998, 2002a; Mueller 2006; Reclamation 2008). Staging and spawning success depend on a single – although large – suite of habitat conditions and critical biological activities. The CEM therefore addresses “staging and spawning” together under a single heading, separate from “ripening.”

The cues that trigger individuals to become physiologically ready to spawn and move toward spawning sites are not well understood. Individuals participating in a spawning cycle presumably forage and use cover to aid foraging, avoid predators, and rest in the same manner as do RASU adults in general. However, foraging does not appear to be a priority. Mueller (2006) summarizes reports that RASU are frequently emaciated following participation in spawning, at which time they move to locations with substantial food resources (Mueller et al. 2000). Within the connected river-reservoir environment, RASU swim to and from their spawning sites over large scales limited only by the distribution of dams (Mueller et al. 2000; Albrecht et al. 2010a; Kesner et al. 2012; Wydoski and Lantow 2012). Adults moving to or from spawning sites presumably use currents to facilitate movement and presumably may be swept along involuntarily only by the largest/strongest flow events/currents. They also spawn within isolated ponds (Mueller 2006; Dowling et al. 2011; LCR MSCP biologists, personal communications, September 2013).

The spawning of RASU in isolated ponds, with non-riverine hydrologic regimes, in fact suggests that RASU can spawn without any cues from changes in depth or flow. They select spawning sites based on a suite of criteria (e.g., for substrate texture, depth, and flow) about which much uncertainty remains (Minckley et al. 1991; Modde and Irving 1998; USFWS 1998, 2002a; Mueller 2006; Reclamation 2008; Schooley et al. 2008; Albrecht et al. 2010a; Bestgen et al. 2011, 2012; Patterson et al. 2012; Valdez et al. 2012). Given the evidence for spawning in isolated ponds, however, the criteria may be fairly broad.

RASU reportedly exhibit fidelity to individual or limited sets of spawning sites (Tyus and Karp 1990; Modde and Irving 1998; Mueller et al. 2000; Wydoski et al. 2010; Wydoski and Lantow 2012). However, it is not known whether this is a matter of fidelity to the natal site or simply to a site at which an individual has successfully spawned in the past. Females may visit multiple sites (Mueller 2006), indicating that at least female fidelity is not specific to the natal site. Males may be territorial in the vicinity of spawning sites when ripe females are not present (Mueller 2006; Flamarique et al. 2006).

Spawning RASU may prepare sites for holding eggs by agitating the surface of the benthic substrate to remove fine sediment and/or by excavating nest-like depressions (Bozek et al. 1984; Minckley et al. 1991; Snyder and Muth 2004; Mueller 2006). However, these depressions are not actual nests (Minckley et al. 1991). Further, the dispersing of fine sediments and creation of depressions may be a secondary consequence of patterns of agitation associated with the spawning itself (see chapter 3). As noted for life stages 1 and 2, further, the agitation may also drive the eggs into the substrate.

Success for spawning adults involves their ripening, potentially triggered by environmental cues; presumably developing sufficient body mass to sustain spawning activity; detecting cues to move toward spawning sites, and surviving their journey to and from these sites; surviving during staging periods when not actively spawning; and engaging in and surviving during spawning itself. The CEM for this life stage differs significantly from the model for adult RASU in general, in three ways. First, the model for spawning adults recognizes seven critical biological activities and processes for this life stage that resemble those for adults in general but, in this case, exclusively concern spawning and movement to and from spawning sites. Second, the model for spawning adults recognizes two activities that apply to no other life stage: "ripening" and "staging and spawning," each of which may have its own triggering cues. Third, the model for spawning adults recognizes numerous causal relationships among its nine activities and processes, which affect the success of one central activity, "staging and spawning."

The CEM recognizes the following nine critical biological activities and processes for this life stage (figures 17 and 18), and they are listed here in alphabetical order:

1. *Chemical stress*: RASU spawning adults presumably are vulnerable to chemical stress due to conditions such as depleted DO levels and exposure to harmful dissolved matter, including contaminants, during the time they should be ripening, along their travel routes to and from spawning sites, and at the spawning sites themselves. They are vulnerable in the same manner as adult RASU in general (see "Life Stage 7 – Adults," above). They can remove themselves from settings in which they sense unsuitable conditions, although doing so could disrupt their ripening, staging, or spawning.

2. *Disease*: RASU spawning adults presumably are vulnerable to stress and mortality due to microbial infection during the time they should be ripening, along their travel routes to and from spawning sites, and at the spawning sites themselves. They are vulnerable in the same manner as adult RASU in general (see "Life Stage 7 – Adults," above).

3. *Foraging*: RASU spawning adults feed on a combination of benthos and zooplankton while ripening, along their travel routes to and from spawning sites, and at the spawning sites themselves when not actively engaged in spawning. As noted above, they often move from spawning sites directly to areas of concentrated algal food resources (as summarized by Mueller et al. 2000). The composition of their diet presumably is the same as that of adults in general (see "Life Stage 7 – Adults," above). However, reports that RASU appear emaciated following spawning (Mueller 2006) suggest that foraging is not a high priority activity for RASU over the course of the spawning cycle, following which the RASU replenish themselves at food-rich sites.

Razorback Sucker (*Xyrauchen texanus*) (RASU) Basic Conceptual Ecological Model

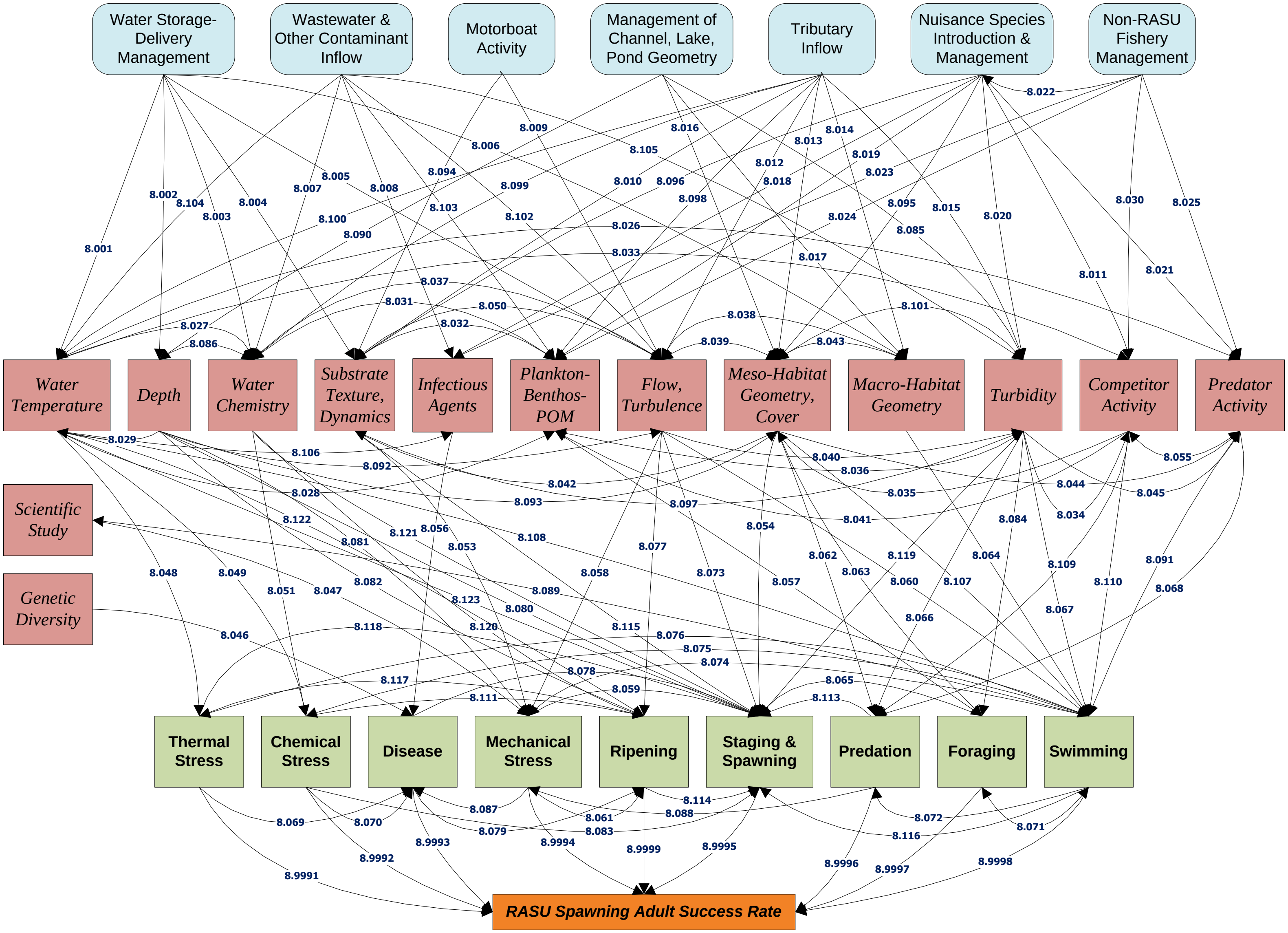

Figure 17.—RASU life stage 8 – spawning adults, basic CEM diagram.

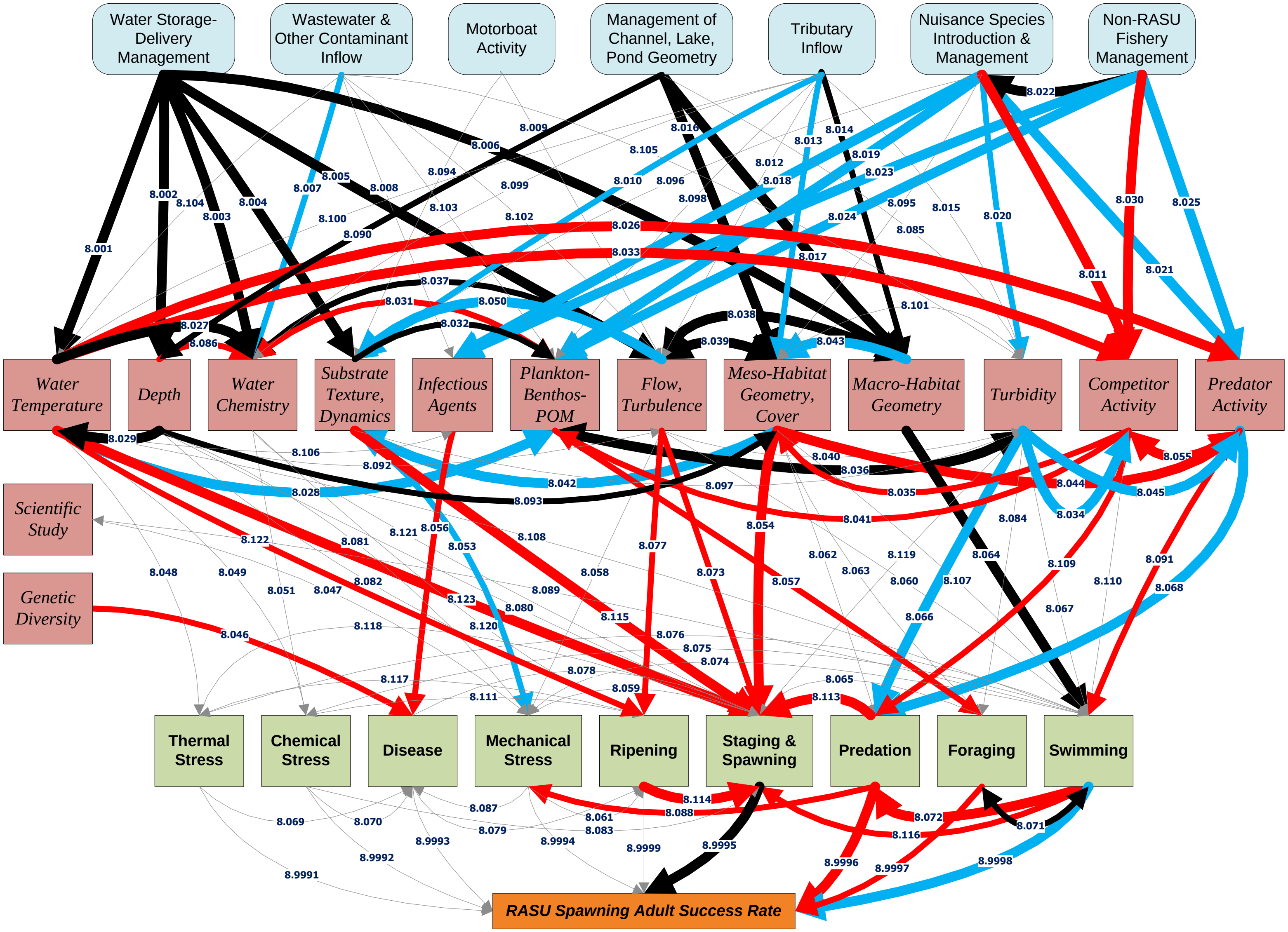

Figure 18.—RASU life stage 8 – spawning adults, high- and medium-magnitude relationships.

4. *Mechanical stress*: RASU spawning adults presumably are vulnerable to stress during the time they should be ripening, along their travel routes to and from spawning sites, and at the spawning sites themselves. The potential causes of such stress include flow velocities and turbulence in excess of tolerable ranges; scour, burial, or exposure; entrainment in propeller wash and dam intakes; wounding from unsuccessful predator attacks; and handling during scientific sampling. They presumably are vulnerable in the same manner as adult RASU in general (see "Life Stage 7 – Adults," above), although they may be more sensitive to disturbance than adults in general. For example, waves from storms may disrupt spawning activity even when not a hazard to individual health (Minckley et al. 1991). Indeed, spawning RASU can remove themselves from settings in which they sense unsuitable conditions, but doing so can disrupt staging or spawning.

5. *Predation*: RASU spawning adults presumably are vulnerable to predation during the time they should be ripening, along their travel routes to and from spawning sites, and at the spawning sites themselves. They presumably are vulnerable mostly in the same manner as adult RASU in general (see "Life Stage 7 – Adults," above), with their large size making them prey to a distinct but presumably limited spectrum of large predators. However, spawning adults may be more vulnerable to avian predation than are adult RASU in general because of the shallowness of staging areas and individual spawning sites (compare Minckley et al. 1991; Mueller 2006; Schooley et al. 2008). Further, it seems plausible that RASU moving toward spawning sites could be less cautious than at other times. Finally, it also seems plausible that emaciation over the course of a spawning cycle would make RASU more vulnerable to predation.

6. *Ripening*: RASU spawning adults presumably respond to cues in the water that trigger their ripening prior to participating in spawning aggregations, although the exact character of such cues is not well understood (Minckley et al. 1991; Modde and Irving 1998; USFWS 1998, 2002a; Mueller 2006; Reclamation 2008; Schooley et al. 2008; Albrecht et al. 2010a; Albrecht et al. 2010b; Bestgen et al. 2011, 2012; Patterson et al. 2012; Valdez et al. 2012). Individuals may exhibit external reproductive traits for many months without becoming ripe (Minckley et al. 1991). Nevertheless, ripening is a different state that is necessary for spawning, and for which other preconditions may in turn be necessary, presumably including the development of sufficient body mass to sustain spawning activity.

7. *Staging and spawning*: RASU adults presumably respond to cues that trigger staging for and participation in spawning. 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 in water levels, as well as general seasonal cues may continue to provide cues in the LCR (Minckley et al. 1991; Modde and Irving 1998; USFWS 1998, 2002a; Mueller 2006; Reclamation 2008; Schooley et al. 2008; Albrecht et al. 2010a, 2010b; Bestgen et al. 2011, 2012; Patterson et al. 2012; Valdez et al. 2012). Spawning of RASU in isolated ponds in refuges along the LCR, with non-riverine hydrologic regimes, indicates that RASU can spawn without any cues from changes in depth or flow (Mueller 2006; Dowling et al. 2011; LCR MSCP biologists, personal communications concerning Imperial Ponds, September 2013). In fact, the importance of the spring flow pulse in dispersing RASU larvae in the river prior to regulation (as discussed in the works cited immediately above) suggests a specific hypothesis: it seems reasonable that, under historic flow regimes, natural selection would have favored responses to cues that *anticipate* rather than coincide with the annual pulse so that the RASU could move into spawning position in time. By that reasoning, evolution would have favored cueing to temperature, seasonal light, or the very beginnings of the rising spring pulse flow. The evidence that RASU spawning in the LCR may precede or follow the timing of flood pulses, and take place in hydrologically isolated ponds, suggests that temperature (and perhaps other seasonal) cues dominate over hydrologic cues (Mueller 2006; Dowling et al. 2011; LCR MSCP biologists, personal communications concerning Imperial Ponds, September 2013). Whether pheromones are also involved in triggering readiness or participation in spawning is not known.

In addition to triggering cues, successful staging requires suitable sites for spawning, where suitability is determined by a suite of possible habitat conditions. However, as stated in chapter 2, 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; Reclamation 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 Imperial Ponds (LCR MSCP biologists, personal communications, September 2013). The understanding of substrate selection for spawning is complicated by a lack of quantitative information on substrates at spawning sites. The literature overwhelmingly uses only qualitative terms such as “cobble” and “gravel” (see review by Valdez et al. 2012) and lacks studies of the differences between sites selected versus ignored for spawning. The present document proposes the hypothesis that, prior to dam construction, natural selection favored behaviors that lead RASU to spawn on sites that most reliably allow for *both* embryo survival and the successful dispersal of RASU larvae into habitats suitable for their own survival and maturation (see life stages 1–4, above).

From this perspective, RASU spawning site selection would be expected to favor settings with the following three characteristics: (1) substrates with the right combination of particle sizes to receive and hold the eggs for embryo development, including a minimal presence of fine sediment or biological accretions that occlude pore spaces, and possibly also including characteristics that reduce visibility or accessibility of the eggs to benthic predators; (2) low exposure to flow conditions that would disturb the substrate or involve velocities or turbulence along the substrate surface in ways that would dislodge or bury the developing embryos and freshly emerged larvae; and (3) positioning along a flow path that can disperse motile larvae to suitable habitat for their continuing growth. Natural selection thus would favor spawning at sites with specific "goldilocks" mesohabitat characteristics: exposed to sufficient flows to keep the substrate relatively clean of fine sediment and biological accretions, but not sufficient to disturb larger (pebble and cobble) particles, and connected to the overall flow network, but not exposed to the most geomorphically disruptive flows.

Once they arrive at spawning sites, males may be territorial when ripe females are not present (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 summarized in chapter 3 (see Minckley et al. 1991). Mueller (2006) and Reclamation (2008) 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 ("convulsions" in the terms of Minckley et al. 1991) agitate the surface of the benthic substrate, thereby removing fine sediment and excavating nest-like depressions. This activity may also drive the freshly released eggs directly into the substrate (Mueller 2006). The literature does not indicate what specific cueing conditions trigger individual spawning events other than the arrival of a ripe female on the spawning grounds. The spawning act itself takes place during a time span of only a few seconds or minutes. Success presumably depends on the suitability of environmental conditions, including wave turbulence and substrate conditions (Minckley et al. 1991).

8. *Swimming*: RASU spawning adults swim long distances to reach and disperse from their spawning sites, navigating within flow currents and avoiding threats while en route (see "Life Stage 7 – Adults," above). As also noted for adults in general, this swimming could involve solitary movement or movement in "schools." The relative time spent dispersed (solitary swimming) or aggregated (schooling) may affect other activities and processes such as foraging and (vulnerability to) predation, scientific handling, and other causes of stress to individuals participating in a spawning cycle. In turn, RASU swimming behavior at the spawning sites affects the success of staging and spawning activities as noted above.

Reciprocally, the relative degree of solitary versus aggregated movement to and from staging areas may affect the effectiveness of different scientific methods for RASU detection and capture during this life stage and their survey designs.

9. *Thermal stress*: RASU spawning adults presumably are vulnerable to thermal stress during the time they should be ripening, along their travel routes to and from spawning sites, and at the spawning sites themselves (Valdez et al. 2012). They presumably are vulnerable in the same manner as adult RASU in general (see "Life Stage 7 – Adults," above). They can remove themselves from settings in which they sense unsuitable conditions, although doing so could disrupt their ripening, staging, or spawning.

The evaluation of causal linkage magnitude (see figure 18) indicates that, among the nine aforementioned critical biological activities and processes, only four directly affect the success rate for this life stage with high or medium magnitude: staging and spawning, predation, and swimming (with high magnitude) and foraging (with medium magnitude). This evaluation refers to the spawning adult success rate across all reaches of the LCR and in the wildlife refuges and other protected areas along the LCR managed as RASU habitat under the auspices of the LCR MSCP HCP.

The assessment also identifies three critical biological activities and processes that either exclusively or additionally have *indirect* effects on staging and spawning adult success with high or medium magnitude. (1) Swimming behaviors strongly indirectly affect staging and spawning adult success through their effects on predation (high magnitude) and on foraging and on staging and spawning (medium magnitude). Swimming agility and strength, and potential behaviors such as aggregation, help RASU avoid and escape predators; support foraging success; and allow RASU to locate and move to/from staging locations. (2) Predation strongly (high magnitude) affects staging success by determining the abundance of adults that reach and survive at the staging areas. And (3), ripening strongly affects spawning success (high magnitude) by determining the abundance of adults available to spawn.

The assessment indicates that the direct effects of staging and spawning, predation, foraging, and swimming on staging and spawning adult success, and the effects of ripening on staging and spawning, all warrant ratings of high for predictability. That is, their effects on staging and spawning adult success do not depend on the effects of other contingent factors. However, the assessment also indicates that the effects of swimming on foraging have low predictability. RASU spawning adults probably are as strong and agile as full-grown adults, to the extent that these conditions affect foraging; however, RASU engaged in spawning may not forage effectively, and this may affect their swimming strength. Mueller (2006) notes that adults immediately following spawning are often emaciated, indicating that foraging is not a priority during staging and spawning.

The assessment also rates the effects of swimming on predation during this life stage as having only medium predictability. Differences in swimming ability and strength among RASU spawning adults could have some effect on their success in avoiding or escaping predator attack. However, body size among RASU spawning adults could affect predation rates as noted for life stage 7 – adults. The effects of swimming behaviors on staging and spawning success receive a rating of "unknown" for predictability. RASU adult swimming behaviors presumably affect staging, in the ways RASU navigate to and from spawning sites, avoiding hazards and finding resting and foraging opportunities along the way. 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 at spawning sites congregate near the water surface, which could affect their vulnerability to avian predation). However, the literature does not specifically discuss such interactions, making it impossible to assess link predictability.

The assessment found no evidence that any of the other five critical activities and processes are altered in ways that significantly directly affect spawning adult success. Thermal stress, chemical stress, disease, and mechanical stress do not appear strongly linked to altered spawning adult success. However, the effects of such stressors could be invisible in the data because they would simply increase the vulnerability of RASU to mortality from other factors such as predation or starvation. As mentioned previously, data on external markers of stress (e.g., external deformities, eroded fins, lesions, and tumors – *aka* DELT anomalies) (Sanders et al. 1999) might provide a means for assessing rates of sublethal stress. The literature also does not identify altered ripening success as a factor affecting staging and spawning success. However, the topic does not appear to have received specific investigation.

This assessment of the relative impact of different biological activities and processes on spawning adult success comes with an important caveat: these are hypotheses based on the information provided in the literature and by LCR MSCP biologists. Two of the four direct linkages and three of the four indirect linkages between critical biological activities and processes and spawning adult success receive low scores for scientific understanding, indicating that understanding of the relationship is subject to wide disagreement or uncertainty in peer-reviewed studies from within the ecosystem of concern and in scientific reasoning among experts familiar with the ecosystem (see attachment A). For example, the literature suggests that predation on adults, and unsuccessful foraging, both shaped by the availability and proximity of habitat and by swimming behaviors, may be responsible for high rates of mortality in many settings (Minckley et al.

1991; Mueller 2006; Reclamation 2008; Albrecht et al. 2010a, 2010b). By implication, high rates of predation and unsuccessful foraging are implicated as affecting spawning adult success. However, these hypotheses have not received any formal testing. They are supported by evidence for successful survivorship in Lake Mead and some refuge ponds where the availability of suitable – and suitably proximate – resting habitat along with suitable densities of food appears to reduce vulnerability to predation and increase foraging success. However, RASU engaged in spawning may be indifferent to risks from predation: the shallow aggregation that occurs during spawning necessarily increases vulnerability to avian and perhaps other sources of predation. Similarly, the evidence of emaciation among post-spawning RASU (Mueller 2006) suggests that RASU engaged in spawning may be indifferent to foraging needs as well, and emaciation itself is a risk factor for predation. The assessment therefore rates the impacts of predation rates and foraging success on staging and spawning success as having low scientific understanding. Similarly, the assessment suggests a low rating for understanding for the relationship between ripening and staging and spawning. As noted above, the literature does not identify altered ripening success as a factor affecting spawning adult success, but the topic does not appear to have received any specific investigation.

The assessment identifies several habitat elements that directly and significantly (high or medium magnitude) support or limit rates of the four critical biological activities or processes with direct, high- and medium-magnitude impacts on spawning adult success. Specifically, the assessment identifies the following relationships with varying levels of predictability:

- The assessment indicates that the rate of predation strongly depends on (is directly influenced by, at a high magnitude) turbidity and predator activity and moderately depends on (medium magnitude) competitor activity.

    - The effect of turbidity on predation has high predictability through its effect on sight-feeding behavior among predators and sight-based avoidance behaviors among RASU. The effect also receives a medium score for scientific understanding, reflecting a general understanding of the interactions involved but a low understanding of which predators are affected and in what ways.

    - The effect of predator activity on predation has medium predictability due to the intervening effects of habitat conditions. This relationship also receives a medium score for scientific understanding, again reflecting a general understanding of the interactions involved but a low understanding of which predators are involved and in what ways.

  - The effect of competitor activity on predation has low predictability because the intensity of this relationship depends on what predators and what competitors are present and the degree to which these competitors offer attractive alternatives to RASU wild-born juveniles and subadults as prey. The low rating for understanding of this relationship reflects the low level of knowledge of which species compete with RASU at any life stage.

- The assessment indicates that the rate of foraging success among staging and spawning RASU strongly depends on the composition and abundance of the plankton-benthos-POM assemblage. The relationship between the composition and abundance of the plankton-benthos-POM assemblage and foraging success has high predictability. The only factor that might make it less predictable might be the taxonomic composition of the plankton, benthos, and POM if some non-native species were to increase at the expense of preferred food items. However, the relationship receives a low rating for scientific understanding, reflecting the low level of knowledge of how much priority RASU give to foraging while they participate in the spawning cycle, and therefore how much selectivity they exhibit in their foraging activity.

- The assessment indicates that the effectiveness of swimming behaviors during the ripening-staging-spawning cycle strongly depends on the abundance and proximity of macrohabitat types and moderately depends on predator activity.

  - The spatial distribution of macrohabitat types shapes the distribution of suitable spawning sites and the potential movement pathways available within and among river/lake reaches or pond areas for RASU adults traveling to/from spawning sites. This relationship appears to have high predictability because the distribution of macrohabitat features along the LCR and in its refuges is essentially fixed and unvarying.

  - RASU spawning adults have the ability to swim away from (avoid) predators. Doing so during spawning potentially could disrupt spawning activity. As a result, greater densities of predators encountered during this life stage could result in greater disruption of spawning activity. However, descriptions of spawning activity suggest that the participants are relatively heedless of the presence of threats. This relationship has an unknown level of predictability and a low level of scientific understanding due to a lack of studies of how RASU behave in response to the presence of predators or competitors.

- The assessment indicates that the success rate for staging and spawning is strongly shaped by mesohabitat geometry/cover, substrate texture/ dynamics, and water temperature; and moderately shaped by flow/turbulence.

    - Spawning RASU are assumed to select for a specific limited suite of mesohabitat types for spawning. They do not spawn "just anywhere," but do sometimes spawn on substrates unlike those that would have occurred naturally along the LCR, such as the boat ramp at Imperial Ponds (LCR MSCP biologists, personal communication, September 2013). Thus, spatially they may have some flexibility, but are assumed driven to find settings that meet some specific criteria in order to spawn during the narrow window of the spawning period. However, the flexibility exhibited by RASU in their selection of spawning site mesohabitat types makes it uncertain precisely what conditions are suitable for a spawning site. RASU do show fidelity to spawning sites, but this may indicate learned behavior rather than repeated selection of a site for its habitat qualities (Minckley et al. 1991; Mueller et al. 2000; Mueller 2006; Wydoski et al. 2010; Wydoski and Lantow 2012). The relationship therefore appears to have medium predictability but low understanding.

    - Successful staging requires suitable substrate conditions for spawning (see also "Gametes and Eggs" and "Embryos and Larvae"). As discussed above, this document proposes that the characteristics of spawning sites may be understood as an adaptation (product of evolutionary selection) to spawning on sites that most reliably allow for embryo survival and the successful dispersal of RASU larvae into habitats suitable for their own survival and maturation, with substrate stability and a suitable particle size distribution as critical elements of the optimal habitat. However, these relationships presently are poorly understood (Minckley et al. 1991; Modde and Irving 1998; USFWS 1998, 2002a; Mueller 2006; Reclamation 2008; Schooley et al. 2008; Albrecht et al. 2010a, 2010b; Bestgen et al. 2011, 2012; Patterson et al. 2012; Valdez et al. 2012). That is, the literature contains many observations of substrate conditions at spawning sites, but no systematic information on how these observed conditions differ from conditions at other sites that RASU ignore for spawning. Observations of RASU spawning on substrates unlike those they would have encountered in the natural system, such as the artificial boat ramp at Imperial Ponds (LCR MSCP biologists, personal communications, September 2013), further challenge knowledge of substrate preferences during spawning. Unfortunately, too, available descriptions of spawning site substrate use only qualitative terms such as "cobble" and "gravel" rather than quantitative measurements (see review by Valdez et al. 2012). Consequently, it is not yet possible to frame hypotheses concerning substrate selection for spawning in quantitative terms for testing.

The relationship between staging and spawning and substrate texture/dynamics therefore also appears to have medium predictability but low understanding.

  - Most discussions of the cues for 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 provide cues in the LCR (Minckley et al. 1991; Modde and Irving 1998; USFWS 1998, 2002a; Mueller 2006; Reclamation 2008; Schooley et al. 2008; Albrecht et al. 2010a; Albrecht et al. 2010b; Bestgen et al. 2011, 2012; Patterson et al. 2012; Valdez et al. 2012). Whether pheromones are also involved in triggering spawning is not known. This relationship appears to have low predictability and low scientific understanding, reflecting the strong lack of consensus on whether and how water temperatures trigger staging and spawning.

  - A change in water flow/turbulence conditions may be one of the cues that trigger staging, although water temperature and, perhaps, depth appear more likely to cue staging in the LCR (see above). On the other hand, excessive flow velocities or turbulence at staging/spawning sites can disturb spawning adults, potentially disrupting spawning activity temporarily or for the season. Further, RASU may select spawning sites in part based on their moderate flow velocities and lack of turbulence, and their spawning quite close to the substrate may minimize their exposure to potentially unsuitable flows or turbulence (see above). This relationship appears to have high predictability but low scientific understanding of the specifics involved.

- The assessment indicates that the success rate for ripening is moderately shaped by flow/turbulence and water temperature.

  - Theoretically, a change in water flow conditions may be one of the cues that trigger ripening, but the subject has not been investigated. Ripening takes place in isolated, hydrologically controlled ponds as well as in open environments, so flow conditions may not have a strong bearing on ripening. The relationship therefore receives low ratings for both predictability and scientific understanding.

  - Theoretically, a change in water temperature also may be one of the cues that trigger ripening. However, the literature presents no evidence concerning whether or how changes in water temperature, over a period of perhaps several months prior to the spawning season, directly trigger ripening. Individuals may exhibit external reproductive traits for many months without becoming ripe (Minckley et al. 1991); this indicates that sexual maturation and ripening are at least partially independent, making it difficult to determine what factors affect ripening. Water temperature might affect ripening only indirectly via effects on health and foraging success. The relationship therefore receives a rating of "unknown" for predictability and a low rating for scientific understanding.

The assessment also identifies several habitat elements that significantly but *indirectly* support or limit the rates of those critical biological activities or processes with high-magnitude impacts on survivorship for this life stage. Specifically, the assessment identifies the following relationships:

- Water temperature affects predator activity, competitor activity, and the composition and abundance of the plankton-benthos-POM assemblage (high magnitude).

- Competitor activity and predator activity affect each other with high magnitude. Predators on RASU may also prey on species that compete with RASU for food or habitat, and species that compete with RASU may also prey on them.

- Turbidity affects both predator activity and competitor activity with high magnitude.

- Mesohabitat geometry/cover affects predator activity with high magnitude because predators may use cover during their foraging, and RASU may use cover to avoid predators.

- Competitor activity affects mesohabitat availability (medium magnitude) when other species compete with RASU not just for food but also for habitat space.

- Macrohabitat geometry strongly shapes the abundance and spatial distribution of mesohabitat types.

- Competitor activity strongly shapes the composition and abundance of the plankton-benthos-POM assemblage, and reciprocally, the composition and abundance of the plankton-benthos-POM assemblage also strongly shapes competitor activity.

- Turbidity and the composition and abundance of the plankton-benthos-POM assemblage strongly shape each other. Plankton concentrations directly affect light penetration, and the depth of light penetration strongly affects the depth to which phytoplankton and periphyton may grow.

- Water chemistry and the composition and abundance of the plankton-benthos-POM assemblage reciprocally affect each other with medium magnitude. Water constituents may support or limit phytoplankton growth, golden alga blooms release toxins, and the invasive quagga and zebra mussels can directly affect DO concentrations.

- Substrate texture/dynamics moderately shapes the composition and abundance of the plankton-benthos-POM assemblage.

- Both flow/turbulence and mesohabitat geometry strongly shape substrate texture/dynamics, and flow/turbulence strongly shapes mesohabitat geometry and the abundance and spatial distribution of mesohabitat types. Flow/turbulence thus shapes substrate texture/dynamics directly as well as indirectly through its influence on mesohabitat conditions.

Among the direct and indirect causal relationships, through which habitat elements support or limit critical activities or processes, the assessment again rates roughly half as having low understanding in the literature. For example, as noted for earlier life stages, hypotheses concerning the influence of mesohabitat geometry/cover on predator activity or actual predation rates; swimming, resting, or drifting behaviors; or foraging rates have not received detailed consideration, let alone formal testing. Hypotheses concerning which species prey on or compete with RASU spawning adults, how the ecology (e.g., habitat preferences) of these species interacts with the ecology of RASU spawning adults, and whether RASU spawning is affected by predator and competitor activity have not been subjected to detailed discussion or analysis.

Finally, the assessment permits an analysis of the cumulative magnitude of impact of individual habitat elements that affect critical biological activities or processes for this life stage. Across the five critical biological activities and processes for this life stage with the strongest direct or indirect impact on spawning adult success, the following nine habitat elements have the highest cumulative magnitudes of impact. Each of these nine is strongly influenced (high or medium magnitude) by one or more other habitat elements, and the list below identifies those with the highest impacts on the listed habitat element:

- Competitor activity
    - Habitat elements with the strongest influence on this element include predator activity, turbidity, and water temperature.
- Flow/turbulence
    - Habitat elements with the strongest influence on this element include macrohabitat geometry and mesohabitat geometry/cover.
- Macrohabitat geometry
    - The habitat element with high- or medium-magnitude influence on this element is flow/turbulence.
- Mesohabitat geometry/cover
    - The habitat element with the strongest influence on this element is macrohabitat geometry.
- Plankton-benthos-POM
    - Habitat elements with high- or medium-magnitude influence on this element include competitor activity, predator activity, substrate texture/dynamics, turbidity, water chemistry, and water temperature.
- Predator activity
    - Habitat elements with the strongest influence on this element include water temperature, competitor activity, mesohabitat geometry/cover, and turbidity.
- Substrate texture/dynamics
    - Habitat elements with the strongest influence on this element include flow/turbulence and mesohabitat geometry/cover.
- Turbidity
    - The habitat element with the strongest influence on this element is plankton-benthos-POM assemblage abundance and composition.
- Water temperature
    - The habitat element with the strongest influence on this element is depth.

Chapter 7 – Effects of Controlling Factors on Habitat Elements

Each of the 7 controlling factors discussed in chapter 5 directly affects some of the 16 habitat elements as show in table 5. The influence of these controlling factors is the same across all life stages for which those habitat elements matter. Table 7 shows the magnitudes of *direct* influence of the seven controlling factors on the 16 habitat elements. The structure of table 7 is the same as for table 5, but shows the magnitudes of the relationships instead of just their presence/absence. The paragraphs following the table discuss the relative effects of the different controlling factors on each habitat element.

Table 7.—Magnitude of influence of controlling factors on habitat elements

Controlling factor ➔ **↓ Habitat element affected**	**Management of channel, lake, pond geometry**	**Motorboat activity**	**Non-RASU fishery management**	**Nuisance species introduction and management**	**Tributary inflow**	**Wastewater and other contaminant inflow**	**Water storage-delivery management**
Competitor activity			**High**	**High**			
Depth	**Med.**						**High**
Flow/turbulence		**Low**			**Low**	**Low**	**High**
Genetic diversity	*(n/a)*						
Infectious agents			**High**	**High**		**Unk.***	
Macrohabitat geometry	**High**				**Med.**		**High**
Mesohabitat geometry/cover	**High**			**Low**	**Med.**		
Plankton-benthos-POM			**High**	**High**	**Low**	**Low**	
Predator activity			**High**	**High**			
Pre-release conditioning	*(n/a)*						
Scientific study	*(n/a)*						
Substrate texture/dynamics		**Low**		**Low**	**Med.**		**High**
Transport/release	*(n/a)*						
Turbidity	**Low**			**Med.**	**Low**	**Low**	
Water chemistry					**Low**	**Med.**	**High**
Water temperature					**Low**	**Low**	**High**

* "Unknown" (insufficient information to assess).

COMPETITOR ACTIVITY

Two controlling factors – non-RASU fishery management and nuisance species introduction and management – strongly shape competitor activity. Both relationships have high-impact magnitudes. However, both relationships also have low ratings for scientific understanding, reflecting the lack of systematic studies of which species – at which stages in their life cycles – may compete with RASU at different stages in its life cycle for food and/or habitat.

DEPTH

Water depths along the LCR and in its refuges is strongly shaped by water storage-delivery management, and moderately shaped by the management of channel, lake, and pond geometry. The lower rating for impact magnitude for the latter relationship reflects the fact that areas of active dredging along the channel, and dredging/shaping of refuge ponds, are spatially limited and only moderately frequent (LCR MSCP biologists, personal communications, April–September 2013). Both relationships have ratings of high for scientific understanding, reflecting the high level of knowledge and monitoring of water management and dredging operations and their effects on depths across the system.

FLOW/TURBULENCE

The locations and magnitudes of water flow volumes, velocity fields, and turbulence fields along the LCR and in its refuges are strongly shaped by water storage-delivery management for the many reasons presented in chapter 5. Motorboat activity, tributary inflow, and wastewater inflow have much more localized impacts and therefore receive ratings of low for magnitude. The impacts of water storage-delivery management and tributary inflow have high ratings for scientific understanding, reflecting the high level of knowledge and monitoring of water management across the system. The major tributary inflows – from the Virgin, Muddy, Bill Williams, and Gila Rivers – are all highly regulated. The impacts of motorboat activity and wastewater inflow have low ratings for scientific understanding, reflecting the lack of specific studies of their impacts.

INFECTIOUS AGENTS

Infectious agent diversity and abundance are shaped strongly by two controlling factors – non-RASU fishery management and nuisance species introduction and management. Both effects have high-impact magnitudes. Both also have medium ratings for scientific understanding, reflecting the relatively paucity of studies of which species may infect RASU at different stages in their life cycle. Conceivably, wastewater and other contaminant inflow may also affect the diversity and abundance of infectious agents in the system. However, this last relationship has not been studied and so receives a rating of "unknown" for magnitude and a low rating for scientific understanding.

MACROHABITAT GEOMETRY

Water storage-delivery management and management of channel, lake, and pond geometry have high-magnitude effects on the distribution and abundance of different macrohabitats along the LCR and in its refuges. Tributary inflow also affects the distribution and abundance of different macrohabitats along the LCR, with medium magnitude, because the tributary confluences constitute distinct macrohabitats. All three relationships have ratings of high for scientific understanding, reflecting the high level of knowledge and monitoring of water management, dredging operations, and tributary inflows and their effects on the overall geometry of the system, including its refuges.

MESOHABITAT GEOMETRY/COVER

Management of channel, lake, and pond geometry affects the distribution and abundance of different mesohabitats and the types and densities of cover along the LCR, and in its refuges, with high magnitude. Tributary inflow also affects the distribution, abundance, and cover characteristics of different mesohabitats along the LCR, with medium magnitude, because the tributary confluences constitute distinct macrohabitats that incorporate distinct sets of mesohabitats. Nuisance species introduction and management also affects – with low magnitude – the distribution, abundance, and cover characteristics of different mesohabitats along the LCR. This last relationship recognizes that some nuisance species can alter mesohabitat conditions. For example, Phragmites can alter cover in shallow-water and wetland settings, quagga and zebra mussel beds can completely cover benthic surfaces, and filtering by these two mussel species potentially can increase water clarity, allowing more growth of emergent macrophytes across a given shallow-water setting (see chapter 5). These three relationships receive ratings of, respectively, high, medium, and low for scientific understanding, reflecting the different levels of knowledge available for each.

PLANKTON-BENTHOS-POM

Non-RASU fishery management and nuisance species introduction and management have strong impacts on the composition and abundance of plankton, benthic organisms, and POM along the LCR and in its refuges. The introduction and management of sport fishery species affects LCR plankton, benthos, and POM because the introduced species may consume plankton, benthos, or POM, or they may prey on species that do. In turn, the introduction and management of nuisance species affects LCR plankton, benthos, and POM in three ways: (1) the introduced species may become members of the plankton, benthos, or wetland vegetation communities along the LCR; (2) the introduced species may consume plankton, benthos, or POM as do, for example, the filter-feeding zebra and quagga mussels; and (3) management activities to control nuisance species may involve the use of biocides or mechanical removal that also affect other organisms within the plankton, benthos, or wetland vegetation communities. Two other controlling factors have low-magnitude impacts on this habitat element: tributary inflow and wastewater and other contaminant inflow. Both of these factors introduce POM, and affect water chemistry, which in turn affects planktonic and benthic productivity. All four relationships receive ratings of medium for scientific understanding because such impacts are widely known in other freshwater ecosystems, but simply have not been studies specifically in the LCR.

PREDATOR ACTIVITY

Predator activity is shaped strongly by two controlling factors, as discussed in chapter 5: non-RASU fishery management and nuisance species introduction and management. Both relationships have high-impact magnitudes. Both relationships also have ratings of medium for scientific understanding, reflecting the need for more systematic studies of which species – at which stages in their life cycles – may prey on RASU at different stages in its life cycle.

SUBSTRATE TEXTURE/DYNAMICS

Water storage-delivery management strongly shaped substrate texture/dynamics along the LCR. Most dams trap sediment unless managed to allow for pulses of sediment releases, and the dams along the LCR are not managed to allow sediment transport. They thus strongly affect sediment availability and particle sizes along the LCR (Reclamation 2004). In turn, the hydrologic isolation of many of the refuges from the main stem river prevents any river-transported sediment from affecting substrates within those refuges. Tributary inflow has a medium-magnitude influence. As noted above, the vast majority of the water flowing through the LCR originates upstream in the UCRB, but the LCR also receives water from its own natural tributaries, including the Virgin, Muddy, Bill Williams, and Gila Rivers. The first two flow into Lake Mead, the Bill Williams into Lake Havasu, and the Gila River into the Colorado at Yuma, Arizona. All these tributaries are highly regulated, but nevertheless contribute sediment to their respective confluence reaches, creating/sustaining deltas and affecting sediment particle size distributions and dynamics in and near these deltas. The medium rating for magnitude recognizes the limited spatial distribution of these deltas. These two relationships receive ratings of high and medium, respectively, for scientific understanding, reflecting the high level of knowledge of the effects of dams and other water control infrastructure on sediment management, and intermediate level of knowledge concerning sediment dynamics at tributary confluences.

Motorboat activity and nuisance species also affect – with low magnitude – substrate dynamics. Turbulence from intensive boating activity in areas of shallow depths, and boat grounding in such settings, could disturb substrate sediments. If nuisance species such as quagga and zebra mussel – or a biofilm-forming species – colonize an area at sufficient density, they will change substrate stability and texture (see "Mesohabitat Geometry/Cover," above). These latter two relationships receive ratings of medium and low for scientific understanding, respectively, reflecting the level of knowledge of the two topics in the LCR.

TURBIDITY

No controlling factor within the LCR has a direct, high-magnitude impact on turbidity in the present system. Sediment dynamics strongly controlled turbidity in the LCR prior to regulation, but the near-elimination of sediment transport by the dams of the Colorado River (see above) has choked off this source of variation in turbidity. On the other hand, nuisance species introduction and management has a medium-magnitude direct impact. This latter relationship results from three processes: (1) the introduced species may be organic sources of turbidity in the form of, for example, algal blooms or particulate plant matter; (2) the introduced species may consume organic sources of turbidity, for example, as do the filter-feeding zebra and quagga mussels; and (3) management activities to control nuisance species may involve the use of biocides or mechanical removal that also affect other organisms that affect turbidity in the areas of these management activities. However, these impacts are also likely small compared to the overarching impacts of the dams in preventing transport of suspended sediment and the impacts of lake chemistry on primary productivity within the LCR waters and along its shores. This relationship receives a rating of medium for scientific understanding, reflecting the fact that such interactions are well known elsewhere, but have not been studied specifically along the LCR.

Water storage-delivery management, tributary inflow, and wastewater and other contaminant inflow have low-magnitude direct impacts on turbidity. Channel, shoreline, and pond management activities such as dredging, bank maintenance, etc., disturb sediment in ways that can produce localized turbidity that disperses with distance from the location of the activity. The HCP specifically recognizes this as one of the ways in which Federal actions may routinely affect RASU (Reclamation 2004). Tributaries provide the only remaining natural inputs of suspended sediment to the LCR and therefore produce zones of distinct turbidity at their immediate confluences whenever they are flowing. Concentrated wastewater inflows, such as from Las Vegas Wash, carry their own loads of suspended particulate matter (turbidity) to the main stem LCR. All three relationships receive ratings of high for scientific understanding.

WATER CHEMISTRY

Water storage-delivery management has a high-magnitude impact on water chemistry throughout the system. Water released from dams often comes from a single thermal layer in the upstream reservoir, either the epilimnion or the hypolimnion, each of which has a unique chemistry that in turn affects water chemistry for some distance below each dam. For example, hypolimnetic water typically has little or no DO and contains metal ions that are soluble in such anoxic conditions but are insoluble in fully oxygenated water where they are oxidized (Reclamation 2004). Groundwater pumped into hydrologically disconnected ponds similarly arrives with a distinctive water chemistry that shapes the overall chemistry of the affected pond. This relationship receives a rating of high for scientific understanding, because the principles are well understood and the system well monitored.

Wastewater and other contaminant inflow has a medium-magnitude impact on water chemistry along the river and its impoundments. As noted above (see chapter 5), the LCR receives inputs directly from municipal wastewater systems, most notably from Las Vegas via Las Vegas Wash, and diffuse wastewater input, for example, from the septic systems of Lake Havasu City. Finally, non-point source pollution, including via irrigation return flows and storm runoff from individual sites of chemical contamination, bring additional contaminants into the river. Perchlorate contamination from an industrial site near Las Vegas is perhaps the most widely mentioned site contributing non-municipal contamination, and irrigation inputs of selenium from the UCRB also are commonly noted (Seiler et al. 2003; Reclamation 2004; Hamilton et al. 2005a, 2005b; Sanchez et al. 2005; Reclamation 2005; Acharya and Adhikari 2010a, 2010b; Reclamation 2010; Adhikari et al. 2011; Turner et al. 2011; Reclamation 2011a, 2011b; Stolberg 2009, 2012). This relationship receives a rating of medium for scientific understanding because, although the principles for understanding contaminant transport and fate are well established in general, there are gaps in understanding the sources, transport, fate, and possible biological effects of some contaminants specifically in the LCR.

Finally, tributary inflow has a low-magnitude impact on water chemistry along the river and its impoundments. Tributary inflows necessarily carry their own loads of dissolved substances to the main stem LCR, including contaminants. However, the effects are likely brief, spatially limited, and unpredictable due to the high variability in precipitation across the basin, and they have not been specifically studied.

WATER TEMPERATURE

Water storage-delivery management has a high-magnitude impact on water temperature throughout the system. Water released from dams often comes from a single thermal layer in the upstream reservoir, either the epilimnion or the hypolimnion, each of which has a unique temperature spectrum that in turn affects water temperatures for some distance below each dam (Reclamation 2004). Groundwater pumped into hydrologically disconnected ponds similarly arrives with a distinctive range of water temperatures that shapes the pattern of temperature variation in the affected pond. This relationship receives a rating of high for scientific understanding because the principles are well understood and the system well monitored.

Wastewater and other contaminant inflow has a low-magnitude impact on water temperature along the river and its impoundments. As noted above (see chapter 5), the LCR receives inputs directly from municipal wastewater systems, most notably from Las Vegas via Las Vegas Wash. The thermal impacts of these inflows will be spatially highly localized and vary with inflow volumes. Tributary inflow also has a low-magnitude impact on water temperature along the river and its impoundments. Tributary inflows necessarily affect water temperatures at and around their confluences. However, the effects are likely brief, spatially limited, and unpredictable due to the high variability in precipitation across the basin, and they have not been specifically studied. Both these latter relationships receive ratings of high for scientific understanding because the principles are well understood and the system well monitored.

Chapter 8 – Discussion and Conclusions

This chapter summarizes the findings of the assessment in three ways by posing three questions: (1) which critical biological activities and processes most strongly affect the individual life stages across all life stages; (2) which habitat elements, in terms of their abundance, distribution, and quality, most strongly affect the most influential activities and processes; and (3) which of these causal relationships appear to be the least understood in ways that could affect their management?

MOST INFLUENTIAL ACTIVITIES AND PROCESSES ACROSS ALL LIFE STAGES

Figure 19 identifies the critical biological activities and processes that the assessment found most strongly directly or indirectly affect the success of each life stage (high or medium magnitude). The findings presented in this diagram may be summarized as follows:

- The rate of predation strongly affects the success rate of every life stage. This is consistent with the literature on RASU, which overwhelmingly identifies or hypothesizes that predation (mostly by non-native piscivorous fishes) is the leading cause of their population decline. The rate of predation is indirectly affected by other critical biological activities in most life stages. The duration of exposure of eggs above the substrate and the effectiveness of spawning agitation in driving eggs into the substrate both affect the vulnerability of RASU eggs to predation. A range of swimming behaviors among larvae, juveniles, subadults, and adults affects predation, as do aspects of larval drifting, as discussed below. The ability of larval and more mature RASU to find resting locations with suitable cover and other forms of concealment also affect predation rates.

- The rate of foraging success moderately or strongly affects the success rate of all six mobile life stages. This is consistent with numerous suggestions that, while poor foraging success may affect RASU in some settings, possibly shaped by the presence of numerous competitors, the availability of suitable foods for RASU in fact remains one of the positive conditions in the LCR – a counterweight to other stressors. Foraging success in turn depends on the ability of RASU to swim to settings with suitable forage and on their ability to forage for increasingly large invertebrates as they mature. The apparently lowered priority that spawning RASU give to foraging may make them vulnerable to other threats such as predation.

Razorback Sucker (*Xyrauchen texanus*) (RASU) Basic Conceptual Ecological Model

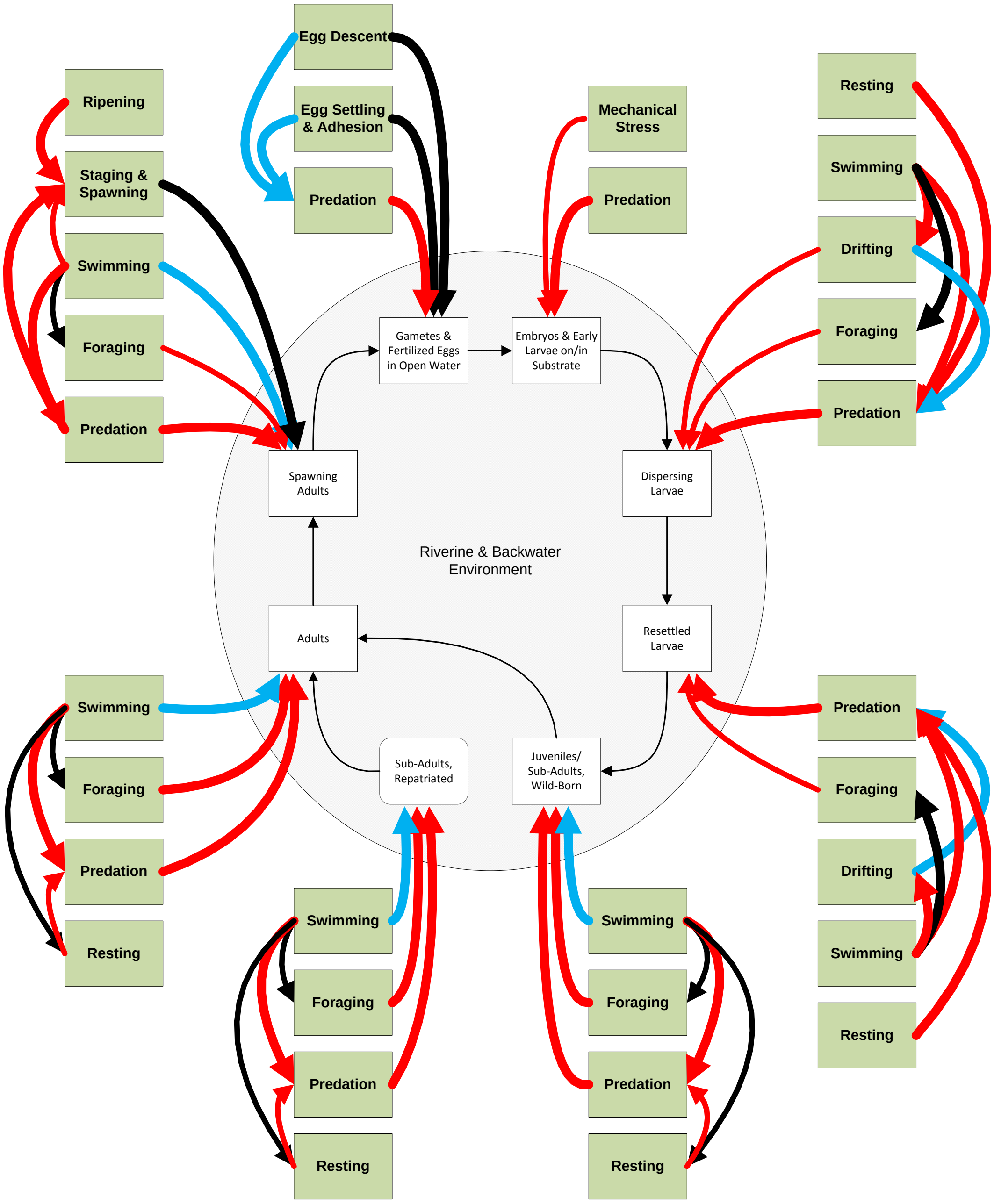

Figure 19.—Most influential biological activities and processes affecting each life stage.

- The effectiveness of swimming behaviors in allowing RASU to navigate among habitats and avoid predation strongly affects the success rate for all juveniles, subadults, and adults, including during spawning, in both positive and negative ways. The dams along the river and the restricted sizes of the off-channel refuges do restrict the range of RASU movement within the system. However, the assessment indicates that neither RASU development nor reproduction are limited by their confinement to smaller swimming ranges than they experienced prior to river regulation. Further, RASU of every mobile life stage appear to possess a range of swimming capabilities that help them avoid predators, although these behaviors may sometimes be compromised by the lower turbidity and lack of opportunities to take cover in the present-day system. On the other hand, RASU rearing in hatcheries prior to repatriation may result in their learning behaviors, such as surface congregation for feeding, that increase their vulnerability to predation after release or result in their not learning crucial predator avoidance behaviors or not acquiring adequate swimming stamina before release.

- The rate of occurrence of mechanical stress moderately affects the success of embryo and protolarval development on/in the substrate at spawning sites. The literature identifies mechanical disturbance of spawning sites during embryo development as a risk factor for the embryos due to the possibility of storm-driven turbulence and changes in water levels along the river. However, it is not clear whether the range of variation in such conditions in the present system lies outside the natural range of variation.

- The dynamics of drifting moderately affect the success rate for dispersing larvae. RASU larvae reach nursery habitats largely by drifting, at least in the river and its reservoirs. RASU larvae today may confront longer drift pathways, with lower turbidity, and fewer settings with suitable shelter/cover, resulting in greater exposure to predation and possibly poorer forage. Drift pathways along the river and its reservoirs also may simply not deliver the larvae to suitable nursery habitat.

- Finally, the CEM indicates that the rates of success of egg descent and egg settling/adhesion strongly affect the success rate for gametes and eggs in the open water essentially by definition. The rate of ripening strongly affects the rate of success of staging/spawning, and the rate of success of staging/spawning strongly affects the success rate for spawning, again essentially by definition.

These findings are noteworthy for what they do not include: the assessment does not identify disease, chemical stress, or thermal stress as significant factors affecting RASU survivorship and reproduction. The literature presents clear evidence of egg mortality due to infection (e.g., fungal infections) (Mueller 2006) and of parasitization of RASU, but does not indicate that these conditions play any significant role in RASU survivorship. The literature on parasites, in fact, specifically reports that adult RASU live with parasite infestations without obvious impairment, and while the earlier literature on RASU endangerment often posited that chemical or thermal stress could be contributing factors, the evidence at least from the LCR and its refuges does not support this hypothesis for the present-day system. Chemical stress from exposure to golden algal toxin could become a problem in the future.

POTENTIALLY PIVOTAL ALTERATIONS TO HABITAT ELEMENTS

Figure 20 identifies the habitat elements that the assessment indicates most strongly directly or indirectly affect the critical biological activities and processes identified on figure 19 across all life stages (high or medium magnitude). The findings presented in this diagram may be summarized as follows:

- Mesohabitat geometry/cover directly strongly or moderately influences 6 of the 10 most influential critical biological processes or activities. It directly shapes site suitability as spawning, resting, and foraging habitat; provision of cover for avoiding predation; drifting and swimming distances among habitats; and the likelihood of encounters with potential competitors and predators. Mesohabitat conditions, in turn, affect local flow patterns within macrohabitats; substrate texture and stability; and the spatial distribution of predators and competitors, all habitat elements that have their own direct impacts on various critical biological processes and activities.

- Flow/turbulence also directly strongly or moderately influences 6 of the 10 most influential critical biological processes or activities at multiple spatial scales. At the scale of individual spawning sites, it directly affects the suitability of sites for spawning and the likelihood of successful egg descent and settling/adhesion and mechanical stress to embryos following adhesion. At larger spatial scales, it shapes drift pathways for dispersing larvae, and at the largest scales may contribute to the triggering of reproductive ripening and staging. Flow/turbulence at multiple spatial scales also shape macro- and mesohabitat distributions and abundance, water chemistry (through effects on mixing), and the spatial distribution of different types of substrates, all habitat elements that have their own direct or indirect impacts on various critical biological processes and activities.

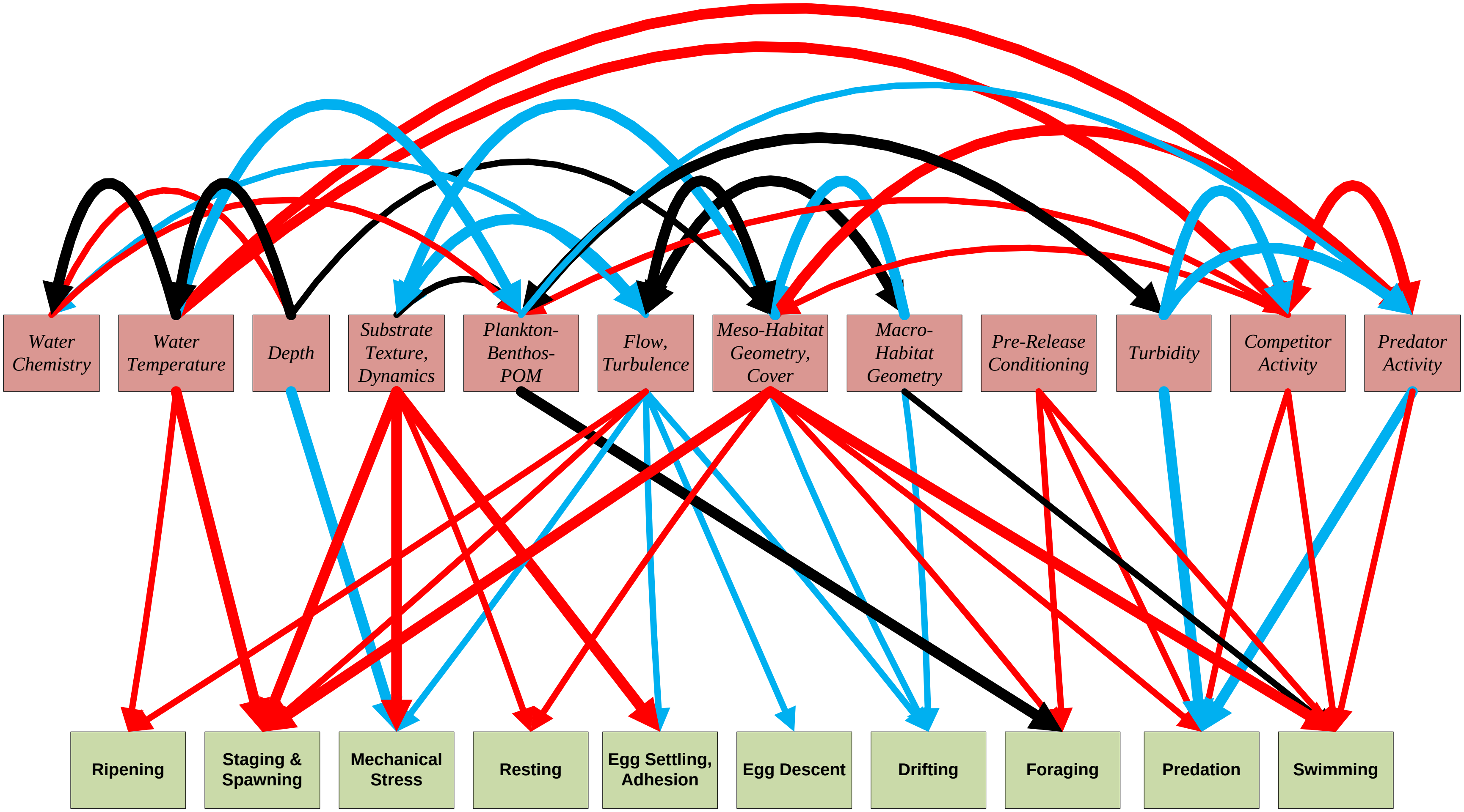

Figure 20.—Habitat elements that directly or indirectly affect the most influential biological activities and processes across all life stages.

- Substrate texture/dynamics strongly or moderately influence 4 of the 10 most influential critical biological processes or activities at the scale of individual habitat sites. It directly affects the suitability of sites for spawning, egg settling/adhesion, and embryo development, and it shapes the suitability of resting sites for all mobile life stages. Substrate texture/dynamics also shape local patterns of flow/turbulence at individual spawning and resting sites, and the suitability of sites for supporting different assemblages of benthic organisms, all habitat elements that have their own direct impacts on various critical biological processes and activities.

- Pre-release conditioning strongly or moderately influences 3 of the 10 most influential critical biological processes or activities, specifically for life stage 6 – repatriated subadults: foraging behaviors, swimming behaviors, and predator avoidance.

- Water temperature strongly or moderately influences 2 of the 10 most influential critical biological processes or activities, specifically for life stage 8 – spawning adults. In this life stage, changes in water temperature may provide crucial cues for adult reproductive ripening and for participation in spawning itself. Water temperature or its pattern of variation over time and space also shapes plankton and benthos biological activity, and activity levels of competitors and predators, all habitat elements that have their own direct impacts on various critical biological processes and activities. Finally, water temperature shapes water chemistry, which in turn affects several habitat elements with direct impacts on various critical biological processes and activities.

- Macrohabitat geometry also strongly or moderately influences 2 of the 10 most influential critical biological processes or activities. Specifically, it directly shapes drifting and swimming distances among habitats. The spatial distribution of different macrohabitat types, in turn, affect flow patterns among macrohabitats and the spatial distribution and abundance of different mesohabitat types, both habitat elements that have their own direct impacts on various critical biological processes and activities.

- Competitor activity and predator activity both strongly or moderately influence 2 of the 10 most influential critical biological processes or activities: predation and swimming behaviors. Species that compete with RASU also provide alternative food resources for predators, and the presence of competitors or predators may prompt RASU avoidance (swimming) activity. Competitor and predator activity also strongly influence each other. Competitor activity also shapes the abundance and composition of the planktonic and benthic biological assemblages, and some species may compete with RASU not only for food resources but for cover. Competitor activity thus affects three other habitat elements with direct impacts on various critical biological processes and activities.

- Depth strongly influences 1 of the 10 most influential critical biological processes or activities. Changes in depth during the short period of embryo development can cause mechanical stress to RASU embryos by exposing them to desiccation or inundating them to excessive depths. Both water chemistry and water temperature also vary with depth, and changes in depth can change the mesohabitat type of a site. Depth thus affects three other habitat elements with direct or indirect impacts on various critical biological processes and activities.

- Plankton-benthos-POM strongly influences foraging, 1 of the 10 most influential critical biological processes or activities for all RASU mobile life stages. Specifically, the abundance and composition of the planktonic and benthic biological assemblages, and the availability of POM, determine the availability of food resources for each mobile life stage. The abundance and composition of the planktonic and benthic biological assemblages also shape predator activity since some benthic organisms may prey on RASU eggs, larvae, and juveniles, and the abundance and composition of the planktonic and benthic biological assemblages together with the availability of POM helps shape the composition and abundance of the assemblage of species that compete with RASU for food. Finally, plankton contribute to turbidity. Plankton-benthos-POM thus affects several other habitat elements with direct impacts on various critical biological processes and activities.

- Turbidity strongly affects predation, possibly the most influential critical biological process or activity for all RASU life stages, by shaping the ability of different predators to forage. Spatial and temporal variation in turbidity also shape the abundance and spatial distribution of both competitors and predators in general and the abundance and composition of the planktonic and benthic biological assemblages in different settings.

- Finally, figure 20 also includes water chemistry. This habitat element has no *direct* influence on any of the 10 most influential critical biological processes or activities across all RASU life stages. However, water chemistry moderately influences primary productivity along the LCR, and in its refuges, and therefore moderately shapes the abundance and composition of the planktonic and benthic biological assemblages and the abundance and distribution of POM.

GAPS IN UNDERSTANDING

Figures 19 and 20 use the conventional color coding of individual causal relationships to identify relationships that the CEM identifies as having high, intermediate, or low levels of scientific confirmation. As noted in the attachment A, "low" scientific understanding of a relationship means that it is "… subject to wide disagreement or uncertainty in peer-reviewed studies from within the ecosystem of concern and in scientific reasoning among experts familiar with the ecosystem." In many cases, the scientific principles are well understood, but the factual details are insufficiently understood within the LCR and its refuges. The two figures show large numbers of red arrows, indicating relationships that the assessment identifies as having a low level of scientific understanding. Each of these red arrows identifies a causal relationship that may warrant further field, laboratory, or literature investigation. The following paragraphs highlight some potentially important areas of low understanding.

- The assessment identifies predation as an important factor shaping survivorship for every life stage in the present-day system, and the literature on RASU overwhelmingly points to introduced species as the culprits. A few laboratory studies and field observations demonstrate that particular native and non-native species can/do prey on RASU larvae (Horn et al. 1994; Mueller 2006; Mueller et al. 2006; Carpenter and Mueller 2008), and a few studies of stomach contents document or suggest predation on larger RASU by both native and non-native piscivores (Portz and Tyus 2004; Karam and Marsh 2010). However, knowledge concerning the ecology of the process of predation on RASU is very limited for all life stages. For example, no studies provide information on which species may be taking the heaviest toll, in which habitat settings, or which life stages. The hunting behaviors, size selection, and gape limitations among the present assemblage of piscivorous fishes in the LCR system also differ from those of the predators that RASU faced prior to human manipulation of the river and its flow rigime, but no study has quantified these changes and their implications for RASU management. In contrast, several studies indicate that RASU possess a variety of life-stage-specific behavioral and physical adaptations for avoiding or escaping predation, shaped by their evolutionary histories. The challenge that non-native predators pose for RASU therefore may not lie in the mere presence and abundance of these novel predators, but in the specific ways in which their densities, hunting behaviors, and capabilities differ from those of the predators that shaped RASU evolution, and the ways in which mesohabitat conditions shape these interactions.

  Several studies in fact provide indications that mesohabitat conditions can affect predation rates, allowing RASU to survive the present-day gauntlet of native and non-native predators and grow to adulthood (Mueller 2006;

Albrecht et al. 2010b). For example, aspects of mesohabitats that potentially affect survivorship among dispersing and settled RASU larvae include the availability of benthic vegetative and substrate interstitial cover, the distances across which the larvae are exposed to predation during drifting, and whether movement pathways and nursery habitat also present habitat conditions (e.g., turbidity) that affect their predators. Altered mesohabitat conditions in fact show up as a potentially strong influence on several of the activities and processes that affect survivorship in all life stages in part because of their effects on predation rates. Several studies in the UCRB further indicate that non-native predation on RASU may vary with season and a variety of habitat conditions (Franssen et al. 2007; Pilger et al. 2008). These findings suggest a need to improve the understanding of the ecology of predation on RASU, how this may vary among predator species and across different habitat settings, and whether it may be possible to manipulate habitat conditions to improve RASU survival even in the presence of predators.

- The assessment identifies a low level of scientific understanding of the ways in which mesohabitat conditions and substrates shape RASU behaviors and survivorship in all life stages. For example, as noted several times in chapters 3 and 6, 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; Reclamation 2008; Schooley et al. 2008; Albrecht et al. 2010a; Bestgen et al. 2011, 2012; Patterson et al. 2012; Valdez et al. 2012). The understanding of substrate selection for spawning is complicated by a lack of quantitative information on substrates at spawning sites – the literature almost exclusively relies on qualitative terms such as “cobble” and “gravel” (see review by Valdez et al. 2012) – and by a lack of substrate data comparing sites selected versus ignored for spawning.

  As discussed in chapter 6, this document proposes that the mesohabitat characteristics of sites selected for spawning may be understood as a consequence of natural selection for a preference for spawning at sites that most reliably allow for embryo survival and the successful dispersal of RASU larvae into habitats suitable for their own survival and maturation. That is, natural selection would be expected to produce patterns of spawning site preference that favor embryo survival and subsequent larval survival. From this perspective, spawning site selection would be expected to favor settings with: (1) substrates of the right combination of particle sizes to receive and hold the eggs for embryo development, including a minimal presence of fine sediment or biological accretions that occlude pore spaces, and possibly also including characteristics that reduce visibility or accessibility of the eggs to benthic predators; (2) low exposure to flow conditions that would disturb the substrate or involve velocities or turbulence along the substrate surface in ways that would dislodge or bury the developing embryos and freshly emerged larvae; and (3) positioning along a flow path that can disperse motile larvae to suitable habitat for their continuing growth. As stated in chapter 6, therefore, natural selection would favor spawning at sites with specific “goldilocks” mesohabitat characteristics: exposed to sufficient flows to keep the substrate relatively clean of fine sediment and biological accretions, but not sufficient to disturb larger (pebble and cobble) particles, and connected to the overall flow network, but not exposed to the most geomorphically disruptive flows.

The literature on RASU behavioral selection and use of cover by different life stages is similarly weak. For example, as summarized by Valdez et al. (2012), dispersing larvae may use interstitial spaces in the substrate as resting locations, and it would be reasonable to assume that this behavior affords some degree of protection from predators. However, the literature provides insufficient information to determine suitable or optimal hiding conditions for application to management deliberations.

- The assessment identifies a low level of scientific understanding not only about the ecology of predation on RASU but also about the ecology of competition. A review of online databases of biological information for the non-native fishes of the LCR (chapter 5) indicates that, during one or more of their life stages, all of the species deliberately introduced for sport fisheries or as bait or forage for these fisheries could compete with RASU for food. However, the topic has not received specific study in the LCR or elsewhere in the Colorado River system. Similarly, the present assessment also did not find evidence that food availability has affected RASU recruitment (e.g., larval survival) in the LCR or its refuges. However, the literature on RASU across the entire Colorado River system identifies foraging failure as a possible limitation on RASU recruitment – again, particularly for larvae. Conceivably, the influx of anthropogenic nutrients into the LCR and the lowered levels of turbidity support higher rates of primary productivity, compared to the system prior to regulation, and this higher productivity allows the LCR to support the great diversity of non-native fish species found there today without limiting food availability for RASU. However, no studies address this possibility. As a result, the literature does not provide a clear picture of the possible roles of food availability and competition in shaping RASU recruitment.

- The assessment reflects ongoing uncertainty concerning the conditions that may trigger or cue RASU spawning. As discussed in chapter 6, 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 in water levels, as well as general seasonal cues (e.g., photoperiod) may continue to provide cues in the LCR (Minckley et al. 1991; Modde and Irving 1998; USFWS 1998, 2002a; Mueller 2006; Reclamation 2008; Schooley et al. 2008; Albrecht et al. 2010a; Albrecht et al. 2010b; Bestgen et al. 2011, 2012; Patterson et al. 2012; Valdez et al. 2012). Given the apparent importance of the spring flow pulse in dispersing RASU larvae in the river prior to regulation, the literature suggests a hypothesis that natural selection would have favored responses to cues that *anticipate* rather than coincide with the annual pulse so that the RASU could move into spawning position in time. By that reasoning, evolution would have favored cueing to temperature, seasonal light, or the very beginnings of the rising limb of the spring flow pulse. Spawning in the LCR in fact may precede or follow the timing of flood pulses, suggesting that temperature (and perhaps other seasonal) cues dominate over hydrologic cues (Mueller 2006). The literature does not indicate whether pheromones may also be involved in triggering readiness or participation in spawning. Similarly, the assessment reflects ongoing uncertainty concerning the conditions that may trigger or stimulate ripening in individual adult RASU or shape the fraction of the adult population that ripens in any single year.

- Finally, the assessment reflects a widespread concern that repatriated subadults may experience high rates of stress and mortality due to their lack of conditioning to the foods available and flow velocities they experience after release and due to their lack of experience with predators. Further, the assessment reflects recognition that the effects of pre-conditioning – or its absence – are not well understood. This is a subject of ongoing investigations as noted in chapters 3–6. Similarly, ongoing investigations address concerns that handling during transport from rearing to release sites may also cause hatchery-reared RASU unacceptable levels of stress sufficient to impair their survival following release.

This list of uncertainties is not meant to be exhaustive, but only to highlight topics the literature, and gaps in the literature, identify as potentially particularly pivotal to RASU recruitment in the LCR and its refuges.

CONCLUSIONS

This document presents a CEM for the razorback sucker (*Xyrauchen texanus*) (RASU). It addresses the RASU population along the river and lakes of the LCR and in wildlife refuges and other protected areas along the LCR managed as RASU habitat under the auspices of the LCR MSCP HCP. It does not include facilities managed exclusively for rearing RASU larvae into subadults, but does include protected areas into which RASU subadults are repatriated as part of the augmentation program (Reclamation 2006). As stated in the chapter 1, the purpose of this 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 habitat and species restoration, and the methods used to measure RASU habitat and population conditions.

The model integrates numerous sources of information and knowledge. The basic sources are Minckley et al. (1991), USFWS (1998, 2002a), Reclamation (2004, 2008), Mueller (2006), and Valdez et al. (2012). The model also integrates numerous additional sources, particularly reports and articles completed since these publications; information on current research projects; and the expert knowledge of LCR MSCP and USFWS biologists. The review of RASU habitat requirements by Valdez et al. (2012) strongly complements the present document.

The model identifies and separately assesses eight stages in the RASU life cycle, each of which is characterized by a distinct set of critical biological activities and processes. The rates of these activities and processes depend on the abundance, distribution, and/or condition of specific habitat elements. In turn, the abundance, distribution, and/or condition of these habitat elements depend on the operation of a suite of controlling factors. Because the LCR and its refuges comprise a highly regulated system, the controlling factors exclusively concern human activities. The CEM identifies the causal relationships among these model components and also assesses each relationship in terms of its character and direction, magnitude, predictability, and level of scientific understanding.

The analysis of the causal relationships shows which critical biological activities and processes most strongly support or limit the success of each life stage in the present-day system, which habitat elements most strongly affect the rates of these critical activities and processes, and which controlling factors most strongly affect the abundance, distribution, or condition of these habitat elements. The analysis further shows which are the most versus least understood in terms of the level of agreement or certainty evidenced in peer-reviewed studies within the ecosystem and among experts familiar with the ecosystem. The results of the analysis of uncertainty highlight several relationships that may strongly affect RASU survivorship and recruitment but about which scientific understanding remains low. These may warrant attention to determine if improved understanding might provide additional management options for improving RASU survivorship and recruitment in the LCR and its refuges.

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ATTACHMENT 1

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

OVERVIEW OF METHODOLOGY FOR BUILDING CONCEPTUAL ECOLOGICAL MODELS

The conceptual ecological models (CEMs) for species covered by the Lower Colorado River Multi-Species Conservation Program (LCR MSCP) expand on a methodology developed by the Sacramento-San Joaquin Delta Ecosystem Restoration Program (ERP): https://www.dfg.ca.gov/ERP/conceptual_models.asp.

The ERP is jointly implemented by the California Department of Fish and Wildlife, U.S. Fish and Wildlife Service, and the National Marine Fisheries Service. The Bureau of Reclamation participates in this program.

The ERP methodology for building CEMs incorporates common best practices for presenting these models for species covered by the LCR MSCP and identified in Habitat Conservation Plan (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 transitions from one stage/event to the next.

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

- It characterizes these interrelationships using a "*driver-linkage-outcomes*" approach. Linkages are cause-and-effect relationships between drivers and outcomes. Outcomes are the transition rates and their associated metrics (such as larval production or mortality).

- 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 status (certainty) of present scientific understanding of the effect. Below, we present the draft definitions for these four variables, after DiGennaro et al. (2012).

The LCR MSCP conceptual ecological models will expand this ERP methodology, incorporating the recommendations of Kondolf et al. (2008) and Burke et al. (2009) for a more hierarchical approach. This expanded approach provides greater detail on causal linkages and outcomes by dividing outcomes into two types: (1) activities and processes and (2) habitat elements. This expansion therefore calls for identifying **three** model components for each life stage or transition, and the causal linkages among them, as follows:

- **Critical biological activities and processes** – These consist of the activities in which the species must engage and the biological processes that must take place during each life stage to sustain an acceptable rate of transition (recruitment) to the next life stage. Examples of activities and processes include mating, foraging, avoiding predators, avoiding other specific hazards, egg maturation, and seed germination.

- **Habitat elements**– These consist of the specific habitat conditions that are necessary or sufficient for the critical activities and processes to take place or that interfere with critical activities or processes. Defining the full "template" of these elements for each life stage or transition also requires identifying habitat conditions that can interfere with these critical activities and processes. The abundance and distribution of habitat elements control the rates (intensities) of the activities and processes that they affect. Defining the habitat template also 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 begin to fail – if the state of the science supports such estimates.

- **Controlling factors** – These consist of environmental conditions and dynamics –including human actions – that determine the abundance, spatial and temporal distribution, and quality of important habitat elements. Controlling factors are also called "drivers." There may be a hierarchy of such factors affecting the system at different scales of time and space (Burke et al. 2009). For example, the availability of breeding territories may depend on factors such as river flow rates and flow-path morphology, which in turn may depend on factors such as watershed geology, vegetation, and climate.

This expanded approach permits the consideration of five possible types of causal linkages on which management actions may focus for each life stage of a species: (1) from one controlling factor to another, (2) from controlling factors to elements of the habitat template, (3) from one element of the habitat template to another, (4) from elements of the habitat template to critical biological activities and processes, and (5) from one critical biological activity or process to others. Each controlling factor may affect more than one element of the habitat template, and each element of the habitat element may be affected by more than one controlling factor. Similarly, each habitat element may affect more than one biological activity or process, and each biological activity or process may be affected by more than one habitat element. 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 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.

Expanding the ERP methodology with this added level of detail will ensure that the CEMs explicitly identify the habitat conditions that support or impede the rates of success of each critical biological activity or process for each life stage and therefore the rate of recruitment from each life stage to the next. Such explicit consideration of habitat conditions is crucial for identifying critical monitoring and research questions and guiding habitat restoration for the species addressed by the LCR MSCP.

Conceptual Ecological Models as Hypotheses

The CEM for each species produced with this methodology will constitute a collection of hypotheses for that species. These hypotheses will concern: (1) the species' life history; (2) the species' habitat requirements and constraints; (3) the factors that control the abundance, spatial and temporal distribution, and quality of these habitat conditions; and (4) the causal relationships among these. Knowledge about these elements and relationships may vary, ranging from well settled to very tentative. Such variation in the degree of 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 these three CEMs will document the degree of certainty of current knowledge concerning each element of the model for each species as indicated in part by the degree of agreement/disagreement among the experts. In some cases, it will be possible also to represent differences in the interpretations or arguments offered by different experts in the form of alternative hypotheses. Categorizing the degree of agreement/disagreement concerning the elements of the CEM will help to more easily identify the topics of greatest uncertainty or controversy.

Documentation and Diagrams

The CEM for each species will include the definition and rationale for each of the following:

(1) Species life cycle, identifying all life stage/events and their transitions.

(2) The critical biological activities and processes for each life stage and transition.

(3) The critical habitat conditions that support or impede each critical biological activity or process.

(4) The controlling factors affecting the abundance, spatial and temporal distribution, and quality of the conditions that comprise the habitat template.

(5) The causal linkages among (2), from (3) to (2), among (3), from (4) to (3), and among (4).

The CEM will also include an assessment of each causal linkage based on the four variables noted above 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 spreadsheet and text will present the rationale for the assessment findings for each of these four variables. The definitions for these four variables will follow those of the ERP methodology.

The CEM for each species will include two types of diagrams: (1) a summary diagram of the species life cycle and the controlling factors affecting each stage and transition and (2) a more detailed diagram for individual life stages that shows the individual elements of the model for that stage (critical biological activities and processes, habitat elements, controlling factors) and their causal relationships. The more detailed diagrams will use many of the conventions of the ERP conceptual ecological models (Williams 2010; DiGennaro 2012), expanded as suggested by Kondolf et al. (2008) and Burke et al. (2009).

Methods for Characterizing Causal Relationships

The following information is adapted from DiGennaro et al. (2012). It incorporates the ERP methodology for assessing causal links among the four dimensions of: (1) the character and direction of the effect, (2) the importance of the effect, (3) the predictability (consistency) of the effect, and (4) the status (certainty) of present scientific understanding of the effect.

- **Character and direction** categorizes a causal relationship as positive, negative, or involving a threshold response. Positive means that an increase (or decrease) in the causal agent results in an increase (or decrease) in the affected element, and negative means that an increase (or decrease) in the agent results in a decrease (or increase) in the affected element.

- **Magnitude** refers to "…the degree to which a linkage controls the outcome relative to other drivers. While the models are designed to encompass critical drivers, linkages, and outcomes, this concept recognizes that some are more important than others in determining how the system works." 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. For purposes of the LCR MSCP conceptual ecological models, the score for magnitude will be calculated as the average of the scores for intensity, spatial scale, and temporal scale (tables 1–3).

- **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 is based on understanding of the driver, and the nature of how it is linked to the outcome, and thus captures variability. For example, understanding of processes may be high, but there may be natural variability either on an inter-annual and/or a seasonal basis that is unpredictable. Or the strength of relationships and the magnitude of effects may vary so much that properly measuring and statistically characterizing inputs to the model are difficult." Table 4 presents the scoring framework for predictability.

- **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 5 presents the scoring framework for understanding.

The ERP methodology applies a consistent approach to characterize these linkage attributes by rating magnitude, predictability, and understanding on a scale of high, medium, or low. The following tables provide the rating definitions for these four increments to assess linkage magnitude, predictability, and understanding.

Table 1.—Criteria for scoring the intensity of a cause-effect relationship, one of three variables averaged to produce the overall score for "magnitude" (after DiGennaro et al. 2012, Table 2)

Intensity – The strength of the effect, either positive or negative, on the population or habitat of a given species. Intensity takes into account the complete driver-linkage-outcome chain leading to the effect of interest.	
High	Expected major effect on natural productivity, abundance, spatial distribution and/or diversity (both genetic and life history diversity), habitat quality, spatial configuration, and/or dynamics at the places and times where the effect occurs.
Medium	Expected moderate effect on natural productivity, abundance, spatial distribution and/or diversity (both genetic and life history diversity), habitat quality, spatial configuration, and/or dynamics at the places and times where the effect occurs.
Low	Expected minor effect on natural productivity, abundance, spatial distribution and/or diversity (both genetic and life history diversity), habitat quality, spatial configuration, and/or dynamics at the places and times where the effect occurs.

Table 2.—Criteria for scoring the spatial scale of a cause-effect relationship (after DiGennaro et al. 2012, Table 1)

Spatial scale – The spatial scale of the effect on the population or habitat of a given species. Spatial scale takes into account the complete driver-linkage-outcome chain leading to the effect of interest.	
High	Effect on natural productivity, abundance, spatial distribution and/or diversity (both genetic and life history diversity), habitat quality, spatial configuration, and/or dynamics occurs at a large spatial scale – landscape or basin scale.
Medium	Effect on natural productivity, abundance, spatial distribution and/or diversity (both genetic and life history diversity), habitat quality, spatial configuration, and/or dynamics occurs at a moderate spatial scale – regional or reach scale.
Low	Effect on natural productivity, abundance, spatial distribution and/or diversity (both genetic and life history diversity), habitat quality, spatial configuration, and/or dynamics occurs at a small spatial scale – local or site scale.

Table 3.—Criteria for scoring the temporal scale of a cause-effect relationship (after DiGennaro et al. 2012, Table 1)

Temporal scale – The time scale of the effect on the population or habitat of a given species. Temporal scale takes into account the complete driver-linkage-outcome chain leading to the effect of interest.	
High	Effect on natural productivity, abundance, spatial distribution and/or diversity (both genetic and life history diversity), habitat quality, spatial configuration, and/or dynamics emerges, persists, or can be reversed only over a very long time scale – decades or longer.
Medium	Effect on natural productivity, abundance, spatial distribution and/or diversity (both genetic and life history diversity), habitat quality, spatial configuration, and/or dynamics emerges, persists, or can be reversed over a time scale of one or two decades.
Low	Effect on natural productivity, abundance, spatial distribution and/or diversity (both genetic and life history diversity), habitat quality, spatial configuration, and/or dynamics emerges, persists, or can be reversed over a time-scale of less than a decade.

Table 4.—Criteria for scoring the predictability of a cause-effect relationship (after DiGennaro et al. 2012, Table 3)

Predictability – The likelihood that a given causal agent will produce an effect of interest.	
High	Magnitude of effect is largely unconstrained by variability (i.e., predictable) in ecosystem dynamics or other external factors.
Medium	Magnitude of effect moderately depends on other highly variable ecosystem processes or uncertain external factors.
Low	Magnitude of effect greatly depends on other highly variable ecosystem processes or uncertain external factors.

Table 5.—Criteria for scoring the 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 and in scientific reasoning among experts familiar with the ecosystem.
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 or uncertainty in peer-reviewed studies from within the ecosystem of concern and in scientific reasoning among experts familiar with the ecosystem.